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Interaction between the predator *Toxorhynchites brevipalpis* and its prey *Aedes aegypti*[1]

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In a circumscribed area in Tanzania where the predacious larvae of Toxorhynchites brevipalpis *were particularly abundant, it was found that water-filled tires and tins containing* Toxorhynchites *larvae had fewer larvae of* Aedes aegypti *than those without the predator larvae. The peaks of infestation with* Toxorhynchites *larvae occurred almost a month later than the peaks of* A. aegypti *infestation. Cannibalism was observed among the predator larvae in these containers.*

Measurement of the effect of predation by the predacious larvae of the mosquito *Toxorhynchites* on the larvae of *Aedes aegypti* is important for the understanding not only of the population dynamics of this yellow-fever vector but also of the results to be obtained when species of *Toxorhynchites* are employed as biological control agents. Predator–prey relationships in entomology may be studied by the use of mathematical models (3, 6), but their characterization in the field is much more difficult. Certain components of the predator–prey system comprising *Toxorhynchites* and *A. aegypti* have already been studied (7, 1, 2). The programme of the WHO East African *Aedes* Research Unit in Tanzania offered an opportunity to study in detail the predator–prey relationships of one important species of *Toxorhynchites*.

Toxorhynchites brevipalpis is a treehole-breeding mosquito widely distributed in the tropical zone of Africa. Its larvae occur commonly in the axils of plants such as *Strelitzia* and *Dracaena* in some regions of South Africa (7) but not in East Africa. Breeding in man-made containers has also been recorded in the past (5). At present breeding in treeholes is still more extensive than breeding in artificial containers, although the author has found larvae in coconut shells and in *Achatina* snail shells very occasionally. The occurrence of *T. brevipalpis* in unusually high numbers in the Buguruni automobile dump located in one of the Dar es Salaam suburbs, where the larvae of this species were breeding mostly in tires, provided a unique opportunity for study.

This one-hectare habitat contained about 500 wrecked automobiles, 3 000 discarded motor tires, 190 tins, 160 coconut shells, and 380 *Achatina fulica* snail shells. The number of tires increased from 2 500 in April 1969 (when this study began) to 3 240 in August 1969 and to 4 000 in May 1970.

The purpose of the present investigation was to demonstrate the predator–prey relationship of *Toxorhynchites* and to follow the oscillations in relative numbers of predator and prey. In the laboratory, the author has found that one *T. brevipalpis* larva destroys an average of 154 *A. aegypti* larvae when reared at 26°C, and as many as 359 *A. aegypti* larvae at 32°C (10). In the field, the effect of predation of *T. brevipalpis* on *A. aegypti* can be found (*a*) indirectly, from the frequency distribution of the numbers of prey larvae per container in the presence and absence of the predator larvae, or (*b*) directly, by a field experiment with known numbers of predator and prey larvae in marked breeding sites.

METHODS

Nine tires grouped according to size (3 small and capable of holding 3 litres of water, 3 medium-sized holding 6 litres, and 3 large holding 9 litres of water) were sampled weekly. A 15-mm hole was made in the centre of the tires for transferring all the *T. brevipalpis* and *A. aegypti* larvae into a large (500 × 300 × 100 mm) plastic pan, for transport to the laboratory for identification and counting. The physical condition of the tires (presence or absence of water) was recorded. Nine tins were also sampled, similarly

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divided into groups of three, the large tins having a capacity of 2.5 litres, the medium-sized 750 ml, and the small 250 ml. The figure for the population density of the larvae of both predator and prey per one hectare automobile dump was derived from the mean number of larvae per container and the percentage of containers with water.

The data for rainfall were obtained from the Meteorological Station at Dar es Salaam Airport (about 5 km from the study area) from April 1969 to December 1969. In January 1970 a rain-gauge was placed in the study area and checked daily by the members of the East Africa *Aedes* Research Unit until the end of the study.

RESULTS

Effect of Toxorhynchites *on* Aedes aegypti

Of the total of 381 assessments in which water was present in the tires sampled weekly, 159 showed that *A. aegypti* was present alone, and 222 that *Toxorhynchites* was also present (Table 1). When the assessments are grouped into infestation size-classes according to the number of *A. aegypti* found present, it is seen that the presence of *Toxorhynchites* altered the frequency distribution in the direction of the smaller size-classes. In the presence of the predator, no infestation exceeded 50 per tire, whereas 3.4% of samples exceeded 50 in its absence. The frequency of the class where no *A. aegypti* was present increased from 47% in the absence of *Toxorhynchites* to 83% in its presence.

To demonstrate its predatory activity in the field, ten 4th-instar larvae of *T. brevipalpis* were left in each medium-sized tire colonized by this species; then 200 4th-instar larvae of *A. aegypti* were introduced into the tires. The number of prey consumed was recorded and added daily. Three experiments were conducted simultaneously and the observation was continued for 7 days. During 24 hours, the water temperature varied between 22°C and 25°C. It was found that one 4th-instar larva of *T. brevipalpis* living in tires consumes on average 12.3 *A. aegypti* larvae per 24 hours. In laboratory experiments, it has been shown that one 4th-instar predator larva consumes on average 16 prey larvae per 24 hours at a temperature of 26°C (10).

Table 1. Distribution of infestation size (number of larvae). Frequency of occurrence of larvae of *Aedes aegypti* in tires in the absence and in the presence of the predator *Toxorhynchites brevipalpis* larvae

Number of *A. aegypti* larvae per tire	In absence of predator		In presence of predator	
	Number	%	Number	%
0	75	47.2	184	83.0
1–10	51	32.1	27	12.1
11–20	16	10.1	8	3.6
21–50	10	6.3	3	1.3
51–100	5	3.1	0	0.0
101–300	2	1.2	0	0.0
Total	159	100	222	100

Intra-species effects and size of breeding sites

In *Toxorhynchites*, as a treehole-breeding mosquito, intra-species competition for food and space results in cannibalism. In large breeding sites such as tires containing leaves, tree branches, debris, etc., its larvae can find shelter that to some extent protects against cannibalism. Thus, a container as large as a tire can shelter as many as 22 larvae (Table 2). On the other hand, the maximum density of predator larvae found in tins was 10, and this density occurred with a frequency of only 1.8%. Tins are smaller and offer less shelter than tires. One larva per container was found most frequently in both tires and tins. The survival of only one predator larva is most probably the result of cannibalism, because every time that 10–50 1st-instar predator larvae were placed in 100–250-ml beakers without prey, only one larva in the 3rd or 4th instar was found after 5–7 days.

We have found that *T. brevipalpis* females readily lay their eggs in black jars in the laboratory. It was supposed that these containers could be used for detecting seasonal variation in the relative density of a larval population in both suburban and feral biotopes. Ten black jars (ovitraps) 80 mm in diameter and 125 mm deep were placed in the Buguruni and Pugu forest biotopes, and filled three-quarters full with water. They were examined weekly for mosquito larvae over a period of one year. Almost 72% of the ovitraps in the Buguruni biotope and 85% in Pugu forest were found to be negative for *Toxorhynchites* larvae (Table 2). This might indicate that there are perhaps more attractive sites for oviposition than black jars, such as motor tires in Buguruni or treeholes in the Pugu forest. The relatively low number of jars could hardly compete with thousands of tires or hundreds of treeholes.

A single larva per jar was the most frequent finding in both these biotopes. However, the black jars were

Table 2. Frequency distribution of infestation size (number of larvae) of *Toxorhynchites brevipalpis* in various containers

Infestation size (no. per container)	Tires		Tins		Oviposition jars			
					Buguruni		Pugu Forest	
	No.	%	No.	%	No.	%	No.	%
0	99	28.8	137	83.0	377	73.9	170	85.4
1	104	30.4	13	7.9	101	19.8	21	10.6
2	59	17.2	8	4.8	23	4.5	5	2.5
3	35	10.2	4	2.5	3	0.6	3	1.5
4–5	24	7.0	3	1.8	6	1.2	—	—
6–10	18	5.2	—	—	—	—	—	—
11–15	3	0.9	—	—	—	—	—	—
16–22	1	0.3	—	—	—	—	—	—
Total	343	100.0	165	100.0	510	100.0	199	100.0

not suitable for indicating the seasonal variation in density of a larval population of *T. brevipalpis*, and no distinct oscillations in predator–prey density could be detected with them. The small size of the jars and the absence of shelter within facilitated cannibalism. Only in the periods when the prey and predator density was very high did more than one larva occur per jar.

Predator–prey oscillations between Toxorhynchites *and* A. aegypti

The monthly averages for the weekly samples of predator and prey (Table 3) show that the density of the prey was high in April 1969, when these studies began. Four peaks and three depressions in density of prey were recorded during the period of one year extending from April 1969 to March 1970. As has been shown (9), the density of *A. aegypti* in this area depends on the pattern of rainfall. The main rainy season in Dar es Salaam occurs in April and early May. From mid-May to the end of August there is a dry cool season, and the prey population was found to decrease steadily from April to August (Fig. 1). From September to November, when the short rains occurred, the prey population increased again, only to fall in December. The third peak occurred in January, during a dry hot season punctuated by occasional short showers. The decrease in rainfall in February caused a decrease in the prey density. Around the middle of March the new main rainy season started, having the effect of increasing the numbers of prey.

The density of the predator followed the pattern of the prey numbers. Larvae of *T. brevipalpis* showed a direct numerical relationship with the density of *A. aegypti*. However, the effect was not immediate; there was always a time lapse between the emergence of the predator and its active predation. This period includes the pupal stage, the time until the females are able to lay eggs, and the duration of embryonic development until the hatching of new larvae.

The interaction between predator and prey can be demonstrated, e.g., in the oscillation during the period from August to December 1969, when the prey density rose from zero (in August) to 11 708 in October, 2 347 in November, and 272 in December (Fig. 2, A). Neither the larval nor the adult population of the predator fell to zero after a long dry period. However, the predator is not present in large enough numbers to control the prey at the beginning of the rainy season. Eggs of *A. aegypti* laid from the end of the main rainy season until the beginning of the short rainy season remain dormant in breeding sites (9). The hatching of *A. aegypti* at the onset of heavy rain causes a sudden eruption of the population which the predator is not able to reduce because of its low density (Fig. 2, A).

In other invertebrate predator–prey systems, the predators die off rapidly when their prey is depleted. The *Toxorhynchites* predator–prey system is different in this respect. When the prey is depleted the *Toxorhynchites* 4th-instar larvae are capable of starving for 6 months or longer. The drop in population of the predator occurs when there is a shortage of

Table 3. Condition of breeding sites, predator–prey interaction, and population dynamics of larvae of prey (*A. aegypti*) and predator (*Toxorhynchites brevipalpis*) in the Buguruni automobile dump, Dar es Salaam.

Date		No. of tires	Tires with water		Tires positive for mosquito larvae		Tires with *A. aegypti* only			Tires with *T. brevipalpis* only			Tires with *A. aegypti* and *T. brevipalpis*				Estimated population of larvae per one-hectare automobile dump (average of weekly sampling)	
							Tires positive		Mean no. of larvae per tire	Tires positive		Mean no. of larvae per tire	Tires positive		Mean no. of *A. aegypti* per tire	Mean no. of *T. brevipalpis* per tire		
Year	Month	Sampled	No.	%	No.	%	No.	%		No.	%		No.	%			*A. aegypti*	*T. brevipalpis*
1969	April	27	27	100	16	59	8	50	4.1	8	50	3.7	0	0	0.0	0.0	7 492	2 711
	May	36	36	100	27	75	1	4	15.0	19	70	4.6	7	26	7.3	3.7	5 963	7 943
	June	36	36	100	27	75	2	7	5.0	17	63	5.1	8	30	5.4	2.6	4 862	7 687
	July	36	21	58	17	81	2	12	3.0	11	65	4.1	4	24	10.5	3.8	3 652	4 182
	August	36	2	6	2	100	0	0	0.0	2	100	3.0	0	0	0.0	0.0	58	532
	September	45	22	49	8	36	3	38	12.7	5	63	2.2	0	0	0.0	0.0	2 766	1 367
	October	18	18	100	6	33	3	50	12.4	1	17	2.2	2	33	5.0	3.0	11 708	2 508
	November	33	33	100	32	97	3	9	3.7	26	81	3.8	3	9	5.3	4.0	2 347	10 163
	December	45	31	69	24	77	1	4	4.0	22	92	3.6	1	4	4.0	2.0	273	5 448
1970	January	36	34	94	30	88	4	13	2.0	20	67	2.9	6	20	42.7	2.3	10 490	7 731
	February	27	22	82	22	100	1	4	34.0	19	86	2.0	2	9	9.0	2.0	3 133	6 377
	March	36	29	80	18	62	4	22	14.2	11	61	2.4	3	17	5.7	1.7	8 250	3 247
	April	45	32	71	32	100	7	22	11.6	23	72	1.8	2	6	9.5	1.5	10 282	2 654
Total or average		456	343	78	261	76	39	18	9.3	184	68	3.2	38	14	8.0	2.0	—	—

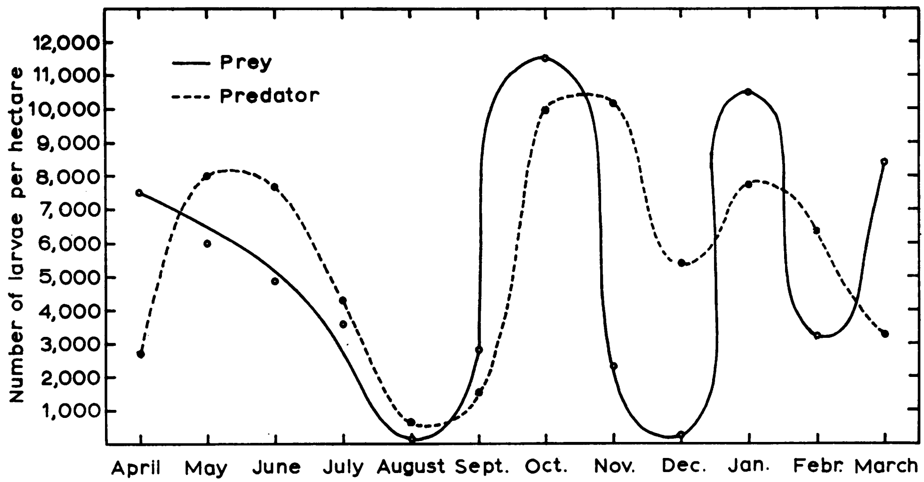

Fig. 1. Oscillations in density showing the predator–prey relationship between mosquito larvae of *Toxorhynchites brevipalpis* (predator) and *Aedes aegypti* (prey) in a suburban habitat in Dar es Salaam.

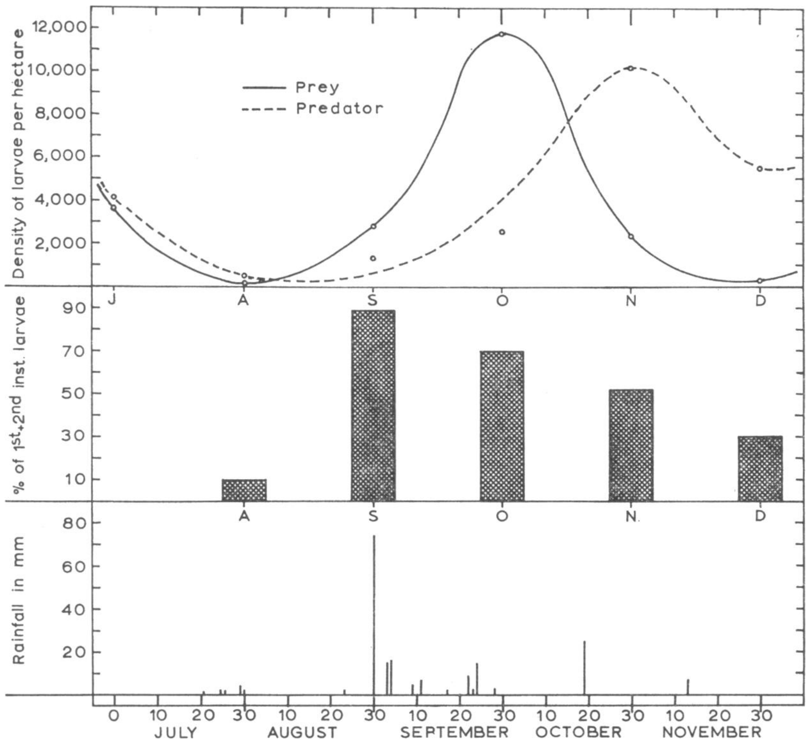

Fig. 2. Growth of the larval population of *Aedes aegypti* and *Toxorhynchites brevipalpis* during the short rainy season in East Africa.

A. One oscillation in the population of prey (*A. aegypti*) and predator (*T. brevipalpis*).

B. Change in the composition of larval instars of the predator during one oscillation.

C. Rainfall of the short rainy season in the coastal zone of Tanzania (Dar es Salaam) in 1969.

A. aegypti. The 4th-instar larvae of *T. brevipalpis* start eating the earlier larval instars of their own species (10). When the larval density of *T. brevipalpis* reaches its peak there is a high population of adults in the area. There is no shortage of predator eggs but all freshly hatched larvae are eaten by higher instars. Density of the 1st- and 2nd-instar larvae of the predator increased after prey population increased (Fig. 2, B). Apparently the higher instars of predator larvae eat the prey larvae. On the descending part of the prey–predator curves cannibalism occurs more intensively (Fig. 2, A).

The data presented in this paper show that the oscillations in the population densities of both prey and predator in the field are such that the reduction in *A. aegypti* larvae soon after the rains is accompanied by an increase in the production of *Toxorhynchites* larvae. This undoubtedly contributes to the suppression of the prey almost to zero level. However, the presence of water in some tires even during the dryest period of the year in the heavily shaded Buguruni biotope prevents extinction of the predator population. At the same time the prey population is mostly in the egg stage, comprising dormant embryos. At the end of the dry season *T. brevipalpis* (whose embryos are not able to resist desiccation) is at a low density level and cannot control the prey population when it erupts at the first heavy rain. Since the predator's life-cycle is almost 3 times as long as that of the prey, the predator begins to be effective as a control agent only when the prey is already at all developmental stages. This delay in control can be eliminated by the release of adult *T. brevipalpis* at the end of the dry season, as the females must be at least 6 days old to produce eggs in time for the first rains. Since *T. brevipalpis* has been colonized (11) and its mass production developed (Dr E. J. Gerberg, personal communication), it would be possible to effect such a release.

Among mosquito predators the larvivorous fish *Gambusia affinis* has been studied most, and probably not enough attention has been given to the study of *T. brevipalpis.* Considering the quantity of prey consumed, it is at least as effective in the control of mosquito larvae as *Gambusia affinis.* Naturally the application of *Toxorhynchites* larvae is limited to a certain group of biotopes, as *Gambusia* is limited to others. However, at present *Toxorhynchites* larvae seem to be good potential predators that can be used for the biological control of some disease-carrying mosquitos in thick rain-forests or in peridomestic habitats. The release of laboratory-reared adults at the end of the dry season would ensure a good production of predator larvae by the beginning of the rainy season, when they are most needed.

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RÉSUMÉ

INTERACTION ENTRE LE MOUSTIQUE PRÉDATEUR *TOXORHYNCHITES BREVIPALPIS* ET SA PROIE *AEDES AEGYPTI*

L'étude de la distribution de fréquence des taux d'infestation des gîtes larvaires par *Aedes aegypti* montre que la présence de larves prédatrices de *Toxorhynchites brevipalpis* a pour effet de réduire fortement le nombre de larves d'*A. aegypti* partout où ce dernier se reproduit. Ces observations ont été faites à Dar es-Salaam, Tanzanie. Le plus souvent, on ne décèle qu'une larve de *T. brevipalpis* par gîte ce qui indique que les larves de cette espèce se dévorent aussi entre elles. Une larve de *T. brevipalpis* au 4e stade consomme en moyenne 12,3 larves d'*A. aegypti* au 4e stade par 24 heures.

L'emploi d'ovipièges est apparu comme une méthode peu sensible pour mesurer les variations saisonnières des populations de *Toxorhynchites* ou du rapport prédateur/proie dans les biotopes suburbains ou sauvages. Le faible volume des récipients utilisés favorise le cannibalisme des larves prédatrices. Dans la plupart des cas, on n'a trouvé qu'une larve de *T. brevipalpis* par piège.

La densité des populations de *T. brevipalpis* dans les gîtes varie en fonction directe de la densité des moustiques proies. La prédation est plus active à la fin qu'au début de la saison des pluies. La faible vitesse de croissance des larves prédatrices freine l'action destructrice sur les larves proies, au développement rapide. On pourrait y remédier en lâchant des *Toxorhynchites* adultes, élevés au laboratoire, peu de temps avant le début de la saison des pluies.

Le système prédateur/proie où *T. brevipalpis* est le prédateur diffère des autres systèmes. Dans la plupart de ces derniers, le prédateur meurt d'inanition lorsque la proie a été complètement détruite; en revanche, les larves de *T. brevipalpis* au 4[e] stade sont capables de supporter un jeûne prolongé (6 mois ou plus). La baisse de la densité du prédateur, quand il n'y a plus de proie disponible, est due au cannibalisme.

REFERENCES

1. Corbet, P. S. Observations on *Toxorhynchites brevipalpis conradti* Grub. (Diptera, Culicidae) in Uganda. *Bull. ent. Res.*, **54**: 9-17 (1963).
2. Corbet, P. S. & Griffith, A. Observations on the aquatic stages of two species of *Toxorhynchites* (Diptera: Culicidae) in Uganda. *Proc. roy. Soc. A*, **38**: 125-135 (1963).
3. Holling, C. S. Principles of insect predation. *Ann. Rev. Entomol.*, **6**: 163-182 (1961).
4. Holling, C. S. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.*, **48**: 1-86 (1966).
5. Hopkins, G. H. E. Mosquitos of the Ethiopian region. I. Larval bionomics of mosquitos and taxonomy of culicine larvae, London, British Museum (Natural History), 1952, pp. 1-355.
6. Morris, R. F. The effect of predator age and prey defense on the functional response of *Podisus maculiventris* Say to the density of *Hyphantria cunea* Drury. *Can. Entomol.*, **95**: 1009-1020 (1963).
7. Muspratt, J. The bionomics of African *Megarhinus* (Diptera, Culicidae) and its possible use in biological control. *Bull. ent. Res.*, **42**: 355-370 (1951).
8. Trpis, M. Adult population estimate of *Toxorhynchites brevipalpis*. *Bull. Wld Hlth Org.*, **48**: 758-759 (1973).
9. Trpis, M. Seasonal changes in the larval populations of *Aedes aegypti* in two biotopes in Dar es Salaam, Tanzania. *Bull. Wld Hlth Org.*, **47**: 245-255 (1972).
10. Trpis, M. Development and predatory behavior of *Toxorhynchites brevipalpis* (Diptera, Culicidae) in relation to temperature. *Environ. Entomol.*, **1**: 537-546 (1972).
11. Trpis, M. and Gerberg, E. J. Laboratory colonization of *Toxorhynchites brevipalpis*. *Bull. Wld Hlth Org.*, **48**: 637-638 (1973).