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PREDATORY HABITS OF DIPTERAN LARVAE INHABITING *NEPENTHES* PITCHERS

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ABSTRACT. - The food habits of some dipteran immatures inhabiting the fluid in *Nepenthes* pitchers were observed in Indonesia and Singapore. Predation by *Aedes (Alanstonea) treubi* (Culicidae), *Nepenthosyrphus* (Syrphidae), *Nepenthomyia* and *Wilhelmina* (Calliphoridae) and *Pierretia* (Sarcophagidae) is confirmed for the first time. The predatory behaviour of *Lestodiplosis* (Cecidomyiidae), *Xenoplatyura* (Mycetophilildae), *Nepenthosyrphus, Pierretia* and *Phaonia* (Muscidae) is described. Prey selection experiments carried out reveal that *Tripteroides tenax* (Culicidae) and *Dasyhelea* (Ceratopogonidae) are most susceptible to attack by *Toxorhynchites* (Culicidae), *Nepenthosyrphus* and *Nepenthomyia*, whereas *Tripteroides nepenthis* is most resistant, with *Culex* and *Uranotaenia* mosquitoes of intermediate susceptibility. *Corethrella calathicola* (Chaoboridae) attacks *Dasyhelea, Tr. tenax* and if prey is unavailable, also becomes cannibalistic. Predation is very severe in at least some *Nepenthes* pitchers, suggesting the importance of adaptive prey character traits for escape from predation in this habitat.

INTRODUCTION

Phytotelmata are small and discrete water bodies held by plants. They provide habitats for aquatic arthropods, especially immatures of Diptera, and thus have received the ecologist's attention as habitats suitable for studying some aspects of biotic communities (Maguire, 1971; Frank & Lounibos, 1983). Pitchers of the carnivorous plant *Nepenthes* (Nepenthaceae) contain a fluid that is a mixture of plant secretions (including digestive enzymes) and of rain water. Small insects, most abundantly ants (Mogi & Yong, 1992; Kato et al., 1993), are attracted to nectar glands densely distributed on the under surface of the lid extending over the pitcher opening and slip off into the fluid where they are digested and absorbed by the plant. Withstanding this digestive power, some dipteran larvae exclusively inhabit the pitcher fluid. Thienemann (1932) compiled animals recorded from *Nepenthes* pitchers and coined the word "nepenthebiont" for inhabitants specific to this habitat. However, these animals were not dealt with as a community until Beaver (1979a, b) illustrated food webs in pitchers

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of *Nepenthes albomarginata* Lobb and *Nepenthes ampullaria* Jack of Peninsular Malaysia. Since then, this community has been analysed for regional and local variation in food web structure (Beaver, 1983, 1985; Kitching & Pimm, 1985; Kitching & Beaver, 1990; Clarke & Kitching, 1993; Kato et al., 1993), the meaning of food web patterns (Pimm et al., 1991) and competition and predation in patchy habitats (Mogi & Yong, 1992).

The basis for such analyses is the precise knowledge of food habits of inhabitant animals. Although Beaver (1979a) reported some direct observations, the food habits of *Nepenthes* inhabitants have often been inferred from those of related species. They are therefore inconsistent among researchers. By comparing prey communities in *N. ampullaria* pitchers with and without predators, Mogi & Yong (1992) hypothesized that some of the competitively superior prey species are more susceptible to predation, but they gave no substantiating data. Here we report (1) newly confirmed predacity of some dipteran larvae, (2) predatory behaviour of these and some other predators, and (3) selective predation revealed by laboratory experiments.

MATERIALS AND METHODS

Species studied - Species used for study and their origins are compiled in Table 1. Some taxa have not yet been identified to species or described. Therefore, for the sake of convenience, these species (some probably new to science) are designated by their generic names with their country of origin (i.e. collection regions) appended. Species from different *Nepenthes* species in the same region are also distinguished. Some of the congeneric insects from different regions or *Nepenthes* species may finally prove to be conspecific.

Observation on predatory habits - Feeding habits were observed under room temperature (ca. 25°C) and natural daylength conditions (12-13 h = astronomical daylength + durations of morning and evening civil twilight) near the collection sites. Some observations with substitute prey (see below) were conducted in the insectary with 20°C and 12 h photophase.

Predators and prey were placed in 10 ml (diameter 2 cm, height 3.5 cm) plastic tubes with 2 ml (depth 7 mm) of pitcher fluid or 100 ml (diameter 4.5 cm, height 7 cm) plastic bottles with 15 ml (depth 1 cm) fluid. As far as possible, nonpredator nepenthebiont dipteran larvae collected together with predators were used as prey; they were *Culex coerulescens* (Edwards), *Culex eminentia* (Leicester), *Tripteroides nepenthis* (Edwards), *Tripteroides nepenthisimilis* Mattingly, *Tripteroides tenax* (De Meijere), *Tripteroides* sp. 1 (Mattingly, 1981), *Uranotaenia gigantea* Brug, *Uranotaenia moultoni* Edwards, *Dasyhelea* spp. and *Megaselia* spp. When these natural prey species were unavailable, *Aedes aegypti* (L.), *Aedes scutellaris* (Walker) and *Culex quinquefasciatus* Say larvae from laboratory colonies were substituted. Known numbers of prey individuals were given and the number attacked (consumed and/or killed) within one day was recorded.

Prey selection experiments - A single predator individual of the last larval instar was placed together with two to five different taxa or stages of prey (three individuals per taxa/stage) for all the predators studied, namely, *Toxorhynchites, Corethrella calathicola, Nepenthosyrphus* and *Nepenthomyia.* The numbers of surviving prey were recorded at 12-h intervals for the first 10 days (at room temperature) and daily thereafter (at 20°C). Prey survival rates at observation time *t* were subjected to the improved angular transformation

Table 1. Nepenthebiont Diptera for which food habits were observed

Family	Species	Site	Date	*Nepenthes* species*
Culicidae	*Aedes treubi* (DeMeijere)	Sumatra	1994 Aug 16-19	*N. singalana* Becc.
	Toxorhynchites acaudatus (Leicester)	Singapore	1994 Oct 22	*N. ampullaria* Jack
	Toxorhynchites sp.	Borneo 1	1993 Aug 25	*N. ampullaria*
	Toxorhynchites sp.	Borneo 2	1993 Aug 26	*N. reinwardtiana* Miq.
	Uranotaenia gigantea Brug	Sumatra	1994 Aug 19	*N.* sp.
Chaoboridae	*Corethrella calathicola* Edwards	Singapore	1994 Oct 22	*N. ampullaria*
Cecidomyiidae	*Lestodiplosis* sp.	Singapore	1994 Oct 25	*N. gracilis* Korth
Mycetophilidae	*Xenoplatyura beaveri* Matile	Singapore	1994 Oct 25	*N. ampullaria*
Syrphidae	*Nepenthosyrphus* sp.	Borneo 1	1993 Aug 25	*N. ampullaria*
	Nepenthosyrphus sp.	Borneo 2	1993 Aug 26	*N. reinwardtiana*
	Nepenthosyrphus sp.	Borneo 3	1993 Aug 27	*N. gracilis*
	Nepenthosyrphus sp.	Sumatra	1994 Aug 18	*N. ampullaria*
	Nepenthosyrphus sp.	Singapore	1994 Oct 20	*N. ampullaria*
Calliphoridae	*Wilhelmina nepenthicola* Villeneuve	Sumatra	1994 Aug 17	*N. gracilis*
	Nepenthomyia sp.	Borneo 4	1993 Aug 23	*N. ampullaria*
	Nepenthomyia sp.	Borneo 1	1993 Aug 25	*N. ampullaria*
	Nepenthomyia sp.	Singapore	1994 Oct 20	*N. ampullaria*
Sarcophagidae	*Pierretia* sp.	Irian Jaya	1993 Aug 4	*N. maxima* Nees
	Pierretia sp.	Biak	1993 Aug 11	*N. insignis* Dans.
Muscidae	*Phaonia nepenthicola* Stein	Java	1993 Sep 4	*N. gymnamphora* Nees
	Phaonia sp.	Sumatra 1	1994 Aug 12-19	*N.* sp.
	Phaonia sp.	Sumatra 2	1994 Aug 16	*N. singalana*

* Following Kurata (1976) except for *Nepenthes* sp. from Sumatra.

[arcsin $\sqrt{(n_t + 3/8) / (n + 3/4)}$, where n_t = no. survivors at time t, n = no. exposed to the predator (Sokal and Rohlf, 1981)]. Means and standard errors (SE), calculated from replicates, were backtransformed to percentages.

RESULTS

1. Species confirmed to be predatory

Table 2 shows species proved to be predatory in this study. Due to unavailability of sufficient prey individuals, the maximum consumption rate could not be determined. However, the proportion of days when predation was confirmed to the total observation days might be an index of predation efficiency. *Aedes (Alanstonea) treubi* attacked both *Ae. aegypti* and *Ur. moultoni* efficiently. *Nepenthosyrphus* from Borneo also exhibited predatory habits at high rates and attacked as many as 30 4th instar *Ae. aegypti* per day. *Nepenthosyrphus* Singapore is an efficient predator against *Dasyhelea* and nepenthebiont mosquito larvae (see 3 below, prey selection experiments). A single individual of *Wilhelmina nepenthicola* attacked both *Ur. gigantea* and *Ae. aegypti* larvae efficiently. *Nepenthomyia* Singapore attacked *Dasyhelea* and nepenthebiont mosquito larvae (see selection experiments). *Nepenthomyia* Borneo 2 also attacked *Ae. aegypti* at a low rate, but *Nepenthomyia* Borneo 1 did not attack this prey during eight observations. *Pierretia* Biak attacked *Ae. aegypti* efficiently. One *Pierretia* larva from Irian Jaya, when collected, devoured a newly drowned carabid beetle (length ca. 1 cm) floating at the fluid surface. *Phaonia nepenthicola* and *Phaonia* Sumatra also were efficient predators against *Ae. aegypti*, *Ae. scutellaris* and *Cx. quinquefasciatus* and attacked at least 20 4th instar *Ae. aegypti* per day. However, attack rates were substantially lower against nepenthebiont *Ur. gigantea* coexisting in the field. Larvae of *Ur. gigantea* are exceptionally large among *Uranotaenia* species and comparable to substitute prey in body size. Thus, lower vulnerability of *Ur. gigantea* to *Phaonia* predation was not due to size differences. Despite its large size, *Ur. gigantea* was not predatory and never attacked 3rd or 4th instar larvae of *Ur. moultoni*, a smaller coexisting species.

Table 2. Nepenthebiont Diptera proved to be predatory[a]

Species	Prey[b]	n[c]	% with predation[d]	Maximum no. prey given per day	Maximum no. prey attacked per day[e]
Ae. treubi	*Ur. moultoni*	26	89	3	3
	Ae. scutellaris	58	100	2	2
Nepenthosyrphus Borneo 1	*Ae. aegypti*	51	100	30	30
	Cx. quinquefasciatus	8	100	1	1
Nepenthosyrphus Borneo 2	*Ae. aegypti*	6	83	1	1
Nepenthosyrphus Borneo 3	*Ae. aegypti*	8	75	10	10
Nepenthosyrphus Singapore	See selection experiment				
Wilhelmina nepenthicola	*Ur. gigantea*	4	75	1	1
	Ae. scutellaris	15	100	4	4
Nepenthomyia Borneo 2	*Ae. aegypti*	11	46	3	3
Nepenthomyia Singapore	See selection experiment				
Pierretia Biak	*Ae. aegypti*	7	86	2	1
Phaonia nepenthicola	*Ae. aegypti*	9	100	20	20
	Cx. quinquefasciatus	6	100	1	1
Phaonia Sumatra 1	*Ur. gigantea*	26	69	1	1
	Ae. scutellaris	93	98	2	2
Phaonia Sumatra 2	*Ur. gigantea*	48	44	1	1
	Ae. scutellaris	46	78	2	2

a - Observed in 10 ml bottle at 25°C (observations with nepenthebiont prey) or 20°C (observations with substitute prey).
b - 4th instar larvae
c - No. observations (= day x predator number).
d - 100 x no. observations when predation was confirmed / no. all observations,
e - Including prey individuals killed but not consumed.

2. Predatory behaviour of nepenthebiont Dipteran larvae

Lestodiplosis - Mature larvae of the cecidomyiid *Lestodiplosis* Singapore (ca. 1.2 mm long) did not attack 1st to 3rd instar larvae of the mosquito *Tr. tenax* and 2nd instar larvae of *Megaselia*. They crawled actively on and among the detritus, and attacked 3rd and 4th instar larvae of *Dasyhelea* (respectively about 3 mm and 6 mm long on maturity). They attached themselves to the prey body with their mouthparts (Fig. 1A) and often coiled round the prey. The prey wriggled violently but, within a few minutes, became immobile and then completely motionless. At the initial phase of the attack, the predator often dropped off due to the vigorous wriggles of the prey, but, later, it stuck to the prey firmly and rarely was detached from the wriggling prey. The wriggling or motionless victim was seized by other *Lestodiplosis* larvae, and often several predator individuals were seen feeding on a single victim (Fig. 1B). They sucked the prey's body fluids, leaving its dead body behind.

Xenoplatyura beaveri - The larvae of this mycetophilid spun a dense sticky net (web) above the water with secretions produced from their mouthparts (Fig. 1C). Mosquito adults emerging from pupae were all caught by this net. When the victim on the net struggled, the predator approached it and strengthened the net around the prey. The predator did not devour the victim's whole body immediately but often consumed it over 2-3 days. This predator often crawled over and strengthened the net but, when it touched the water surface, would quickly retract from the water.

Nepenthosyrphus - The resting larvae of the syrphid *Nepenthosyrphus* Borneo 1 most often stayed motionlessly on the submerged part of the bottle wall with their anal respiratory horn touching the water surface, or, sometimes, stayed on the wall above the fluid. When prey mosquito larvae were added to the fluid, the predator laid on the bottom or floated upside down (Figs. 1D, E), and very quickly coiled round the approaching mosquito larvae (Figs. 1F, G). While still coiled round the victim on the bottom of the container, it consumed the victim within 15 minutes. The predator then uncoiled and actively crawled over the bottom, demonstrating a behaviour that was completely different from its resting posture. The predatory behaviour of *Nepenthosyrphus* Borneo 2 and 3 was not observed. One individual *Nepenthosyrphus* Borneo 3 was once seen to seize a live mosquito larva with its mouthparts and to eat the prey without coiling.

Nepenthomyia - The predatory behaviour of this calliphorid was not directly observed.

Wilhelmina nepenthicola - A single larva of this calliphorid was observed to float near the water surface and to often strike the space below with its body in a manner that suggests capture of prey by "hooking" it. However, the moment of "hooking" its mosquito larval prey was not observed.

Pierretia - The larva of this sarcophagid coiled round its prey (a mosquito larva offered) in the same manner as *Nepenthosyrphus* Borneo 1, but while feeding (Fig. 1H) it was floating and not lying on the bottom.

Phaonia - Slender larvae of the muscid *Phaonia nepenthicola* rested on the bottle wall above the fluid (head either upward or downward), in the fluid (head downward) or half in the fluid (head in the fluid with the posterior body above the fluid). The predatory attack was done only from the last position. With their posterior body on the wall, they stretched or swung their anterior body into the fluid (Fig. 1I), and hooked mosquito larvae approaching

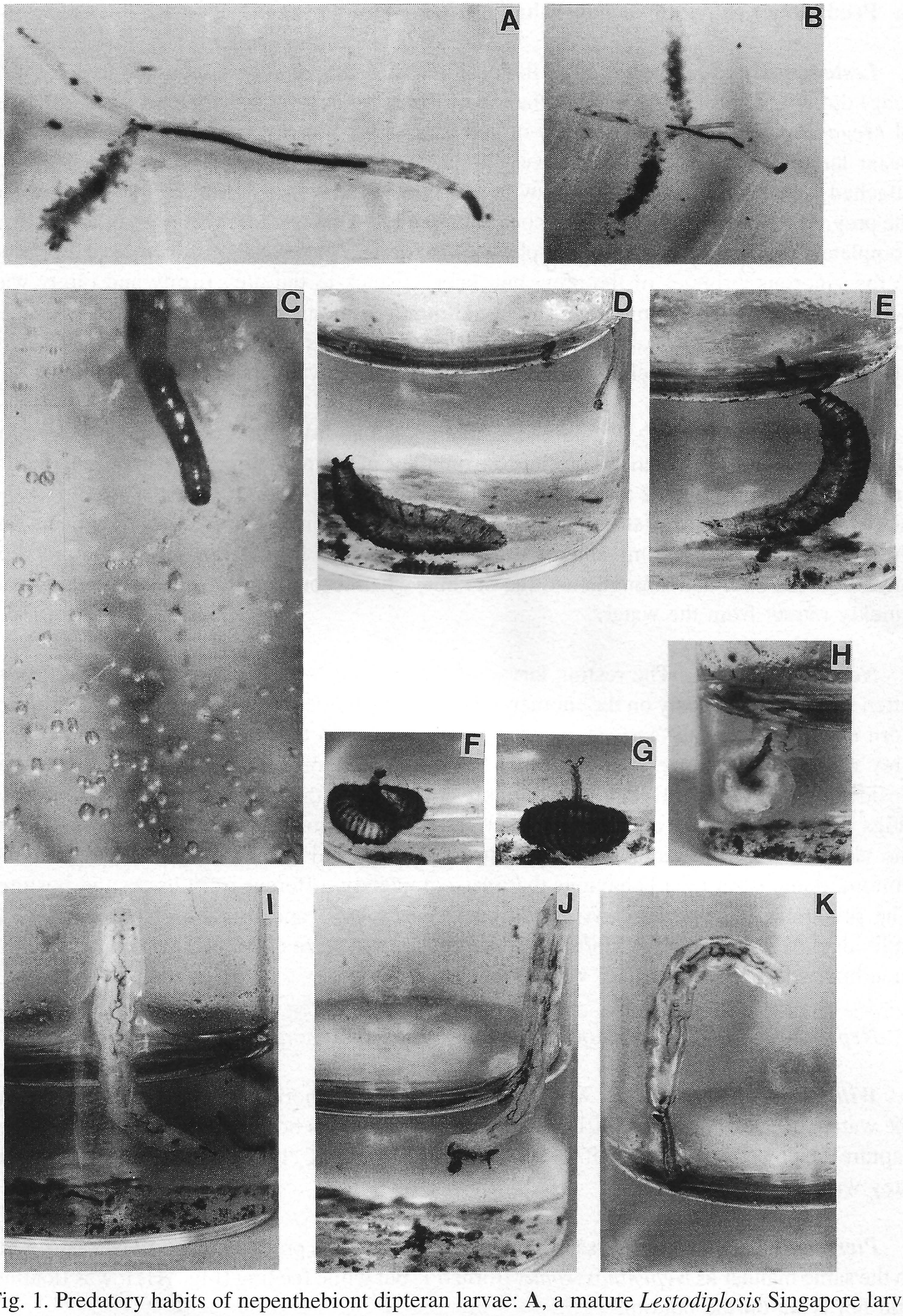

Fig. 1. Predatory habits of nepenthebiont dipteran larvae: **A**, a mature *Lestodiplosis* Singapore larva attacking a 4th instar *Dasyhelea* larva; **B**, two mature larvae of *Lestodiplosis* Singapore sucking the fluids from a 3rd instar *Dasyhelea* larva; **C**, webs with sticky droplets of various sizes and a mature *Xenoplatyura beaveri* larva (the head and anterior body is seen); **D,E**, mature larvae of *Nepenthosyrphus* Borneo 1 lying (**D**) or floating (**E**) upside down in preparation for predatory attack; **F,G**, mature larvae of *Nepenthosyrphus* Borneo 1 consuming 4th instar *Aedes aegypti* larvae (the victim's anterior [**F**] or posterior [**G**] part of the body is seen); **H**, a mature larva of *Pierretia* Biak consuming a 4th instar *Ae. aegypti* larva; **I,J,K**, mature larva of *Phaonia nepenthicola* aiming at [**I**], catching [**J**] and pulling up [**K**] a 4th instar larva of *Ae. aegypti*.

the head with a quick motion (Fig. 1J). As soon as the prey was caught the predator pulled up the victim above the water by moving backwards and then consumed it (Fig. 1K). *Phaonia* Sumatra attacked and consumed its prey in the same manner.

3. Prey selection experiments

Toxorhynchites - In 100 ml bottles, 4th instar larvae of the mosquito, *Toxorhynchites*, attacked *Dasyhelea* larvae most readily. They attacked, less readily, larvae of the mosquitoes *Cx. eminentia, Tripteroides* sp. 1, *Tr. nepenthisimilis* and *Tr. tenax* (Figs. 2A,B,C). *Culex coerulescens* was more resistant to *Toxorhynchites* predation while *Tr. nepenthis* and *Ur. moultoni* were highly resistant. After the disappearance of the susceptible species, a few resistant prey larvae managed to survive, some individuals coexisting with the predators for >30 days.

In 10 ml bottles (Fig. 2D), *Ur. moultoni* was attacked most easily and disappeared within 2-5 days, whereas *Tr. nepenthes* was still highly resistant to *Toxorhynchites* predation.

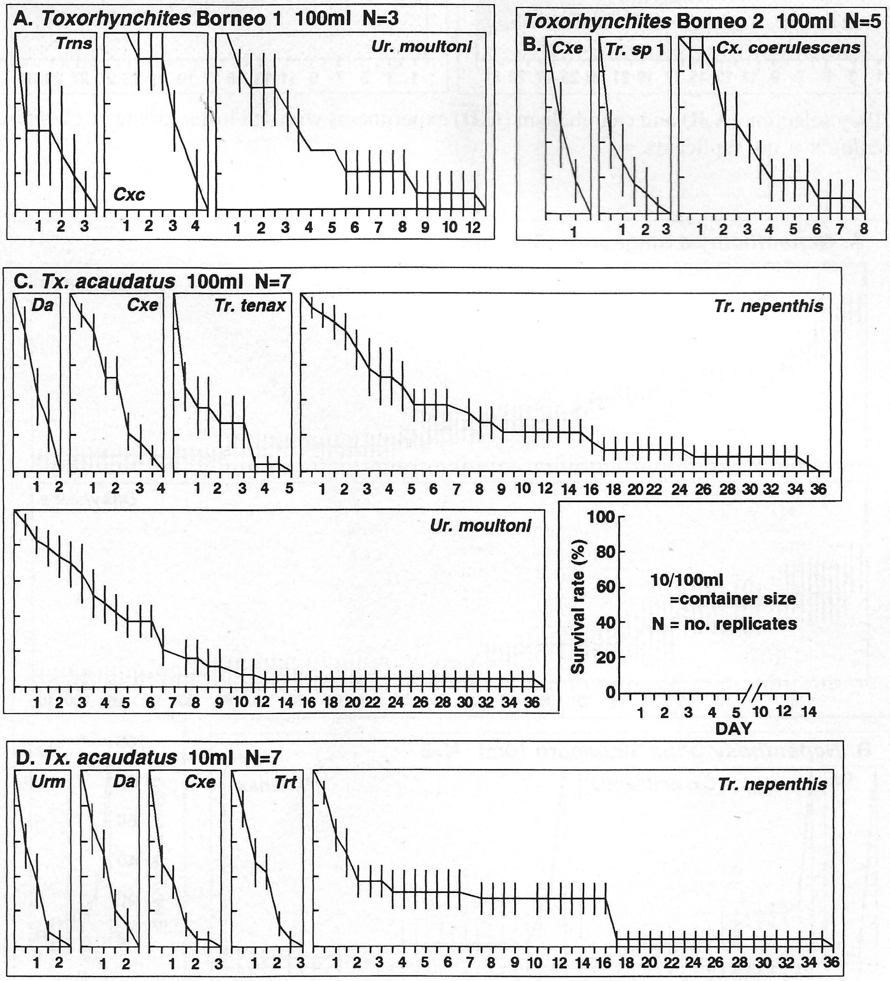

Fig. 2. Prey selection experiments with 4th instar larvae of *Toxorhynchites* Borneo 1 (**A,B**) and *Tx. acaudatus* (**C,D**). *Trns = Tr. nepenthisimilis; Cxe = Cx. emenentia; Da = Dasyhelea; Urm = Ur. moultoni*. Mature larvae of prey were offered. N = no. replicates.

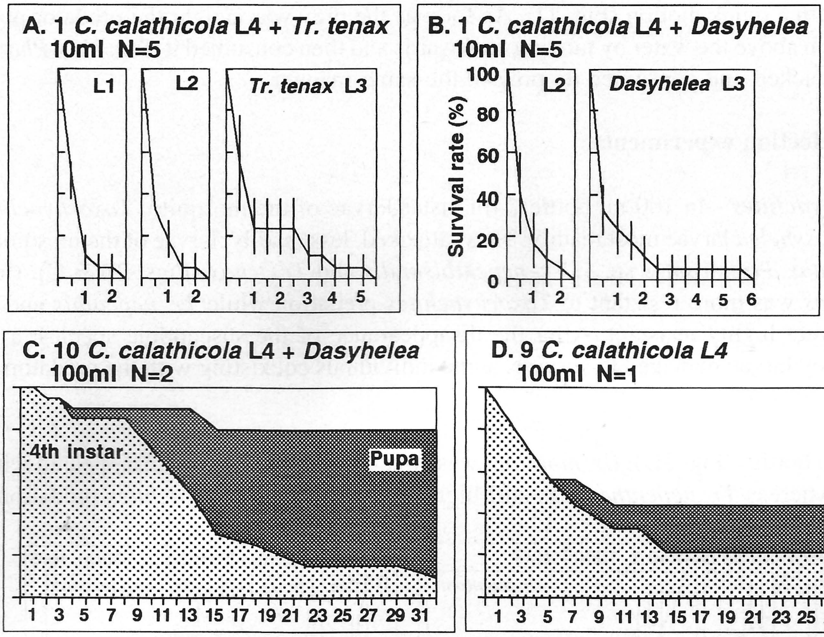

Fig. 3. Prey selection (**A**,**B**) and cannibalism (**C**,**D**) experiments with 4th instar larvae of *Corethrella calathicola*. N = no. replicates.

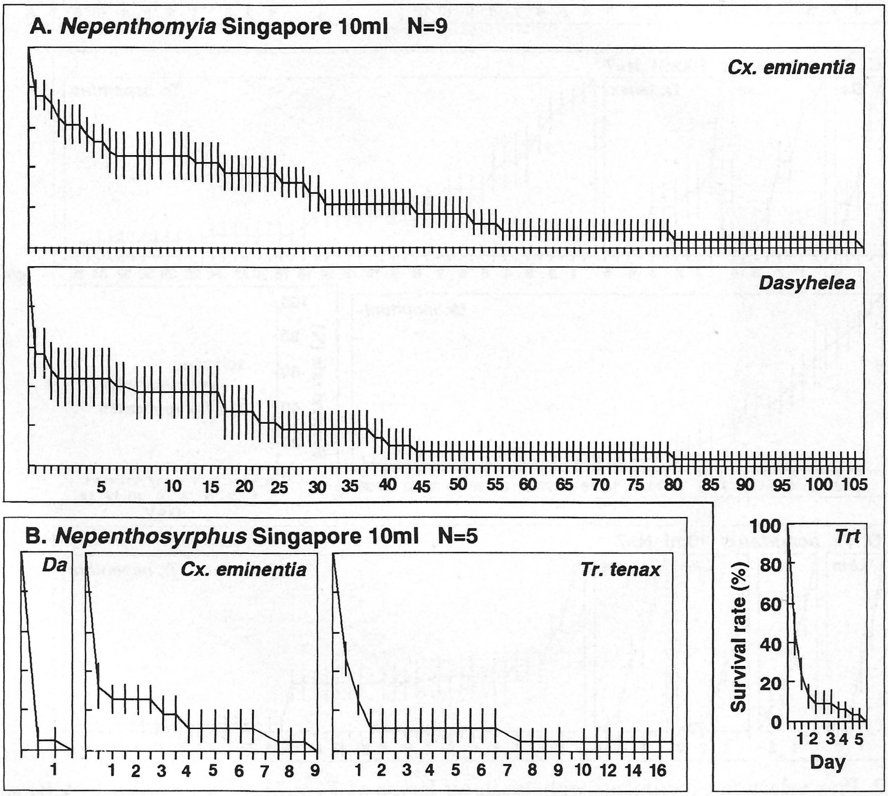

Fig. 4. Prey selection experiments with mature larvae of *Nepenthomyia* (**A**) and *Nepenthosyrphus* (**B**). Mature larvae of prey were offered. N = no. replicates.

Corethrella calathicola - This small chaoborid predator preyed on 1st to 3rd instar larvae of *Dasyhelea* and *Tr. tenax*, consuming younger instars more quickly (Figs. 3A,B). More than 65% of the 4th instar larvae supplied with *Dasyhelea* larvae pupated within 20 days (Fig. 3C), whereas those kept without *Dasyhelea* killed one another and the pupation rate was only 20% (Fig. 3D).

Nepenthomyia - *Nepenthomyia* Singapore consumed 90% of *Tr. tenax* larvae within 2 days and all of them within 6 days (Fig. 4A). However, both *Cx. eminentia* and *Dasyhelea* were resistant to this predator except for some individuals consumed within the first 1 or 2 days. The remaining individuals were killed infrequently and a few coexisted with the predator for >100 days in 10 ml bottles.

Nepenthosyrphus - *Nepenthosyrphus* Singapore attacked *Dasyhelea* larvae most efficiently, killing all within 2 days (Fig. 4B). Seventy percent of *Cx. eminentia* and 90% of *Tr. tenax* were also attacked within 1-2 days, but a few remaining individuals survived for more than 2 weeks.

DISCUSSION

Predation by species of the genera *Nepenthosyrphus, Wilhelmina, Nepenthomyia* and *Pierretia* is confirmed for the first time in this study. Beaver (1983) regards *Nepenthosyrphus* from *Nepenthes albomarginata* of Peninsular Malaysia as a carrion feeder, whereas Kitching (1987) considers *Nepenthosyrphus* from *N. maxima* of North Sulawesi as a predator. Kitching reported the larva's "predatory foray" while staying on the pitcher wall but did not describe its actual predatory behaviour. We also observed that the larvae stayed on the pitcher wall with their heads directed downward and their posterior respiratory horns at the water surface, but this resting posture appears to be different from their pre-attack postures.

Nepenthomyia, Wilhelmina and *Pierretia* are also regarded as carrion feeders by Beaver (1979a, 1983). We also observed *Pierretia* Irian Jaya to feed on recently drowned insects. *Nepenthomyia* Borneo 1 did not exhibit predatory behaviour during the short observation period. Attack behaviour of *Wilmelmina nepenthicola* was not directly confirmed. It is probable that these calliphorid and sarcophagid nepenthebiont fly larvae are facultative predators utilizing both victims and inhabitants of *Nepenthes* pitchers. Large predatory larvae of *Toxorhynchites* mosquitoes attack struggling insects dropped on the water surface (Steffan & Evenhuis, 1981). Thus, the utilization of both types of prey may be common to many dipteran predators. That carrion is also utilized by these fly larvae should be confirmed.

A unique predatory behaviour (coiling) is now reported by us for the first time for the nepenthebiont predators *Nepenthosyrphus* and *Pierretia*. It is possible that *Nepenthomyia* and *Wilhelmina nepenthicola* may also attack their prey in a similar manner. The slender muscid fly larva of *Phaonia* is also an efficient predator, but it differs from the stumpy larvae of *Nepenthosyrphus* and *Pierretia* by staying on the wall and foraging from there.

All of these predators, as well as culicid predators of *Ae. treubi*, *Toxorhynchites* and the chaoborid *Corethrella calathicola*, attacked victims usually smaller than themselves and consumed all or parts of them. In contrast, larvae of *Lestodiplosis* Singapore usually attacked *Dasyhelea* larvae much larger than themselves and sucked only their body fluids. Beaver (1979a) reported that *Lestodiplosis syringopais* (Hering) from *N. albomarginata* of Penang attacked *Megaselia*, but did not describe the attack behaviour. *Lestodiplosis* Singapore attacked neither *Megaselia* nor *Tr. tenax*, and appeared to be a specialist predator of *Dasyhelea*.

Mogi & Yong (1992) divided aquatic dipteran predators in *Nepenthes* pitchers into "nipper type" (Nematocera) and "hook type" (Brachycera). The present study indicates that the actual predatory behaviour is more diverse than such a simple grouping. Mogi & Yong (1992) included a nematoceran cecidomyiid predator, *Lestodiplosis*, in the hook type, because its reduced mouthparts do not allow grasping in a typical nematoceran manner (Gagne, 1981). As described above, this predator with piercing mouthparts, belongs to neither the "nipper" type nor the "hook" type but represents a third feeding type, namely, "sucker". Further studies on the feeding morphology and behaviour of dipteran nepenthebiont predators could reveal more diverse feeding habits than are currently recognized.

Predation among predators was not examined in the present study; but in *Nepenthes* cups the predators themselves, especially of small size or younger stages, are constantly exposed to predation by larger predators of the same and different species. Except for two small predators (*Lestodiplosis, Corethrella calathicola*), the mature larvae of nepenthebiont predators are usually singletons (Beaver, 1979a; Mogi & Yong, 1992), due probably to intraspecific predation. Cannibalism by nepenthebiont *Toxorhynchites klossi* (Edwards) of Peninsular Malaysia was observed to be so severe that mass rearing was impossible even under conditions of ample prey supply (Horio, 1991). *Corethrella calathicola* with aggregated inter-pitcher distribution (Beaver, 1979a; Mogi & Yong, 1992) was considered not to be cannibalistic under usual conditions (Beaver, 1979a). However, the present study shows that cannibalism in this species can also occur under conditions of prey shortage. In contrast, cannibalism among *Lestodiplosis* larvae was not observed and seems unlikely. *Lestodiplosis* larvae, like *Corethrella calathicola*, are distributed aggregatedly among pitchers (Beaver, 1979a). Often, a group of the mature larvae enter a narrow space such as the hollow femur of a fragmented and digested insect before they pupate 'in a group' on the wall above the fluid. The present study shows that they also feed on the prey in a group. Whether the feeding success rate of coexisting *Lestodiplosis* larvae is higher than that of a single larva is an interesting subject for future study.

The terrestrial predator, *Xenoplatyura beaveri*, never shared the pitcher with conspecifics nor with aquatic *Nepenthomyia* larvae (Beaver, 1979a). The latter was observed often to crawl over the pitcher wall and to destroy *Xenoplatyura* webs (Beaver, 1979a). Thus, interspecific interaction also occurs between aquatic and terrestrial predators through behavioural interference.

An important conclusion from the observations described is that predation is very severe in at least some *Nepenthes* pitchers. This suggests that *Nepenthes* pitcher inhabitants, irrespective of predators or nonpredators, must have the ability to escape from predation. One such adaptive trait is to remain motionless. Larvae of the nepenthebiont mosquitoes *Tripteroides, Uranotaenia* and *Culex* usually stick to the pitcher wall upside down with their head directed downwards, and remain motionless in this position for long periods, except for some filtering movements of their mouthbrushes. An exception was *Tr. tenax* larvae, which more frequently lay on the detritus upside down or stayed at the water surface when not disturbed. *Dasyhelea* larvae actively crawled on the bottom of bottles used for prey selection experiments. These behavioural differences may partly explain the results of selection experiments in which *Dasyhelea* and *Tr. tenax* were more vulnerable to predator attacks than were the other prey species. Although phorid larvae were not included in the selection experiments, they may also be susceptible to predation due to their mobility and presence at the water surface when not disturbed. Susceptibility of substitute prey may also be attributed to the active movements of these species in the pitcher fluid which probably was stimulative for them. Extended survival times of a few last individuals also indicated the importance of movement as a key stimulus triggering predator attacks. When density of prey, including mobile ones, is high, disturbance would force even less mobile species to move. In the present selection experiments prey were exposed to predators without refuges. In the field, chitinous parts of victim arthropods accumulate densely on the pitcher bottom. Under such conditions, *Dasyhelea* larvae may be more able to escape predation. Experiments with the prey in field pitchers or under semi-natural conditions are required for a more realistic evaluation of their vulnerability to predator attacks.

Vulnerability of *Tr. tenax*, one of the most common *Tripteroides* species inhabiting *Nepenthes* pitchers from Southern Thailand through Indonesia, is noteworthy. This species is so very close to *Tr. aranoides* (Theobald) inhabiting bamboo stumps that it has often been confused with the latter which is known from India through Indonesia (Mattingly, 1981). These facts might suggest the relatively recent invasion of pitcher habitats by *Tr. tenax* or vice versa.

The role of regional and local processes in determining community structure is currently a subject under debate in ecology (for review see Cornell & Lawton, 1992). Beaver (1985) and Kitching (1987) emphasized the importance of regional (biogeographical) processes determining the richness of communities in *Nepenthes* pitchers: communities in regions near the evolutionary centre of *Nepenthes* are richer. Later, Kitching & Beaver (1990) recognized three levels (biogeographical, population, and stochastic) for the analysis of the processes determining community structure in patchy habitats. They demonstrated geographical (largest scale) and stochastic (smallest scale) level processes for aquatic communities in *Nepenthes* pitchers and tree holes. On the other hand, Bradshaw & Holzapfel (1983) and Mogi & Yong (1992) suggested the importance of population-level interactions (predation and competition) in the organization of aquatic communities in such phytotelmata as well. The present study further suggests the importance of species interactions in determining the structure of communities in *Nepenthes* pitchers. In a separate paper, the role of predation in the organization of communities in *Nepenthes* pitchers in Singapore will be examined by comparing communities with and without predators. *Nepenthes* pitchers are habitats suitable for analysing the significance of processes acting on community organization at various levels, but present knowledge is rather fragmentary. More extensive and intensive studies are necessary.

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