Intra- and Interspecific Predation in Filter Feeding Mosquito Larvae

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Abstract : The larvae of *Culex tritaeniorhynchus* and *Anopheles sinensis* are typical filter feeders. The old larvae of the former species were shown to be potential predators for their own young larvae. They consumed as many as 800 first instar larvae per individual per day. Even when a sufficient amount of suitable food other than young larvae had been supplied, cannibalism was observed. Also, the old larvae of *Anopheles sinensis* were potential predators for the young larvae of *Culex tritaeniorhynchus*. The possible role of intra- and interspecific predation in the population regulation of filter feeding mosquito larvae and the classification and evolution of the feeding habits of mosquito larvae were discussed.

The feeding habits of mosquito larvae have been classified into three basic types, i.e., filter feeders, browsers and predators (e. g., Surtees, 1959). As for predators, cannibalism has been thought to be an usually occurring phenomenon which plays some roles for the regulation and persistence of the species populations, although detailed studies on natural populations are very few. Cannibalism has been recorded also for filter feeders or browsers (e. g., MacGregor, 1915), but generally it seems to be regarded as an unusual phenomenon with little significance at least in natural populations. The report by Reisen and Emory (1976) which suggested the possible role of cannibalism in the population regulation of *Anopheles stephensi* may be a rather rare example. Insofar as I know, the experiments for evaluating the predacious ability of filter feeding or browsing species were scarcely attempted. The main purpose of this report is to show that even in typical filter feeders old larvae are potential predators for the young larvae in the same habitat.

MATERIALS AND METHODS

The larvae of *Culex tritaeniorhynchus* Giles, 1901 and *Anopheles sinensis* Wiedemann, 1828 were derived from each colony of Nagasaki strain which had been maintained in our laboratory

under the condition of 27°C and long–day photoperiod. The experiments were done under the same condition, using glass vials of a diameter of 8.5 cm, each of which contained 50 ml of city water kept at least for one day before the experiments. The depth of water in each vial was 0.88 cm.

The larvae of two different instars were introduced together into each vial. The larvae of advanced instars had spent more than 24 hours in the respective instars before the experiments, while the larvae of less advanced instars were within 24 hours after the last ecdysis or the hatch. After 24 hours, old larvae were removed and the numbers of young larvae were counted with a distinction of living larvae and dead ones. The numbers of young larvae having disappeared during the contact with old larvae were regarded as the numbers of young larvae which had been consumed by the latter.

Further details in each experiment will be explained with the results in the following sections.

RESULTS

1. *Fourth instar larvae of* Culex tritaeniorhynchus *as potential predators for first instar larvae of the same species*

Each fourth instar larva was kept for 24 hours with first instar larvae of various numbers ranging from 20 to 4,800 in seven grades. The relations between the numbers of first instar larvae in each vial and the density per ml of water or cm² of water surface are shown in Table 1. In the vials where more than 2,400 first instar larvae were introduced at the beginning, not a few first instar larvae were so weakened and inactive after 24 hours that they were difficult to be distinguished from dead ones. Therefore, the numbers of all the remaining larvae were counted together for those vials.

The results are shown in Table 2, from which it is seen clearly that the fourth instar larvae of *Culex tritaeniorhynchus* are potential predators for their own first instar larvae. The maximum number of first instar larvae which can be consumed per day could not be determined because of a few replications in the grades of high food density, but it is not likely to be much more than 800 (see Fig. 1).

Table 1. Density of first instar larvae of *Culex tritaeniorhynchus* supplied as food

Density per vial	Density per ml of water	Density per cm² of surface area
20	0.4	0.35
100	2.0	1.76
300	6.0	5.29
600	12.0	10.58
1200	24.0	21.16
2400	48.0	42.32
4800	96.0	84.64

The fourth instar larvae were killed immediately after the experiment and preserved in 70 % alcohol for the later examination of the contents in midguts. Some examples from this examination are shown in Fig. 2. The midguts of fourth instar larvae supplied with more than 300 first instar larvae were almost completely packed with chitinous parts of consumed larvae. They were more or less crashed and no intact larva was found. Therefore, the numbers of larvae in the midguts were difficult to be counted, but at least 30 first instar larvae looked to be packed. This estimated value is only less than 5 % of the maximum number of first instar larvae consumed per day, but it seems to be a reasonable value in view of the high displacement rate of the contents in the midguts of mosquito larvae. Schildmacher (1950) observed for *Anopheles*, *Aedes* and *Culex* that the contents in midguts were displaced completely within an hour or less if sufficient food was consumed without interruption.

A part of first instar larvae may have been consumed after they died for other reasons, but there is no doubt about the fact that many first instar larvae were caught while they were

Table 2.　Numbers of first instar larvae consumed by fourth instar larvae of
Culex tritaeniorhynchus during 24 hours

No. of first instar larvae supplied	No. of replications	Mean No. (range) of first instar larvae living		Mean No. (range) of first instar larvae dead		Mean No. (range) of first instar larvae consumed	
20	10	16.4	(11–19)	0.6	(0–1)	3.0	(0–8)
100	6	78.2	(61–90)	2.7	(1–6)	19.2	(9–38)
300	10	181.2	(72–267)	8.0	(4–14)	110.8	(27–218)
600	9	272.3	(117–437)	24.4	(4–44)	303.2	(119–479)
1200	4	597.3	(494–675)	68.8	(53–79)	534.0	(455–653)
2400	2	1648.0 (1521–1725)*				752.0	(675–829)
4800	1	3979.0*				821.0	

Respective numbers of first instar larvae were supplied per fourth instar larva.
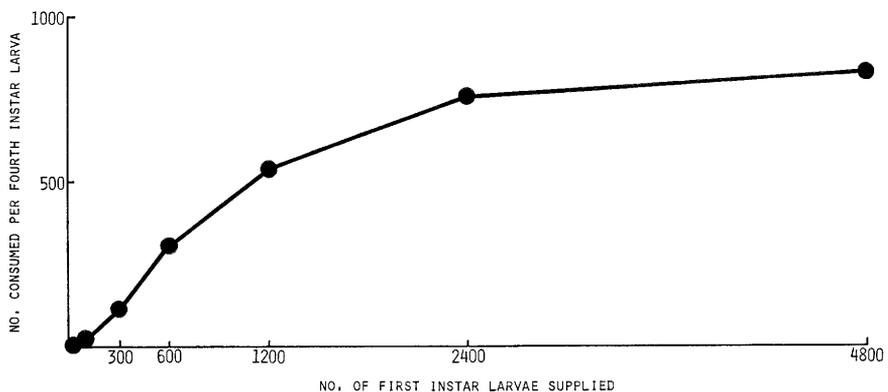* Numbers including living larvae and dead ones.

Fig. 1.　Relation between the numbers of first instar larvae of *Culex
tritaeniorhynchus* supplied as food and those consumed by
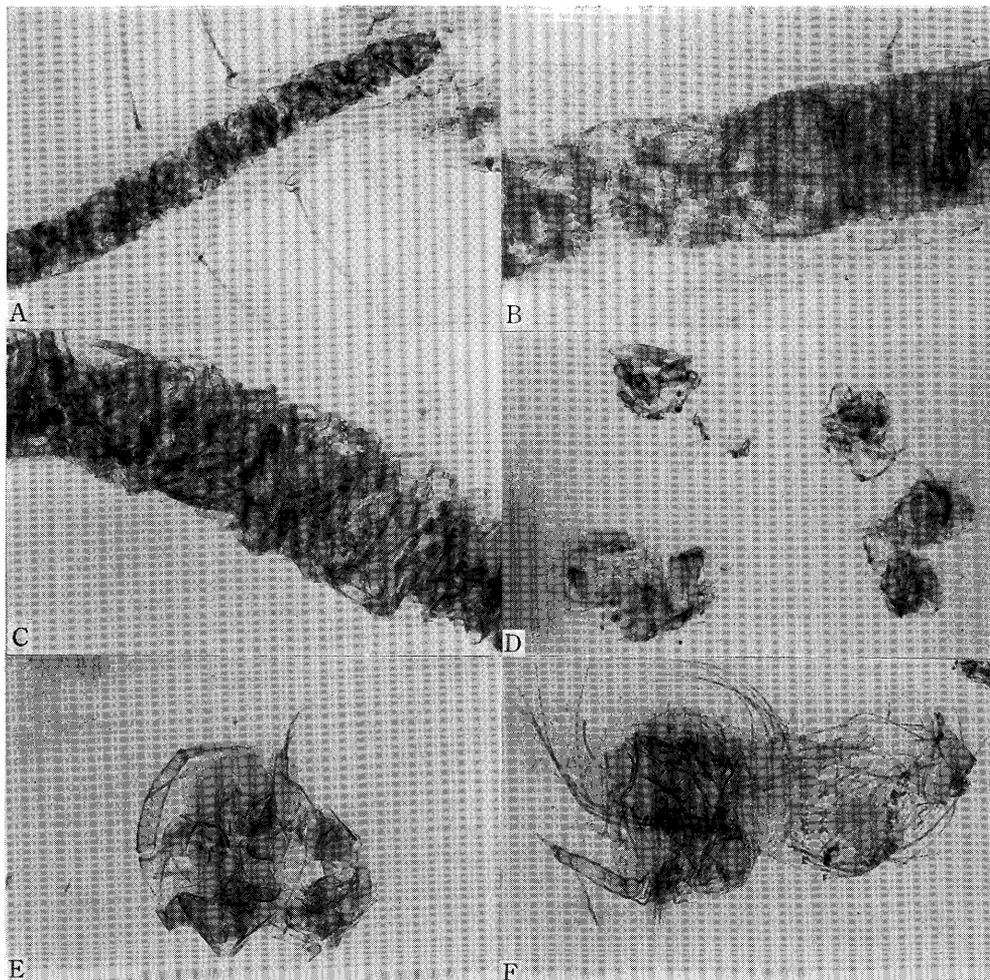fourth instar larvae during 24 hours.

Fig. 2. First instar larvae of *Culex tritaeniorhynchus* in the midguts of fourth instar larvae of the same species. (A) A part of the fourth instar larva supplied with 600 first instar larvae (×20). (B) A part of the midgut of the same individual. See setae of first instar larvae (×50). (C) A part of the midgut taken out from other individual supplied with 600 first instar larvae (×50). (D), (E) and (F) First instar larvae taken out from the midgut of the fourth instar larva supplied with 1,200 first instar larvae, (D) : ×20, (E) and (F) : × 50.

alive. It is easy to observe the scene of predation directly. When 600 first instar larvae, for instance, were supplied per vial, about 300 larvae were consumed during 24 hours. It means that more than 12 larvae were consumed per hour on the average. Therefore, only a five-minutes-observation may give us a chance to observe one first instar larva to be consumed. The first instar larvae which had entered into the effective range of water flow generated by the action of mouthbrushes of fourth instar larvae, were often observed to be drawn towards

and sucked into the mouth. When the fourth instar larvae had caught the first instar larvae, they stopped filtering for a short time. This change of the movement gave me a strong impression that the first instar larvae having been sucked into the mouth were perceived as larger objects than usual food and released some kinds of chewing or crashing processes.

2. *Predation among various instar larvae of* Culex tritaeniorhynchus

Each larva of advanced instars was kept for 24 hours with 20 larvae of less advanced instars. The results presented in Table 3 show that predation is not a phenomenon restricted to the occasion when the fourth instar larvae encounter the first instar ones. Predation occurred also between the fourth instar larvae and the second instar ones and between the third instar larvae and the first instar ones. The efficiency of consuming young larvae in these two combinations was, however, much lower than that of the first combination. Cannibalism was not observed in other three combinations.

Table 3. Numbers of young larvae consumed by old larvae of *Culex tritaeniorhynchus* during 24 hours

Instar of older larvae	Instar of younger larvae	No. of replications	Mean No.(range) of younger larvae living		Mean No.(range) of younger larvae dead		Mean No.(range) of younger larvae consumed	
fourth	third	20	19.8	(19-20)	0.2	(0-1)	0.0	
fourth	second	19	19.3	(17-20)	0.5	(0-2)	0.3	(0-2)
fourth	first	20	17.1	(13-19)	1.2	(0-3)	1.8	(0-6)
third	second	20	19.7	(17-20)	0.4	(0-3)	0.0	
third	first	20	18.5	(15-20)	1.4	(0-4)	0.1	(0-1)
second	first	20	17.7	(15-20)	2.4	(0-5)	0.0	
—	third	2	19.0	(18-20)	1.0	(0-2)	—	
—	second	3	19.3	(19-20)	0.7	(0-1)	—	
—	first	5	19.0	(17-20)	1.0	(0-3)	—	

20 young larvae were supplied per old larva.

3. Anopheles sinensis *larvae as potential predators for* Culex tritaeniorhynchus

Each individual of the fourth or the third instar larvae of *Anopheles sinensis* was kept for 24 hours with 20 individuals of the second or the first instar larvae of *Culex tritaeniorhynchus*. The results are arranged in Table 4 in the same format as Table 2 and 3. It is sure that the old larvae of *Anopheles sinensis* are also potential predators for the young larvae of *Culex tritaeniorhynchus*. Comparing the figures in Table 4 with those in Table 3, it may safely be said that the efficiency of consuming the young larvae of *Culex tritaeniorhynchus* is not significantly different between the same instar larvae of *Anopheles sinensis* and *Culex tritaeniorhynchus*, at least in the condition of the present experiments and also in the range of low food density where the maximum daily consumption rate does not act as a limiting factor. Naturally,

Table 4. Number of *Culex tritaeniorhynchus* larvae consumed by *Anopheles sinensis* larvae during 24 hours

Instar of A. s.	Instar of C. t.	No. of replications	Mean No. (range) of C. t. larvae living	Mean No. (range) of C. t. larvae dead	Mean No. (range) of C. t. larvae consumed
fourth	second	20	18.8 (14–20)	0.9 (0–5)	0.3 (0–2)
fourth	first	20	17.6 (11–20)	0.3 (0–2)	2.2 (0–8)
third	first	20	19.8 (19–20)	0.2 (0–1)	0.1 (0–1)
—	second	5	20.0	0.0	—
—	first	5	19.4 (19–20)	0.6 (0–1)	—

20 larvae of *Culex tritaeniorhynchus* were supplied per larva of *Anopheles sinensis*.

the term "efficiency" here employed means the total efficiency resulting from all the subprocesses influencing the success of predation. Therefore, it is quite probable that the efficiency of each subprocess is different between the two species, even if the total or combined efficiency is nearly the same.

4. Predation in the vials with sufficient food other than young larvae

All the above experiments were done in the vials with no food other than young larvae, although there may have been some micro–organisms or minute fragments of organic matter such as feces excreted by larvae themselves. The following small experiment was attempted to know whether predation occurs in the vials with sufficient food which is thought to be much more accessible than living young larvae. Five vials, each of which contained 10 fourth instar larvae of *Culex tritaeniorhynchus*, were prepared for each of the following conditions.

(A) No food was supplied.

(B) A sufficient amount of the mixture of dried yeast and powdered mouse pellets was supplied. It is normal food for rearing mosquito larvae in our laboratory.

(C) 100 first instar larvae were added per vial per day besides the normal food above stated.

(D) Only 100 first instar larvae per vial per day were supplied. On the 10th day after the initiation of the experiment, all the living fourth instar larvae were gathered in one vial and 100 first instar larvae per day were supplied until the death or the pupation of all the fourth instar larvae.

The results are shown in Fig. 3, from which two important facts can be demonstrated or suggested. Firstly, predation occurred even when a sufficient amount of suitable food was available, although the daily consumption rate was lower than that in the vials without suitable food. This fact can be realized from the results of (B), (C) and (D). Secondly, it can be suggested that the fourth instar larvae feeding on young larvae are able to complete the development to pupae. In other words, young larvae seem to be tolerable food, if not the good one.
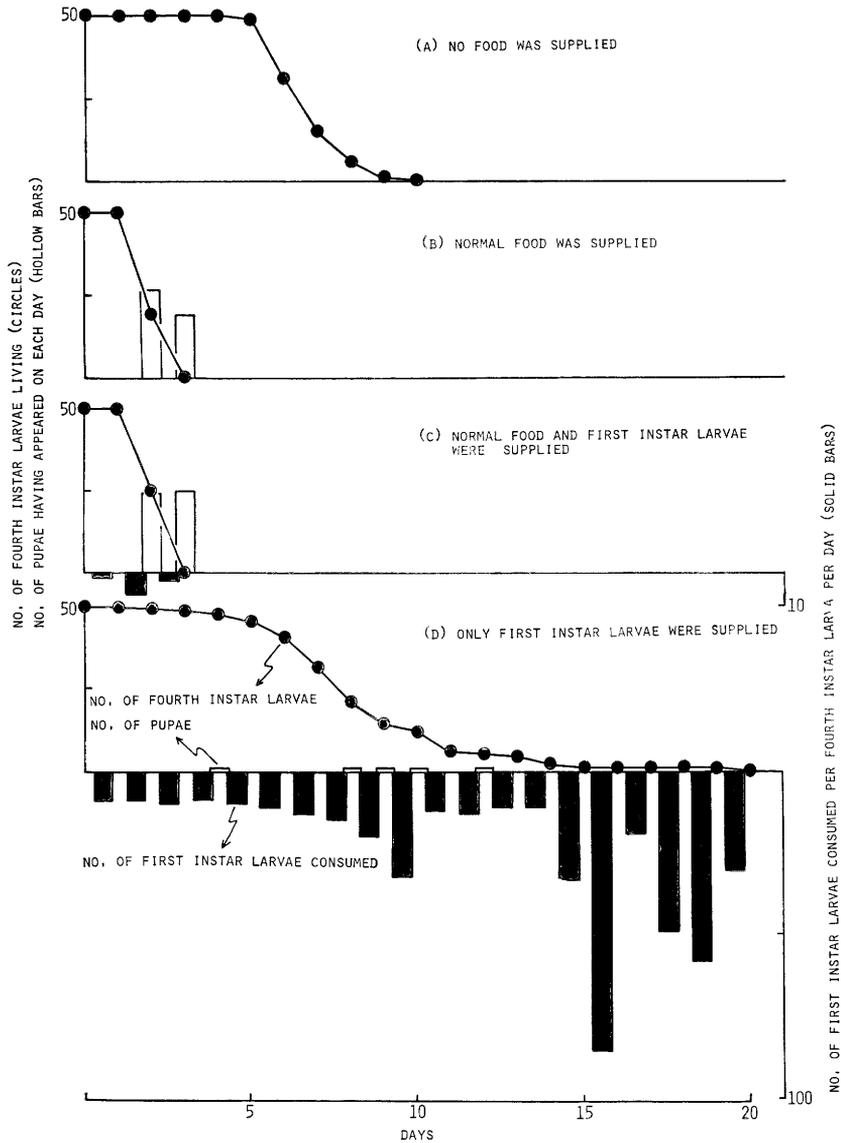
50

(A) NO FOOD WAS SUPPLIED

50

(B) NORMAL FOOD WAS SUPPLIED

50

(C) NORMAL FOOD AND FIRST INSTAR LARVAE
WERE SUPPLIED

50

10

(D) ONLY FIRST INSTAR LARVAE WERE SUPPLIED

NO. OF FOURTH INSTAR LARVAE

NO. OF PUPAE

NO. OF FIRST INSTAR LARVAE CONSUMED

NO. OF FOURTH INSTAR LARVAE LIVING (CIRCLES)

NO. OF PUPAE HAVING APPEARED ON EACH DAY (HOLLOW BARS)

NO. OF FIRST INSTAR LARVA CONSUMED PER FOURTH INSTAR LARVA PER DAY (SOLID BARS)

5   10   15   20

DAYS

100

Fig. 3. Survival and development of fourth instar larvae of *Culex tritaeniorhynchus* under various feeding conditions. Circles : numbers of fourth instar larvae living. Hollow bars : numbers of pupae having appeared on each day. Solid bars : numbers of first instar larvae consumed per fourth instar larva per day. For further explanations, see text.

This is suggested from the results of (A) and (D). The difference of longevity between (A) and (D) seems to show that the first instar larvae consumed were more or less nutritious. Further, pupation was observed only in (D), although the pupae were small and the pupation rate was very low probably because of the small number of first instar larvae consumed. The average comsumption rate in (D) was about 10 larvae per day per individual during the period when about 100 first instar larvae had been supplied for 10 fourth instar larvae. It was only about 1 % of the maximum daily consumption rate which had been expected from the results of the first experiment (see Table 2 and Fig. 1).

The gradual increase of the daily consumption rate during the first 10 days in (D) is due to the decrease of the number of living fourth instar larvae. Therefore, the daily consumption rate returned to its initial level on the 11th day with the recovery of the initial feeding condition. Only one larva survived on the 15th day. This last larva consumed 19–85 first instar larvae per day. This value is much larger than that of the preceding experiment of the same condition (Table 2), where each fourth instar larva consumed only 9–38 first instar larvae. However, there seems to be no evidence for any other factors than the individual difference, to which the different consumption rates between the two experiments are attributable.

The inference that young larvae are more or less nutritious for old larvae may also be supported by another observation by the first experiment whose results were shown in Table 2. The results of this observation are presented in Table 5, for which some additional explanations may be necessary. "Distance moved per 2 minutes" means the difference of the position every 2 minutes measured in a straight line. Therefore, the distance actually covered by the larva may be much grater than it. This observation was done during 20 minutes for each larva. "Swimming" refers to the travelling of larvae by the lashing action of the whole body and does not include "gliding" which means the travelling by the action of mouthbrushes (see Christophers, 1960). This observation was done during 5 minutes for each larva. "10-minutes-quiescence" means that the larva stayed at the same position during 10 minutes. This observation was done during 60 minutes for each larva.

It is clear from the results that the movement of fourth instar larvae changed as the number of first instar larvae consumed increased. The difference was the most drastic between

Table 5. Activities of fourth instar larvae of *Culex tritaeniorhynchus*

Mean No. of first instar larvae consumed per day	No. of replications	Mean distance(range) moved in cm during 2 minutes	Mean frequency(range) of swimming during 2 minutes	Mean frequency (range) of 10-minutes-quiesence during 60 minutes
3.0	10	4.71 (3.80–4.96)	3.4 (1.2–6.4)	0.0
19.2	6	3.24 (1.80–4.56)	0.1 (0.0–0.4)	0.0
110.8	5	0.32 (0.10–0.55)	0.0	1.6 (0–4)
303.2	5	0.14 (0.06–0.20)	0.0	4.2 (2–6)
534.0	4	0.14 (0.09–0.23)	0.0	3.8 (1–6)
752.0	2	0.37 (0.29–0.44)	0.4 (0.0–1.2)	1.0 (1)
821.0	1	0.11	0.0	4.0

Mean numbers of first instar larvae consumed are cited from Table 2. Therefore, they are based upon all the larvae including those whose activities were not observed on.

the larvae which had consumed less than 20 first instar larvae per day and those which had consumed more than 100 ones. The former were very active. They were gliding restlessly and quickly. Swimming was observed frequently. Such a state of larvae can easily be observed when they are reared under the condition of severe food shortage. Contrarily, the larvae which had consumed more than 100 first instar larvae per day were very inactive. Almost always they were gliding quietly and slowly. Swimming was rarely observed. Their movement appeared to be similar to that of the larvae supplied with a sufficient amount of suitable food. The fourth instar larvae which had consumed about 750 first instar larvae per day were more restless than those which had consumed 300–500 first instar larvae. This instability might have been due to the disturbance by too many first instar larvae.

DISCUSSION

1. Significance of cannibalism in the population dynamics of filter feeding species

The larva of *Culex tritaeniorhynchus*, which occurs mainly in open ground pools such as rice fields, is a typical filter feeder with long, fine, unserrated mouthbrushes, large maxillae bearing many fine setae and small cutting organs of mandibles. The occurrence of cannibalism in this typical filter feeder strongly suggests that the phenomenon is universal in filter feeding or browsing species, although it may be usually potential in many species. The extents to which this potency is realized in natural populations must be affected by various factors, of which the depth of water may be one of the most important ones. In the present experiments, the depth of water was 0.88 cm, which may have been the best condition for the realization of cannibalism, because cannibalism is thought to result from the random contact of old and young and larvae (Reisen and Emory, 1976). The more the depth of water increases, the more the chance for old larvae to encounter young larvae must decrease. Therefore, the extents of cannibalism in natural populations must depend on not only the behavior and structure of larvae but also the characteristics of larval habitats.

The classification of habitats of mosquito larvae has been attempted by various authors, of which the system by Mattingly (1969) is here cited.

- A. Running–water habitats
- B. Still–water habitats
  - 1. Ground–water habitats
    - a. Permanent
    - b. Temporary
  - 2. Subterranean habitats
    - a. Artificial
    - b. Natural
  - 3. Container habitats
    - a. Tree–holes
    - b. Bamboos
    - c. Leaf habitats

d. Fruits and husks

e. Artificial containers

f. Miscellaneous

It is expected that cannibalism is the most likely to occur in container habitats which are generally small collections of water. According to Mattingly (1969), the whole of Toxorhynchitinae and Sabethini, at least 40 % of Culicini and a negligible proportion of Anophelinae occupy breeding places of this kind. All the species of Toxorhynchitinae and many of Sabethini are true predators, but most species of Culicini, which is the largest tribe including as many as 2000 species nearly equal to 70 % of the whole family, are filter feeders or browsers. Cannibalism is possible to occur in most, if not all, filter feeding or browsing species breeding in container habitats. Underground habitats are also generally small collections of water, of which crab-holes keep the richest fauna. In those habitats, too, cannibalism may occur as frequently as in container habitats. Another type of habitats interesting from this point of view is temporary ground-water habitats. Generally speaking, they may be larger collections of water than container or subterranean habitats, but they are characterzed by their instability, especially when they are exposed to direct sunlight in open environments. One of the most important habitats of this type, for instance in Japan, are rice fields where the two species employed in the present experiments are dominant. In this habitat, the area filled with water varies so drastically depending upon either the artificial manipulation or the local weather that water not rarely stands only in small depressions such as footprints where many larvae concentrate. On such occasions, cannibalism may be possible to occur.

At present almost nothing is known about either the extents of cannibalism in natural populations of filter feeding or browsing larvae nor its significance in the natural regulation of those species. We often experience that a habitat is occupied exclusively by old larvae. Naturally, such a phenomenon can result from various causes, but there seem to be no reasons to exclude cannibalism from the possible causes. Cannibalism in filter feeding or browsing larvae may be worth examining in some situations as a factor playing some roles in the population regulation of mosquitoes in addition to the major factors such as direct food shortage or overcrowding factors.

2. Significance of predation among different species of filter feeders

The coexistence of different species in the same habitat is so common that the death of young larvae by the predation of old larvae of other species is also probable to be more universal than usually recognized. According to Mattingly (1969), predation of *Armigeres subalbatus* (which is considered to be a browser) plays some role in controlling its associate *Culex pipiens fatigans*. This example may be only one of the similar cases. In some cases, one of the species may become dominant by more seriously damaging other species. In other cases, populations of cohabitants may equally be reduced by mutual predation. On this problem, too, it may be said that almost nothing is definitely known at present.

3. On the classification of feeding habits of mosquito larvae

The concepts of three feeding types in mosquito larvae which were emphasized by Surtees (1959) are convenient, for instance, to express the general feeding habit of each species. But the definitions which were given to the respective types by Surtees (1959) and have been followed by some later investigators seem to be not necessarily quite sufficient. Surtees (1959) stated that filter feeders may be defined as those species which strain out food particles from surrounding medium, such particles being sufficiently small to pass directly into the digestive tract without undergoing any additional breakdown. In the present experiments, however, it was clearly shown that filter feeders consume large objects in more or less crashed conditions if the latter are sufficiently fragile. A few observations which support the results are being cited by Clements (1963). Schremmer (1949) who had studied the feeding mechanisms of the larvae of *Anopheles maculipennis* observed that large objects were crashed between the cutting organs of mandibles and the labiohypopharynx. Farnsworth (1947) and Jones (1960) observed on *Anopheles quadrimaculatus* that the food which had been formed into a large bolus almost filling the pharynx was sent into the midgut by the constriction of both the pharynx and the oesophagus. Such functions are probably common to other filter feeding or browsing larvae, therefore the consumption of such large but fragile objects as young larvae by those species is not surprising. Taking these points into consideration, filter feeders may be defined as those species consuming everything small or fragile which can be sucked into the mouth by the action of mouthbrushes.

Predators, on the other hand, seem to be characterized by its specialized attack behavior as well as the morphological adaptation in their mouthparts. They attack their plays probably in response to the movement of water generated by the movement of preys. Such active attack behavior is never observed in filter feeders and possibly in browsers even when they consume relatively large living organisms as young larvae. Insofar as this attack behavior is concerned, the gap between predators and other two types is very distinct. However, I have not seen predacious larvae other than those belonging to *Toxorhynchites* and *Culex* (*Lutzia*). Therefore, somewhat different types of attack behavior which bridge the gap may be found in other groups of predators.

The evolutionary relationships among three feeding types are one of the interesting but difficult problems. Surtees (1959) considered that feeding habits can be arranged in a serial line ranging from the most primitive filter feeders to the most specialized predators through intermediate browsers. But other explanations may be possible. Filter feeders may be regarded as primitive in the sense that they are omnivorous insects unlike predators. However, they are omnivorous insects with a specialized feeding habit. They can be regarded as specialists in feeding on fine fragments and micro-organisms (as for the significance of micro-organisms as the food of mosquito larvae, see Laird, 1956). The structure of the feeding organs of filter feeders seems not to be explained only as primitive, too. For instance, the comparative study on larval mandibles through the whole family Culicidae by Knight (1971) shows that the structure of mandibles of the filter feeders belonging to the subfamily Anophelinae is different from that of filter feeders belonging to the subfamily Culicinae. For

explaining this difference, at least one of the following suppositions is needed : the filter feeders belonging to Anophelinae and those belonging to Culicinae have different origins or they have adapted for filter feeding differently. The same view may be applicable to the filter feeders in the subfamily Culicinae, too. In other words, typical filter feeders may be specialized and polyphyletic as well as predators. From these point of views, the following hypothesis on the evolutionary relationships among three feeding types may be worth considering : filter feeders and predators were derived repeatedly from the ancestral mosquitoes or their general (being not specialized) descendants whose larvae may have been such general omnivorous insects as scavengers feeding on every dead organism including animals and plants. In this sense, browsers may be said to retain the characteristics of ancestral mosquitoes best.

In this sequence, another type of specialized feeding habits may be definable. It is a type represented by specialized herbivores, i. e., vegetarians. The larvae of some species are well known to have a preference for inhabitation in the dense mass of green algae such as *Spirogyra* and to feed on them. In Japan, for instance, *Culex bitaeniorhynchus*, *C. mimeticus* and *C. orientalis* are good examples. *C. bitaeniorhynchus* of India could not successfully reared without green algae (Mohan, 1950). It is very interesting problem whether this and other species with a preference for the larval habitat of this kind are true vegetarians or they are omnivorous insects which need both animal and plant matter for the development.

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こし取り型摂食をする蚊幼虫における種内および種間捕食現象
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蚊の幼虫をその摂食法から分ける場合には，こし取り型（filter feeder），かじり取り型（browser）および捕食型（predator）の3型に分けるのが普通である．それらのうち，捕食型に属する幼虫は他種の蚊幼虫だけでなく同種の若令幼虫をも普通に捕食することが知られているが，こし取り型，かじり取り型に属する幼虫どうしの捕食は，一般に，特殊な条件下における異常な現象とみなされてきたために，それらの幼虫の捕食能力などについても全く調べられたことがないようであった．そこで，典型的なこし取り型に属するコガタアカイエカとシナハマダラカの幼虫の捕食能力を実験的に調べたところ，コガタアカイエカの高令幼虫はきわめて多数の若令幼虫を捕食する能力を持っていること，我国ではコガタアカイエカとほぼ同じ水域に発生するシナハマダラカの高令幼虫もコガタアカイエカの若令幼虫を捕食する能力を持っていることが明らかになった．上述のように，この2種は典型的なこし取り型に属することからみると，殆んど全てのこし取り型，かじり取り型に属する幼虫が，こうした捕食能力を持っている可能性が大きいと思われる．従って，同種，異種の高令幼虫による若令幼虫の捕食は，これまで一般に考えられていた以上に普通におこっている現象である可能性があり，ある条件下では，個々の種の個体数調節や種間競争において一定の役割をはたしている可能性も考えられる．今後の検討を要する問題であろう．また上記の3型の定義，それら3型の進化史的な関連についても言及した．