

# Natural Prey and Digestion Times of *Toxorhynchites rutilus* (Diptera: Culicidae) in Southern Florida

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**ABSTRACT** Natural prey of *Toxorhynchites rutilus* (Coquillett) were identified from gut contents of 941 larvae collected from treeholes and tires located in an oak-palm woodland in south Florida. Twenty taxa of aquatic prey were recognized in midgut remains, in addition to eggs of Diptera from three families. Ostracods and chironomids were the most abundant aquatic prey in predators from tires, and rotifers and copepods from treeholes. Mosquito larvae accounted for only 6% of prey items from treeholes and 5% from tires. Remains of terrestrial arthropods of nine insect orders plus mites and spiders were also identified, these prey having been captured from the water surface by *T. rutilus* larvae. An electivity coefficient, *R*, was calculated for dipterous prey of each predator instar. Significant heterogeneities among *R* values in tires were attributable, in part, to high electivity for certain mosquito species, especially *Aedes albopictus* (Skuse), and for psychodid larvae, and low electivity for larvae of *T. rutilus* and *Orthopodomyia signifera* (Coquillett), a predator-resistant mosquito larva. Diets were more similar between predator instars in tires than in treeholes, where invertebrate diversity was higher. An associated laboratory study was conducted to determine how long common prey could be detected in guts after ingestion. When alternative prey were provided immediately after consumption, oligochaetes, copepods, and psychodid larvae and adults were detected in >50% of dissected *T. rutilus* for 8-18 h after ingestion. By contrast, if *T. rutilus* fourth instars were starved after ingesting test prey, identifiable remains of psychodid larvae were detectable for >30 d in most predator larvae. Thus, the assessment of *T. rutilus* diet by identification of midgut remains is highly dependent on the consumption of subsequent prey.

**KEY WORDS** mosquitoes, arthropods, electivity, midguts, tires, treeholes

IDENTIFICATION OF PREY consumed in nature is an important consideration for biological control with insect predators (Van Driesche and Bellows 1996). Immunological techniques are frequently used to identify prey taxa consumed by field-collected predators (Greenstone and Hunt 1993), but the isolation and preparation of species-specific antibodies for a large or uncertain suite of prey is tedious, and cross-reactivity can occur. For insect predators that ingest prey whole, the identification of exoskeletal remains in guts or feces permits an inventory of consumed prey with hard body parts (James 1961, Pritchard 1964, Fedorenko 1975).

Predatory mosquitoes of the genus *Toxorhynchites* have been introduced to control the immature stages of container-inhabiting mosquitoes on certain islands or in cities (Rivière et al. 1979, Focks et al. 1983, Gerberg 1985). Although natural populations of *Toxorhynchites* have been shown to depress the abundance of co-occurring mosquitoes (Bradshaw and Holzapfel 1983, Lounibos et al. 1997), a previous analysis of the gut contents of *Toxorhynchites theobaldi* (Dyar and Knab) revealed that mosquitoes were less frequently eaten than other larval aquatic Diptera or surface prey

(Kazana et al. 1983). The potential importance of terrestrial arthropods that alight or fall on the water surface as prey was underscored by Linley (1995), who demonstrated that *T. amboinensis* (Doleschall) and *T. brevipalpis* Theobald actively hunt for surface prey.

Kazana et al. (1983) examined the diet of *T. theobaldi* from flower pots in a Caracas cemetery, where aquatic faunal diversity was low and only six prey taxa were recognized. We report here the results of applying gut content analyses to the native North American *Toxorhynchites rutilus* (Coquillett) collected from treeholes and discarded auto tires, microhabitats frequently occupied by this species in Florida where it is the top predator in the aquatic communities of these containers (Bradshaw and Holzapfel 1983). We also describe experimental results that elucidate the time-course of disappearance of exoskeletal remains of four prey species from *T. rutilus* guts and its dependence on the consumption of subsequent prey.

## Materials and Methods

**Field Studies.** Larvae of *T. rutilus* were collected from 29 treeholes and 30 discarded tires that held water in an oak-palm woodland at the Florida Medical Entomology Laboratory (FMEL) in Vero Beach be-

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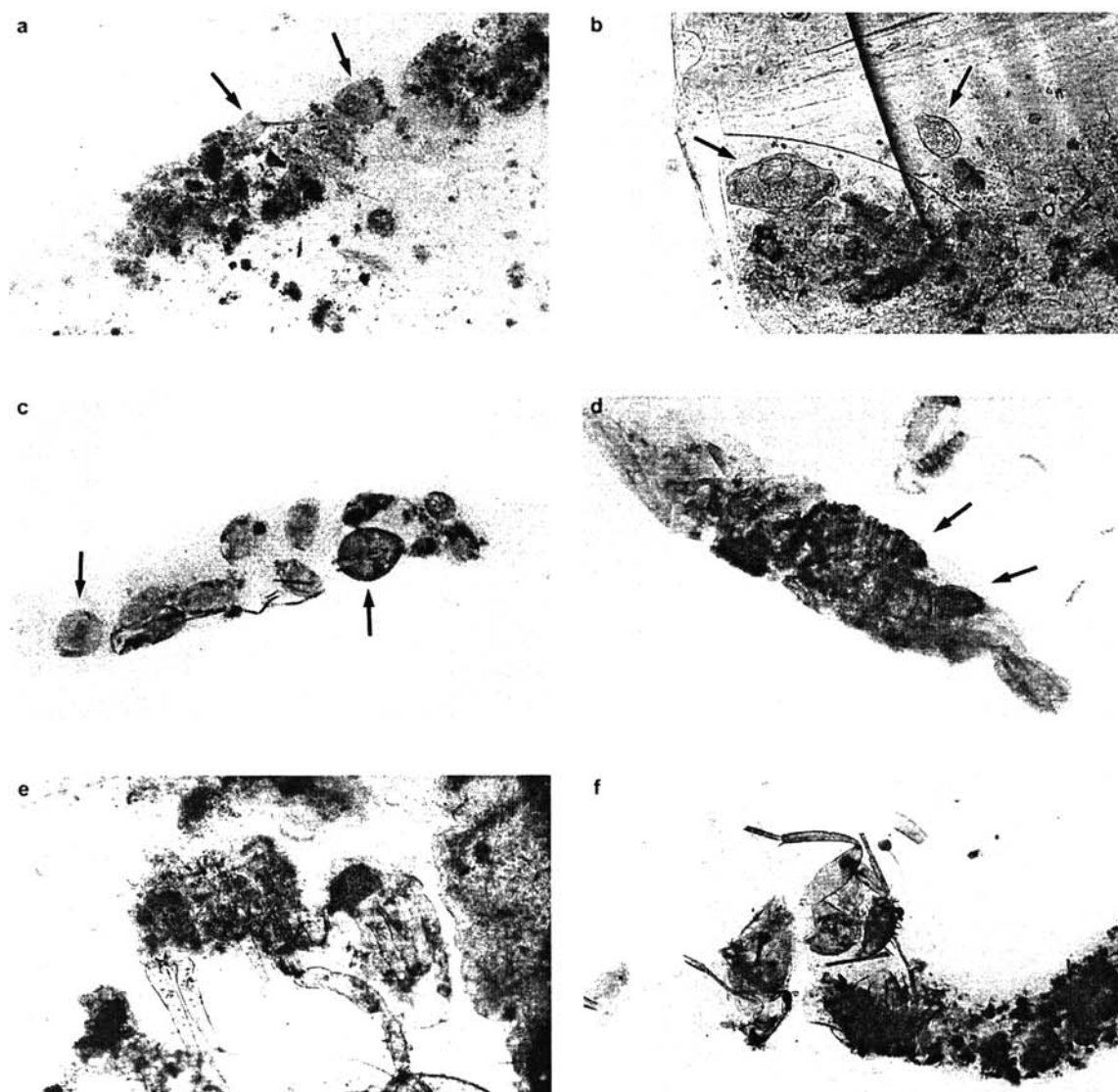


Fig. 1. Examples of prey identified from midguts of *T. rutilus*, structures and specimens noted by arrows where appropriate. a: head capsules of *T. rutilus* larvae in a third instar; b: rotifers in a first instar; c: microcrustaceans (Cladocera, left, Ostracoda, right) in a fourth instar; d: psychodid larvae in a fourth instar; e: Collembola (stained) in a fourth instar; f: adult Diptera in a fourth instar.

tween 21 January and 27 September of 1998. At weekly intervals the entire fluid contents of eight of each container type was suctioned with a hose or ladled with a cup; all debris was extracted from each container for examination. After identifying and counting all aquatic Diptera and removing any *T. rutilus*, each sample was returned to its original habitat. Collected *T. rutilus* larvae were immediately dissected in saline solution under a microscope according to Kazana et al. (1983). Gut contents were examined on microscope slides to identify prey remains (Fig. 1), which were recognized by characteristic chitinous structures. Culicidae were identified to genus and/or species by head capsules, siphons, pecten and comb scales (Fig. 1a). Other Diptera were identified to family: Chirono-

midiae by thoracic and abdominal prolegs; Psychodidae by respiratory tubes and integumentary plates (Fig. 1d); Syrphidae and Ephydriidae by the retractile breathing tube.

Orders of microcrustacea were identified by external morphology (Fig. 1c). In instances of incomplete remains, Copepoda were recognized by the telson, Cladocera by the antenna, and Ostracoda by appendicular structures. Oligochaetes were identified by body setae, and rotifers by morphology of the mastax stage (Fig. 1b). Dipteran eggs were recognized by exochorionic surfaces.

Identifications of prey remains were corroborated by comparisons with intact arthropods collected from the treeholes and tires. Identifications of terrestrial

prey were based on structures characteristic of each order (e.g., Fig. 1e and f). A small proportion of terrestrial prey was unidentifiable (Table 2).

The similarity of diets between *T. rutilus* instars was assessed with Kendall's  $\tau$  coefficient (Ghent 1963), which compared the rank order of importance of prey taxa. Significant values of  $\tau$  indicated that predators of different instars chose prey taxa in similar rank order. A Bonferroni correction was applied to obtain critical  $P$  values appropriate for multiple comparisons (Glantz 1992). Prey items that were observed <5 times in guts were omitted from  $\tau$  calculations to avoid biases attributable to rare taxa (Bullock 1971).

To compare the electivity of *T. rutilus* for particular dipterous prey in the containers, we calculated a coefficient  $R$ , following Kazana et al. (1983):

$$R = P_i / (P_i + P_a),$$

where  $P_i$  is the number of taxon  $i$  in guts divided by number of total dipterous prey in the gut, and  $P_a$  is the number of taxon  $i$  in the container divided by total dipterous prey in the container.  $R$  may range from zero (prey not consumed) to one (all prey eaten); an  $R$  value of 0.5 would indicate predation proportional to prey abundance in the habitat.

In contrast to Kazana et al. (1983), who calculated  $R$  for *T. theobaldi* from summed collections of cemetery fauna, we calculated  $R$  for each sampled *T. rutilus* that contained an aquatic Dipteran in its gut or container. Thus, we obtained suites of  $R$  values for each prey species and predator instar (Tables 4 and 5) that could be evaluated statistically and compared among taxa. Owing to many values of  $R = 0$  when  $P_i = 0$  and  $P_a > 0$ , parametric statistics were not appropriate; instead, the heterogeneity of  $R$  values was assessed by Kruskal-Wallis tests, followed by pairwise multiple comparisons using Dunn's method (Glantz 1992).  $R$  was not calculated for rare taxa because of biases of electivity indices in estimates for rare species (Lechowicz 1982).

**Laboratory Studies.** Experiments were carried out in an insectary at  $27 \pm 0.5^\circ\text{C}$  and a light-dark cycle of 14:10 (L:D) using *T. rutilus* from a colony at the FMEL (Linley and Darling 1993). Recently hatched *T. rutilus* larvae were reared individually and fed *Aedes* spp. larvae of equivalent instar until the start of an experiment. Predators were isolated without food in individual containers with 25 ml tap water for 24 h before an experiment. After consumption of a specific test prey item during a one-hour exposure, each individual predator was placed in a new container and supplied with abundant *Aedes* spp. ( $\approx 25$ ) larvae until dissection. At hourly intervals, ten predator larvae were dissected for remains of test prey. An experiment was terminated when all 10 dissected larvae were negative for test prey remains. These experiments tested four prey types maintained in the laboratory: oligochaetes, copepods, psychodid larvae and psychodid adults. Psychodid larvae were offered in sizes proportional to that of the appropriate *T. rutilus* instar, and psychodid adults were offered only to third and fourth instar predators.

To describe the time course of digestion or elimination of detectable prey remains in starved larvae, fourth instar *T. rutilus*, after consuming a psychodid larva, were isolated in individual containers without *Aedes* spp. larvae. Ten predator larvae were dissected at 24-h intervals for detection of prey remains.

## Results

**Predator Diet in Nature.** Microhabitats positive for *T. rutilus* contained from one to 13 predator larvae (mean = 2.63, SD = 4.47,  $n = 88$ ) in treeholes, and one to 25 (mean = 4.02, SD = 3.83,  $n = 175$ ) in tires. Immature stages of Diptera and microcrustaceans were the most abundant aquatic fauna identified from prey remains (Table 1). Psychodidae were the commonest dipterous prey in treeholes and Chironomidae in tires. Ostracods were the most abundant prey of *T. rutilus* in tires, but more copepods than ostracods were consumed by predators in treeholes. Six species of Culicidae were recognized among prey from treeholes and five from tires, and cannibalism by fourth instar predators was common. Large numbers of rotifers were identified in predators from both microhabitats.

Eight orders of insects plus spiders and mites were identified among remains of terrestrial arthropods in *T. rutilus* guts (Table 2). Collembola were the most abundant terrestrial prey in both treeholes and tires. In general, terrestrial prey were not more common in one microhabitat or another, except for Hemiptera and Hymenoptera, which were found only in *T. rutilus* from tires. Terrestrial arthropods accounted for 8% of prey identified from treeholes and 9% from tires (Fig. 2).

Overall, the most frequently identified prey were microcrustacea, which accounted for 51% of identifications from tires and 20% from treeholes (Fig. 2). Second in abundance were rotifers, which were 52% of food items in treeholes and 12% in tires. Aquatic Diptera were more frequent in the diet of *T. rutilus* in tires than in treeholes owing to the importance of larval Chironomidae in tires.

Inter-instar comparisons of diet composition revealed significant ( $P < 0.008$ ) similarities in all pairs in tires but only for third versus fourth instar predators in treeholes (Table 3). Overall, the degree of diet similarity was higher in tires than in treeholes.

For treehole samples, heterogeneity among  $R$  values for the common dipterous prey was highly significant ( $P < 0.001$ ) only for fourth instar predators (Table 4). Multiple comparison tests showed that *Aedes albopictus* (Skuse), *Corethrella appendiculata* Graham and psychodid larvae were significantly preferred by fourth instar *T. rutilus* to congeners and *Orthopodomyia signifera* (Coquillett). A significant ( $P < 0.05$ )  $H$  value for second instar *T. rutilus* was not accompanied by significant differences in pairwise comparisons.

For tire samples, significant heterogeneity among electivity coefficients was observed for all predator instars (Table 5). In paired comparisons, *A. albopictus*

Table 1. Aquatic prey identified from gut dissections of *T. rutilus* larvae

Prey	Treeholes				Tires			
	I	II	III	IV	I	II	III	IV
Predator instars: No. dissected:	34	33	67	99	196	135	147	230
Mosquitoes								
<i>Aedes albopictus</i>	7/6	8/5	14/8	17/8	17/10	37/22	45/30	150/57
<i>Aedes triseriatus</i>	7/7	9/6	17/12	52/22	2/2	0	2/2	13/7
<i>Anopheles</i> sp.	0	0	1/1	0	0	0	1/1	0
<i>Corethrella appendiculata</i>	0	9/8	25/14	16/9	—	—	—	—
<i>Culex</i> sp.	—	—	—	—	7/4	6/5	28/7	29/10
<i>Orthopodomyia signifera</i>	0	1/1	17/5	6/6	—	—	—	—
<i>Toxorhynchites rutilus</i>	1/1	0	10/9	13/10	2/2	15/15	37/27	101/57
Other invertebrates								
Chironomidae	0	1/1	0	2/2	197/86	276/64	398/86	897/157
Ceratopogonidae	11/7	1/1	5/5	33/12	—	—	—	—
Ephydriidae	0	0	5/1	11/5	—	—	—	—
Psychodidae	7/4	11/5	87/28	153/48	9/7	19/8	39/20	93/38
Syrphidae	1/1	0	5/4	57/12	0	0	0	2/2
Helodidae	0	0	17/12	30/19	—	—	—	—
Aquatic acari	—	—	—	—	0	0	0	5/3
Cladocera <sup>a</sup>	19/7	11/4	16/2	32/8	59/42	88/30	164/33	528/56
Copepoda	21/10	30/7	211/27	213/38	61/41	149/54	322/69	369/98
Ostracoda	0	2/2	44/9	157/22	16/12	51/15	307/39	2,300/140
Oligochaeta <sup>b</sup>	1/1	1/1	5/5	3/3	1/1	7/6	12/12	16/16
Rotifera	120/10	36/7	401/7	1,376/29	232/30	285/18	463/24	141/36
Protozoa	—	—	—	—	0	<sup>c</sup> /2	0	<sup>c</sup> /1
Diptera eggs <sup>d</sup>	0	0	38/2	26/6	0	0	1/1	9/7

Fractions are number of prey identified divided by number of predators containing that prey taxon. —, Prey absent from that microhabitat.

<sup>a</sup> Numerators are estimates.

<sup>b</sup> Because Oligochaeta were not ingested completely, numerators are approximate values.

<sup>c</sup> Counts of Protozoa were not possible.

<sup>d</sup> Culicidae, Syrphidae and Psychodidae.

was significantly preferred over *T. rutilus* by all stages of the predator and preferred over *Culex* sp., Psychodidae and Chironomidae in selected instars. Chironomidae and Psychodidae had significantly higher electivity values than *T. rutilus* in most comparisons. Psychodidae were significantly preferred over Chironomidae by fourth instar predators.

**Prey Detection Times.** When prey consumption was followed by subsequent food, the original item was detectable in midgut dissections from six to 18 h after ingestion, dependent on prey type and predator instar (Fig. 3). In general, copepods and oligochaetes

disappeared faster than remains of Psychodidae, fed as larvae or adults (Fig. 3). Fluctuations over time in percentages of detectable oligochaetes and adult psychodids in third and fourth instar *T. rutilus* were attributable, in part, to incomplete consumption of these prey by some test predators.

When fourth instar *T. rutilus* were starved after consuming a psychodid larva, prey remains were detectable in 80–100% of predator guts up to 31 d after ingestion (Fig. 4), at which point observations were discontinued because of increasing predator mortality. No trend in the elimination of prey remains by

Table 2. Terrestrial prey number identified from gut dissections of *T. rutilus* larvae

Prey	Treeholes				Tires			
	I	II	III	IV	I	II	III	IV
Predator instar: No. dissected:	34	33	67	99	196	135	147	230
Collembola	17/12	15/7	70/35	105/42	58/46	96/48	94/40	195/90
Thysanoptera	0	4/3	7/5	4/4	1/1	10/7	7/5	40/18
Psocoptera	0	0	0	1/1	—	—	—	—
Homoptera	0	0	1/1	0	0	0	1/1	2/1
Hemiptera	0	0	1/1	0	0	2/2	0	14/12
Hymenoptera	0	0	1/1	0	0	0	2/2	18/16
Diptera	0	1/1	9/9	13/12	1/1	0	11/11	63/56
Lepidoptera	0	0	1/1	1/1	0	0	1/1	3/3
Acari	1/1	8/3	6/5	9/9	7/6	21/13	24/17	93/54
Arachnida	1/1	0	1/1	1/1	0	0	1/1	9/9
Unidentified	0	2/2	7/7	11/11	0	1/1	7/7	33/33

Fractions are number of prey identified divided by number of predators containing that prey taxon. —, Prey not recovered from a microhabitat.



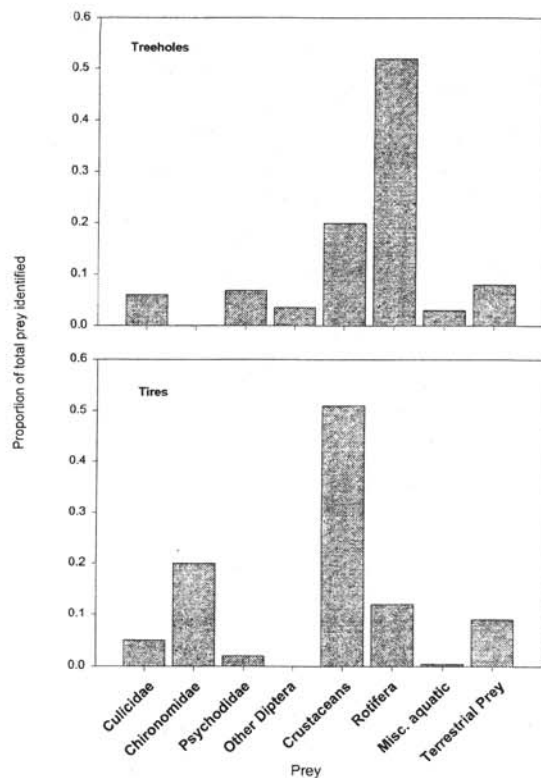


Fig. 2. Relative abundances of important classes of prey identified from *T. rutilus* larvae from treeholes and tires.

predator larvae was observed during the one-month observation period.

### Discussion

Prey consumed by *T. rutilus* in south Florida woodland was far more diverse than the diet of *T. theobaldi* in a Caracas cemetery (Kazana et al. 1983), reflecting the greater variety of invertebrates in woodland treeholes and tires compared with urban cemetery vases. Under both conditions, mosquitoes were relatively minor components of the diet of these two species of predators, challenging the popular assumption that Culicidae predominate among the prey of *Toxorhyn-*

*chites* in nature (Steffan and Evenhuis 1981). Previous, anecdotal reports have noted *Toxorhynchites* larvae consuming tadpoles, damselfly nymphs, and tipulid larvae (Steffan and Evenhuis 1981), but ours is apparently the first to document the numerical dominance of smaller invertebrates, such as microcrustacea and rotifers (Fig. 2), in the natural diet of this predator.

Despite mosquitoes accounting for only 6% of invertebrate remains in *T. rutilus* from treeholes (Fig. 2), two previous investigations of this habitat in Florida have reported significant reductions in numbers of the native treehole mosquito *A. triseriatus* (Say) attributable to predation by this predator species (Bradshaw and Holzapfel 1983, Lounibos et al. 1997). High electivity values for *Aedes*, especially *A. albopictus* (Tables 4 and 5) suggest that *T. rutilus* might consume proportionally more container *Aedes* than other aquatic Diptera when these mosquito prey are abundant.

Significant reductions in the larval abundance of other aquatic Diptera, notably Ceratopogonidae, Psychodidae, and Chironomidae, were caused by predation of *Toxorhynchites hemorrhoidalis* (Fabricius) in Venezuelan phytotelmata (Lounibos et al. 1987). Our current results confirm that *Toxorhynchites* larvae are generalist predators (Murdoch and Bence 1987), capable of reducing the abundance of a broad range of invertebrate prey that cohabit the same containers.

The frequent recovery in midguts of exoskeletal remains of its own species (Tables 1 and 2) further corroborates the regular occurrence of cannibalism in *T. rutilus* (Lounibos et al. 1996, Campos and Lounibos 2000) and other species of this genus (Kazana et al. 1983). Cannibalism was more important in tires, where 25% of all dissected fourth instars contained remains of *T. rutilus*, compared with only 10% in treeholes. Values of *R*, the electivity coefficient, were significantly lower for *T. rutilus* than for most other dipterous prey, indicating that cannibalism occurs despite some intraspecific avoidance of individuals of its own species, which has been documented for similar-sized fourth instar larvae (Lounibos 1985, Lounibos et al. 1996). Eggs of *T. rutilus* were not among those detected in midgut remains, despite experimental and circumstantial evidence for egg cannibalism (Linley and Darling 1993, Campos and Lounibos 2000). Search behavior for intraspecific eggs (Linley and Darling 1993), which causes the active predator to consume floating eggs in a series, may render detection of this food item in midguts less likely because eggs ingested in succession would not remain long in the digestive tract.

Terrestrial prey accounted for eight and 9% of all remains identified, respectively, from treeholes and tires and is, thus, not as important in the *T. rutilus* diet as this prey group was to *T. theobaldi* in cemetery vases (Kazana et al. 1983). Perhaps fewer terrestrial arthropods visit, and fall into, treeholes or tires compared with vases, especially if the latter containers should contain fresh flowers attractive to flying insects. Additionally or alternatively, the relative importance of terrestrial prey may be reduced by the greater abundance and diversity of aquatic prey in treeholes and

Table 3. Comparison between instars of rank order of importance of prey of *T. rutilus*, using Kendall's  $\tau$  as an index of similarity

Container	Instar comparisons					
	I-II	I-III	I-IV	II-III	II-IV	III-IV
Treeholes	$\tau$	0.547	0.185	0.434	0.408	0.317
	<i>P</i>	0.035	0.292	0.015	0.019	0.061
	<i>n</i>	10	20	19	19	21
Tires	$\tau$	0.831	0.866	0.673	0.785	0.701
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001
	<i>n</i>	13	14	20	15	20

*P*, Bonferroni critical  $P = .05/6 = 0.0083$ . *n*, Number of usable ranks (taxa that occurred five or more times) for each inter-instar comparison.

**Table 4.** *R* electivity coefficients for commonest aquatic dipterous prey of *T. rutilus* from treeholes and results of Kruskal–Wallis tests (*H*) to detect heterogeneity of *R* values for each predator instar

Prey <sup>a</sup>	Predator Instar							
	I		II		III		IV	
	<i>n</i>	<i>R</i> (%)	<i>n</i>	<i>R</i> (%)	<i>n</i>	<i>R</i> (%)	<i>n</i>	<i>R</i> (%)
<i>A. albopictus</i>	9	0.52 (0.0–0.88)			10	0.95 (0.51–1.0)	14	1.00AB (0.68–1.0)
<i>A. triseriatus</i>	10	0.52 (0.0–0.63)	9	0.53 (0.38–0.64)	13	0.57 (0.52–0.89)	19	0.79 (0.48–0.82)
<i>O. signifera</i>							10	0.28ACE (0.0–0.47)
<i>T. rutilus</i>	8	0.00 (0.0–0.0)	6	0.00 (0.0–0.0)	13	0.37 (0.0–0.71)	16	0.34BDF (0.0–0.58)
<i>C. appendiculata</i>			14	0.56 (0.0–0.96)	15	0.52 (0.28–1.0)	9	1.0CD (0.75–1.0)
Ceratopogonidae	10	0.96 (0.0–1.0)					10	0.57 (0.35–0.94)
Syrphidae							12	0.65 (0.46–1.0)
Psychodidae	7	0.84 (0.0–0.84)	7	0.82 (0.19–0.99)	29	0.77 (0.75–0.94)	47	0.81EF (0.67–0.90)
<i>H</i>		9.23		8.17		8.94		33.85
<i>df</i>		4		3		4		7
<i>p</i>		0.056		0.043		0.063		<0.001

Significant differences ( $P < 0.05$ ) detected by Dunn's method (Glantz 1992) of pairwise multiple comparisons of fourth instar prey are designated by a common letter after *R* values.

*R* was not calculated for prey that occurred five or fewer times in samples. *R*, Median value of *R* with 25th and 75th percentiles in parentheses.

<sup>a</sup> *Anopheles* sp., Ephydriidae and Chironomidae omitted because of rarity.

tires compared with the cemetery vase habitat. Results of both the current study and that of Kazana et al. (1983) dispel the contention that surface prey are inconsequential in the diet of *Toxorhynchites* larvae (Steffan and Evenhuis 1981).

The identification and quantification of exoskeletal remains provide data only on the frequency of occurrence of prey items (Pritchard 1964) and do not evaluate the energetic importance of different prey taxa. A dipterous larva is, for example, of greater nutritional value than a rotifer or insect egg for the growth and

development of a *Toxorhynchites* larva. Although bio-masses may be estimated for prey items, the extrapolation of energy inputs from midgut remains is confounded by the partial consumption of some prey, e.g., oligochaetes and some terrestrial arthropods, and differences among prey taxa in gut passage times (Fig. 3).

The electivity of *T. rutilus* for *Aedes* mosquitoes was somewhat lower in treeholes than in tires (Tables 4 and 5), where prey diversity was less (Tables 1 and 2). Other swimming Diptera, such as larvae of Ceratopogonidae and Psychodidae, had relatively high elec-

**Table 5.** *R* electivity coefficients for commonest aquatic dipterous prey of *T. rutilus* from tires and results of Kruskal–Wallis tests (*H*) to detect heterogeneity of *R* values for each predator instar

Prey <sup>a</sup>	Predator instar							
	I		II		III		IV	
	<i>n</i>	<i>R</i> (%)	<i>n</i>	<i>R</i> (%)	<i>n</i>	<i>R</i> (%)	<i>n</i>	<i>R</i> (%)
<i>A. albopictus</i>	14	0.78A (0.0–1.0)	23	1.00AB (0.69–1.0)	31	1.00ABC (0.96–1.0)	56	1.00AB (0.62–1.0)
<i>A. triseriatus</i>	9	0.00 (0.0–0.20)					6	0.88CD (0.81–1.0)
<i>Culex</i> sp.	12	0.00 (0.0–0.58)	9	0.38 (0.0–1.0)	9	0.56B (0.29–0.72)	11	0.83G (0.68–0.97)
<i>T. rutilus</i>	94	0.00ABC (0.0–0.0)	54	0.00A (0.0–0.0)	47	0.16ADE (0.0–0.53)	81	0.36ACEGH (0.0–0.56)
Chironomidae	167	0.40C (0.0–0.63)	111	0.50 (0.0–0.59)	102	0.52CE (0.43–0.63)	174	0.53BDFH (0.45–0.60)
Psychodidae	11	0.51B (0.0–0.90)	13	0.00B (0.0–1.0)	22	1.00D (0.89–1.00)	37	1.00EF (1.0–1.0)
<i>H</i>		74.11		53.84		76.87		126.60
<i>df</i>		5		4		4		5
<i>P</i>		<0.001		<0.001		<0.001		<0.001

*R* was not calculated for prey that occurred five or fewer times in samples. *R*, Median value of *R* with 25th and 75th percentiles in parentheses. Significant differences ( $P < 0.05$ ) detected by Dunn's method (Glantz 1992) of pairwise multiple comparisons within instars are designated by a common letter after *R* values.

<sup>a</sup> *Anopheles* sp. and Syrphidae omitted because of rarity.

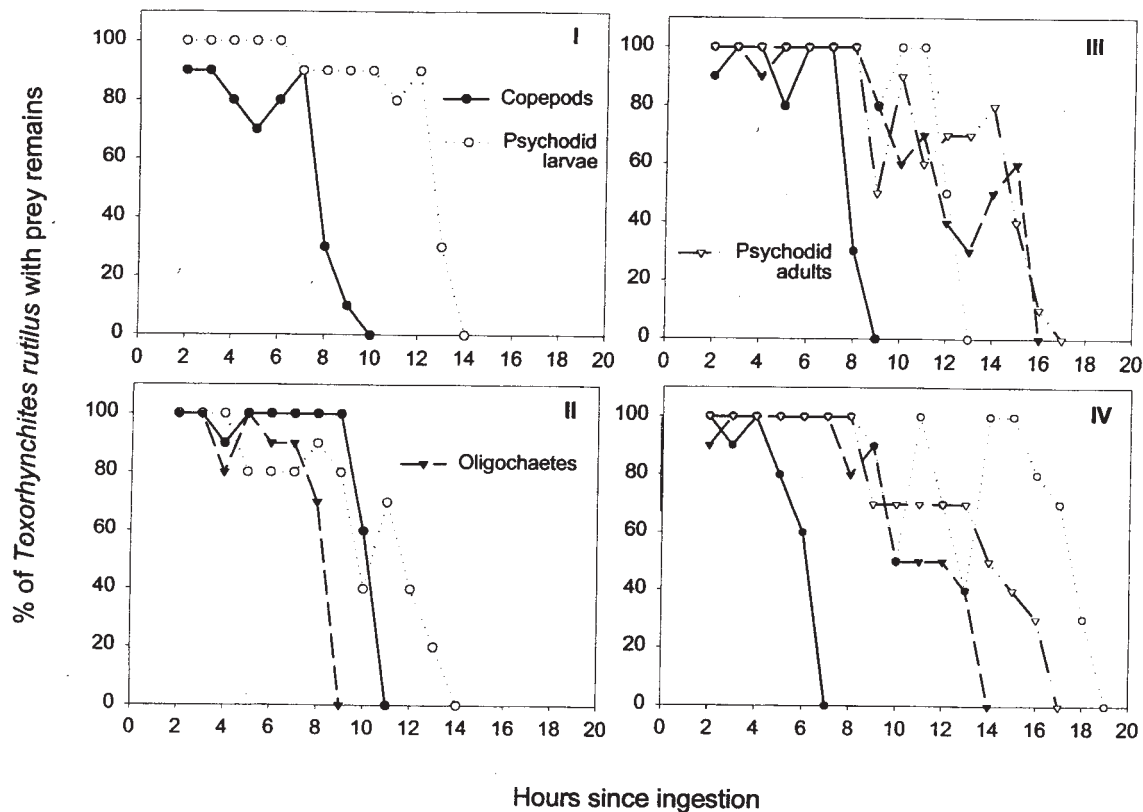


Fig. 3. Percentage of *T. rutilus* instars with prey remains in the gut as a function of time after ingestion. Predators were fed *ad libitum* on *Aedes* larvae after ingestion of test prey. Roman numerals designate predator instars.

tivity values similar to some Culicidae, suggesting that movement behaviors common to these larvae may lead to their capture. The high electivity values for larval Psychodidae should be interpreted with caution because of the comparatively slow gut passage times of remains of this taxon (Fig. 3). Aquatic Chironomi-

dae, despite their numerical importance to predators in tires (Fig. 2), consistently had R values close to 0.5, indicating no preference, perhaps because their larval tubes provide some refuge from predation. The quiescent larvae of *O. signifera* had R values significantly lower than most other dipterous prey, confirming their resistance to predation relative to other mosquito inhabitants of containers (Bradshaw and Holzapfel 1983, Chambers 1985).

Kazana et al. (1983) reported a lack of similarity in the diets of second versus third and second versus fourth instar *T. theobaldi*, based on low values of Kendall's  $\tau$ . These same comparisons were also not similar for *T. rutilus* in treeholes, but all inter-instar diet comparisons were significant in tires (Table 3). Overall, diet similarity between instars was greater in the current study than observed by Kazana et al. (1983). Because we quantified the occurrence of many small invertebrates that are probably not subject to size-selective predation (Fedorenko 1975, Kazana et al. 1983), size constraints may not be important in our inter-instar comparisons. Additionally, we tallied many more prey taxa than Kazana et al. (1983), therefore the statistical significance of  $\tau$  was less sensitive in our study to small changes in the rank order of importance of prey.

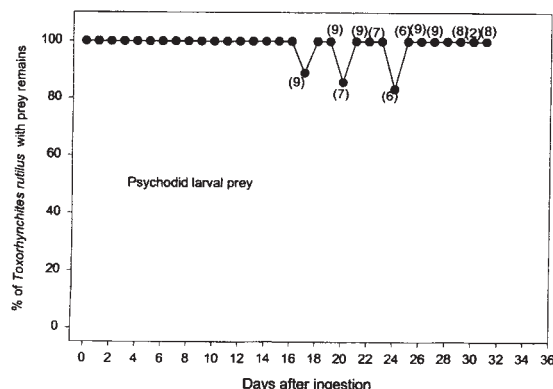


Fig. 4. Percentage of *T. rutilus* fourth instars with psychodid larval remains in the gut. Predators were starved after ingesting test prey. Ten predators dissected per point, except where sample sizes were reduced by deaths to values noted in parentheses.

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