Life Tables of *Toxorhynchites rutilus* (Diptera: Culicidae) in Nature in Southern Florida

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ABSTRACT Stage-specific survivorship curves were constructed for the immature stages of a native, predatory mosquito, *Toxorhynchites rutilus* (Coquillet), by regular censuses in the summer and fall of water-holding treeholes and tires. Survival from egg to adult ranged from 1.8 to 5.6%, and survivorship patterns were significantly heterogeneous between seasons and container types. The probability of death was highest in the first and fourth larval instars. Rainfall and drought were relatively unimportant risk factors during this study, but the probabilities of disappearance of eggs and first and fourth instars were significantly higher in the presence of large conspecifics, suggesting that cannibalism is a major source of mortality.

KEY WORDS *Toxorhynchites rutilus*, life tables, survivorship, mortality, cannibalism

TOXORHYNCHITES IS A cosmopolitan mosquito genus whose larvae occur in natural or artificial water containers where they prey upon other arthropods including vector and pest mosquitoes (e.g., Steffan and Evenhuis 1981, Kazana et al. 1983). Some species of *Toxorhynchites* have been reared and released for mosquito control (e.g., Steffan 1975, Gerberg and Visser 1978, Focks et al. 1982). Predators released for biological control could be more effective if precautions are taken to reduce natural sources of mortality.

Rainfall that may wash floating eggs out of containers has been suspected as a source of mortality for two species of *Toxorhynchites* (Focks and Sackett 1985, Lounibos et al. 1987). Other studies have shown that habitat drying caused temporary, local extinctions of two different species of this genus (Lounibos 1979, Lounibos et al. 1997). Cannibalism of *Toxorhynchites* spp. has been documented in both the laboratory and field (Trpis 1973, Lounibos 1979, Bradshaw and Holzapfel 1983, Corbet 1985), but its role in the reduction of natural populations has not been determined. Mortality caused by other species of predators is common only in tropical phytotelmata where *Toxorhynchites* larvae cohabit containers with larger aquatic fauna such as odonate larvae or anurans (e.g., Lounibos et al. 1987, Caldwell 1993).
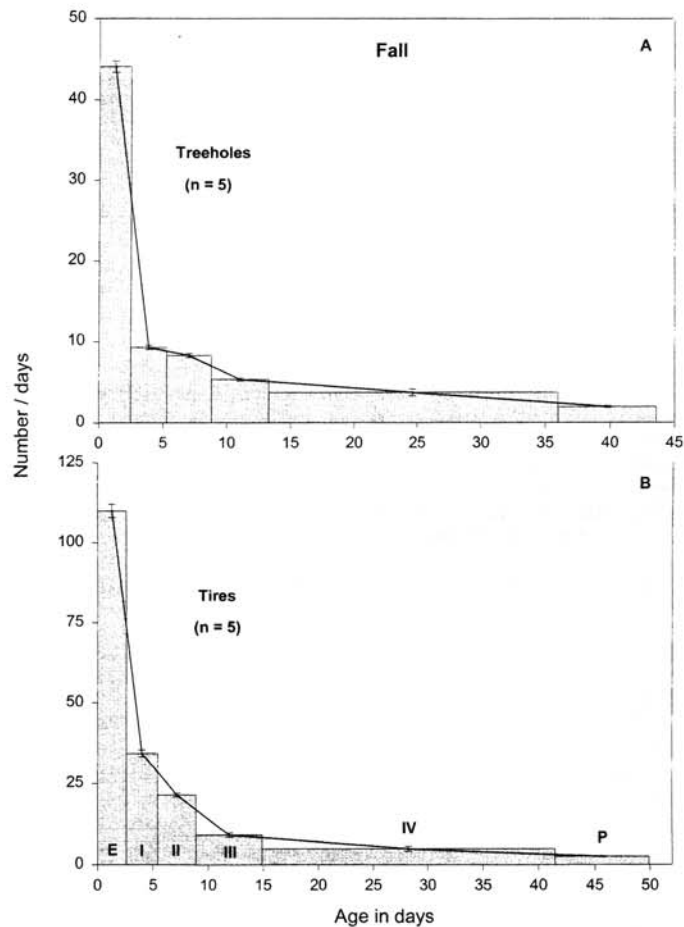
Life tables provide a structured framework for identifying developmental stages most susceptible to mortality and, under some conditions, for inferring sources of mortality. Although life budgets have been tabulated for the immature stages of many mosquito species in nature (Service 1993), the only life tables for *Toxorhynchites* spp. are based on laboratory studies (O'Flynn 1975, Trpis 1981, Amalraj and Das 1996). Yet, the container habitats occupied by *Toxorhynchites* spp. in nature are particularly tractable for the repeated censusing necessary for life table construction (e.g., Frank and Lounibos 1983, Lounibos et al. 1987).

Toxorhynchites rutilus (Coquillett) is the most widespread species of this genus in North America, occurring in the eastern United States from Massachusetts (Dennehy and Livdahl 1999) to Florida, where, as the unique or dominant predator in treeholes and discarded tires, it has been shown to regulate community structure (Bradshaw and Holzapfel 1983) and to reduce abundances of prey mosquitoes significantly (Lounibos et al. 1997). The purpose of this study was to describe and to compare the length of preadult life, stage-specific mortalities, survivorship, and life expectancy of *Tx. rutilus* in water-containing treeholes and discarded tires, the two most common habitats occupied by this species in south Florida. Contemporary weather data and censuses of co-occurring fauna were used to infer the relative importance of several suspected sources of mortality.

Materials and Methods

The naturally occurring immature stages of *Tx. rutilus* were censused in five tires and five treeholes at the Florida Medical Entomology Laboratory (FMEL) during the autumn of 1997 (16 September–16 December) and summer of 1998 (8 July–26 September). Daily rainfall and temperatures were obtained from a weather station 6.5 km NW of Vero Beach. The daily mean temperatures in Vero Beach during these census periods were $22.5°C \pm 0.5$ SE and 27.6 ± 0.1 SE, respectively. The tires and treeholes were located in an oak-palm hammock, where treehole height ranged from 0.20 to 6 m above the ground and tires were propped against trees. Before initiation of censuses, all *Tx. rutilus* immatures were removed from the five tires and treeholes. The water surfaces of these containers
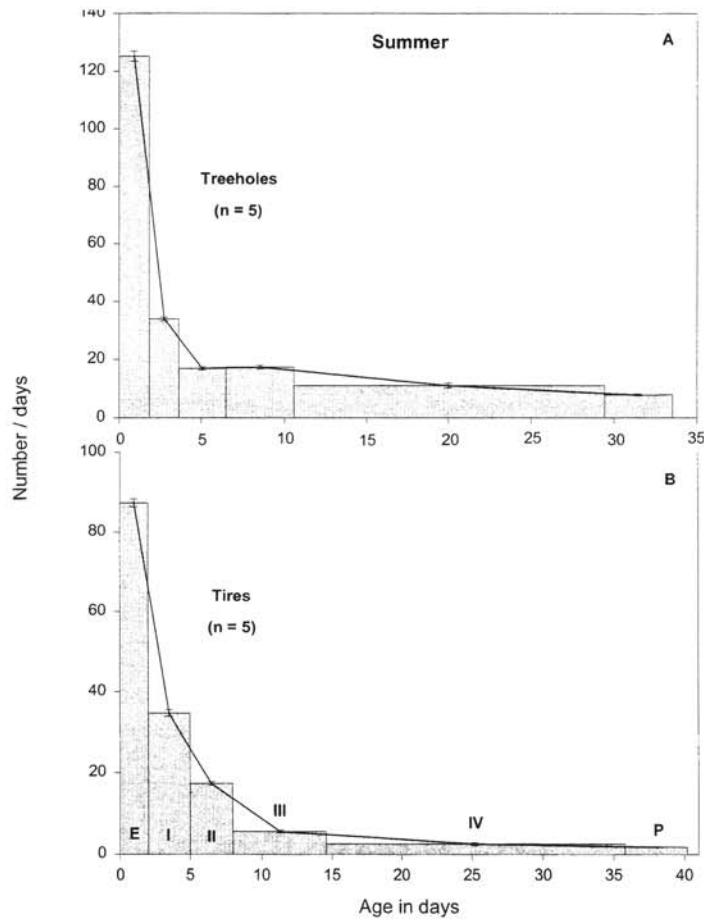
Fig. 1. Stage-specific age distribution and survivorship curves for the immature stages of *Tx. rutilus* in two habitats in the fall of 1997. (A) Treeholes. (B) tires.

were then examined daily with a flashlight for *Tx. rutilus* eggs, which were counted. No other species of *Toxorhynchites* are native or established in Florida, precluding misidentifications of the floating eggs. On every third day, the entire liquid contents of each tire was extracted with a cup and of each treehole with a hose, and brought with all debris to the laboratory in individual containers for examination. Third and fourth instars and pupae of *Tx. rutilus* were recognized individually by clipping a selected seta from an abdominal segment. Adult emergence and sex were recorded from pupal skins. After staging, counting, and identifying *Tx. rutilus* and other aquatic invertebrates, each sample was reconstituted and returned to its original habitat within 1 h after extraction.

Treeholes that held water contained a mean of 908.5 ml (range, 65–2,450 ml, n = 107) liquid in the fall and 3001.7 ml (range, 950–5,500 ml, n = 132) in the summer, and in tires the means were 899.6 ml (range, 30–1,850 ml, n = 116) for the fall and 1,737.4 ml (range, 900–2,200 ml, n = 135) for the summer. Treeholes were more likely to dry out during the fall, when one hole was dry on five consecutive censuses, and two

others were dry on three and four occasions, respectively. In the summer, one treehole was dry on three censuses. Tires were never observed without liquid.

Among aquatic organisms identified, microcrustacea and larvae of Diptera were the most abundant groups in both treeholes and tires, although fewer taxa of Diptera were recognized in tires. Larvae of Chironomidae were the most abundant dipterous prey of *Tx. rutilus* in tires, whereas larvae of Culicidae and Psychodidae predominated among Diptera consumed in treeholes (Campos and Lounibos in prep.).

We constructed life tables for *Tx. rutilus* directly from census data. Instar durations were estimated directly from censuses, but to determine the length of the egg stage we divided the actual counts by three because eggs were censused daily. Using the estimated durations of stages and numbers of immatures collected, vertical stage-specific frequency distributions were calculated (Figs. 1 and 2). Survivorship curves were generated by connecting the midpoints of numbers in each stage (Service 1973, 1977). The numbers of individuals entering each stage were extrapolated from the curves and used for calculating stage-specific

Fig. 2. Stage-specific age distribution and survivorship curves for the immature stages of *Tx. rutilus* in two habitats in the summer of 1998. (A) Treeholes. (B) tires.

mortalities (Service 1973). The relative mortality in different stages was quantified by key-factor analysis and expressed as killing power (k), which is obtained by the subtraction of successive values of log l_x (Varley and Gradwell 1960).

More adult emergences were recorded in censuses than are indicated in Tables 1 and 2, in which the numbers of individuals entering each stage (S_i) were obtained from averaged values for the stage-specific survivorship profiles (Figs. 1 and 2). Developmental times of the actual numbers of adults counted in nature were compared between habitats and seasons by a two-way analysis of variance (ANOVA), performed with the general linear model (GLM) procedure of SAS (SAS Institute 1985) (Table 3).

Heterogeneity of survivorship patterns between habitats and seasons was assessed with the procedure LIFETEST in SAS (SAS Institute 1985). For these analyses, survival distribution functions were generated from the daily proportions of immatures surviving (l_x), calculated according to Service (1973). The survival distribution function evaluated at time x is the probability that a *Tx. rutilus* immature will have a lifetime exceeding the interval x. The significance of heterogeneities was assessed with Wilcoxon and log-rank tests, which are sensitive to different components of the survival distribution function (SAS Institute 1985). After detection of significant heterogeneity, survival distribution functions were compared with z-tests according to Fox (1993).

To examine the effects of rainfall and co-occurring *Tx. rutilus* on stage-specific mortalities, presence-absence data arranged in contingency tables were analyzed by maximum-likelihood methods in the CATMOD procedure of SAS (SAS Institute 1985). Owing to sparse data in some rows or columns of tables, it was necessary to pool certain groups, such as summer with fall or treehole with tire observations, to perform CATMOD analyses.

Results

Immatures of *Tx. rutilus*, as well as larvae of other mosquito species and other invertebrates, were collected on every census, suggesting that the sampling procedure did not disrupt normal growth of these aquatic organisms.

Table 1. Stage-specific mortalities of *Tx. rutilus* from treeholes and tires in the fall

Stage (i)	Age in days at beginning of stage (t_i)	No. entering stage (S_i)	Deaths in stage (D_i)	Relative proportion dying (P_i)	Proportion dying daily (Pd_i)	k
			Treeholes			
Egg	0	44	16	0.364	0.165	0.196
I	2.5	28	19	0.679	0.333	0.493
II	5.3	9	2	0.222	0.069	0.109
III	8.8	7	2	0.286	0.072	0.146
IV	13.3	5	3	0.600	0.039	0.398
Pupa	36.0	2	0	0	0	0
Adult	43.6	2				
		S 0.045				K 1.342
			Tires			
Egg	0	111	36	0.324	0.140	0.170
I	2.6	75	45	0.600	0.279	0.398
II	5.4	30	13	0.433	0.150	0.247
III	8.9	17	8	0.471	0.101	0.276
IV	14.9	9	6	0.667	0.041	0.477
Pupa	41.5	3	1	0.333	0.047	0.176
Adult	49.9	2				
		S 0.018				K 1.744

S, egg to adulthood survivorship (adult/egg); K, sum of "killing power" (k).

Developmental Times and Sexes. The age distributions of *Tx. rutilus* life stages were similar in the fall and summer (Figs. 1 and 2). Preadult development in treeholes and tires was completed in 33.5–40.2 d in the summer and 43.6–49.9 d in the fall (Tables 1 and 2). For individuals that emerged as adults, developmental times were not significantly different between container types ($t_s = -1.76$, df = 38, $P = 0.09$).

Males emerged, on average, sooner than females in both habitats and seasons, but the effects of sex and group on developmental time in a two-way ANOVA were not significant owing to small sample sizes and high variances (Table 3). Sex ratios of adults from treeholes did not differ significantly from 1:1 ($P = 0.08$, Fisher exact test).

Stage-Specific Life Tables. Survivorship from egg to adulthood was higher during the summer in both container types, and survivorship in treeholes was higher than in tires for both seasons (Tables 1 and 2). More than 60% of *Tx. rutilus* eggs survived to an age of 2–3 d and to hatch based on daily mortality estimates (Tables 1 and 2), and age frequency distributions (Figs. 1 and 2). Only 5–13% of the immatures survived to 11–15 d, which approximately marks entry of *Tx. rutilus* into the fourth instar (Tables 1 and 2).

The percent survivorship of *Tx. rutilus* from egg to adulthood, estimated as 1.8–3.4% in tires and 4.5–5.6% in treeholes (Tables 1 and 2), were not significantly different between container types in the fall ($G_{adj} = 0.73, P > 0.1$) or in the summer ($G_{adj} = 0.52, P > 0.1$). The relative proportion dying (P_i) was highest in the first and fourth instars, except for summer tires where third instar mortality was higher than fourth instar.

Table 2. Stage-specific mortalities of *Tx. rutilus* from treeholes and tires in the summer

Stage (i)	Age in days at beginning of stage (t_i)	No. entering stage (S_i)	Deaths in stage (D_i)	Relative proportion dying (P_i)	Proportion dying daily (Pd_i)	k
			Treeholes			
Egg	0	125	47	0.376	0.227	0.205
I	1.8	78	50	0.641	0.429	0.445
II	3.7	28	11	0.393	0.162	0.217
III	6.5	17	2	0.118	0.030	0.054
IV	10.6	15	7	0.467	0.027	0.273
Pupa	29.4	8	1	0.125	0.032	0.058
Adult	33.5	7				
		S 0.056				K 1.252
			Tires			
Egg	0	87	20	0.230	0.122	0.113
I	2	67	42	0.627	0.280	0.428
II	5	25	11	0.440	0.176	0.252
III	8	14	9	0.643	0.144	0.447
IV	14.6	5	2	0.400	0.024	0.222
Pupa	35.8	3	0	0	0	0
Adult	40.2	3				
		S 0.034				K 1.462

S, egg to adulthood survivorship (adult/egg); K, sum of "killing power" (k).

Table 3.   Mean number (±SD) of days from egg to adult for *Tx. rutilus* from treeholes and tires in the fall and summer and ANOVA results (excludes summer tires because no females were recorded) for effects on developmental time

	Treeholes		Tires	
	Male	Female	Male	Female
Fall	35.50	51.67	42.67	54.75
	(6.36)	(14.57)	(13.20)	(9.03)
	$n = 2$	$n = 3$	$n = 3$	$n = 4$
Summer	29.89	35.86	40.20	
	(19.63)	(18.81)	(6.30)	
	$n = 9$	$n = 14$	$n = 5$	
Source	MS	F	df	P
Sex	732.2	2.43	1	0.130
Group	753.8	2.50	2	0.100
Sex × Group	63.7	0.21	2	0.811
Error	301.5		29	

Mortality of eggs, and first and second instars was relatively consistent between seasons and container types, but third-instar mortality was notably higher in tires than treeholes (Tables 1 and 2). Mortality of pupae was consistently very low. The rate of daily mortality (Pd_i) was uniformly highest in the first and lowest in the fourth instar. The total K values (=cumulative "killing power" of Varley and Gradwell 1960) were higher in the fall than summer (Tables 1 and 2).

Daily Life Expectancies and Survival Distributions. Daily life expectancies (e_x) were compared between container types and seasons. In general, life expectancies were initially low but increased rapidly after 3 d, reaching maxima at 5–13 d, the timing depending on container type and season (Fig. 3). These peaks in life expectancy occurred while *Tx. rutilus* were in the third instar (Table 1 and 2); e_x declined in the fourth instar, more uniformly in treeholes than in tires. K-S two sample tests revealed no significant differences in life expectancy distributions between fall and summer treeholes $(D_{max} = 0.25)$, or tires $(D_{max} = 0.27)$ or between fall treeholes and tires $(D_{max} = 0.25)$ or summer treeholes and tires $(D_{max} = 0.24)$ $(D_{0.05} = 0.39$ for $n_1 = 32$, $n_2 = 38)$.

Significant heterogeneity among survival distribution functions was detected from a log-rank test, which is more sensitive than the Wilcoxon test to differences late in survival (Table 4). Paired comparisons showed that the significant heterogeneity was largely attributable to the decreased survivorship of *Tx. rutilus* in fall tires, which was highly significantly different from summer tires and summer treeholes (Table 4).

Mortality Factors. Treehole drying in summer accounted for 6.4% of total *Tx. rutilus* mortality in that habitat and season. No mortality of *Tx. rutilus* was attributable to treehole drying in the fall, and no tires dried out during the two observation periods.

The importance of rainfall and cannibalism as mortality factors for *Tx. rutilus* eggs was tested by partitioning the proportions of deaths that occurred in the presence and absence of recent rainfall (>1 cm in the previous 24 h) and a large predatory conspecific. A maximum-likelihood ANOVA of this contingency ta-
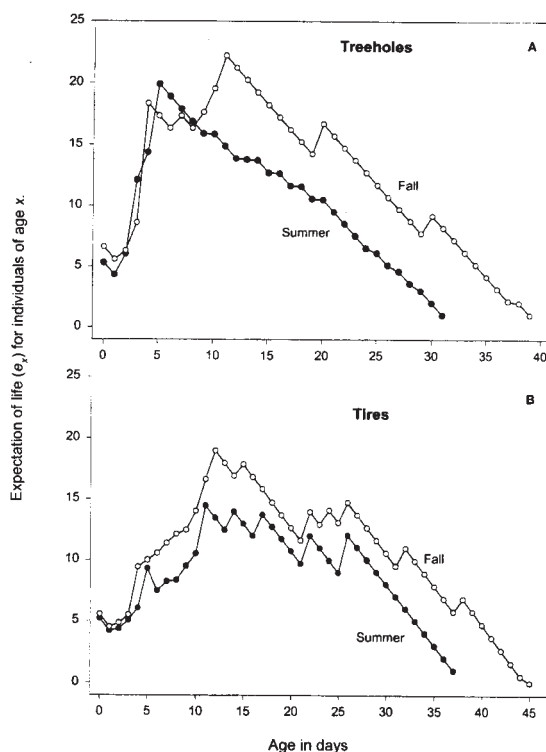

Fig. 3.   Expectation of life (e_x) plotted as a function of age in days for *Tx. rutilus* in (A) treeholes and (B) tires.

ble showed significant effects of season and treatment conditions on the proportion of eggs present or missing (Table 5). Egg mortality was, overall, higher in the presence of a larger conspecific, which influenced survival more than rainfall.

The relative importance of cannibalism as a mortality factor to first and fourth instars was assessed by partitioning total mortalities in the four groups into conditions of presence and absence of a co-occurring predator. The proportion of first-instar mortality that occurred in the presence of a second-instar or later *Tx. rutilus* was significantly higher than in its absence (Table 6).

A significant interaction between season and *Tx. rutilus* presence/absence was attributable to differ-

Table 4.   Tests for significant heterogeneity of survival distribution functions of *Tx. rutilus* immatures and paired comparisons of survival distribution functions based on the log-rank statistics

	Paired comparisons with z-test					
	Tires summer		Treeholes fall		Tires fall	
	z	P	z	P	z	P
Treeholes summer	0.97	0.166	1.46	0.073	3.70	< 0.001
Tires summer			0.47	0.321	2.49	0.006
Treeholes fall					1.96	0.025
Test	χ^2		df		P	
Log-rank	14.11		3		0.003	
Wilcoxon	5.91		3		0.116	

Table 5. Partitioning of egg mortality of *Tx. rutilus* into four conditions and maximum-likelihood ANOVA for pooled data, segregated by season

	No rainfall + no large (≥2nd) *Tx. rutilus*		No rainfall + large (≥2nd) *Tx. rutilus*		Rainfall[a] + no large (≥2nd) *Tx. rutilus*		Rainfall[a] + large (≥2nd) *Tx. rutilus*	
	Eggs present	Eggs missing	Eggs present	Eggs missing	Eggs present	Eggs missing	Eggs present	Eggs missing
Summer treeholes	117	5	239	121	64	32	59	43
Summer tires	109	48	226	39	35	18	36	10
Fall treeholes	24	22	182	68	0	4	9	9
Fall tires	94	30	283	352	12	0	32	30
Totals	344	105	930	580	111	54	136	92

Source	χ^2	df	P
Season	5.8	1	0.016
Conditions	26.0	3	<0.001
Season × Conditions	7.6	3	0.056

[a] Rainfall ≥1 cm since previous census.

ences in mortality trends between seasons in treeholes and tires. First-instar mortality attributable to cannibalism was much higher in the fall than in the summer (Table 6).

Both microhabitat and the presence/absence of a large conspecific produced significant effects in the maximum-likelihood ANOVA for fourth instar mortality. A significant interaction between these factors was attributable to the fact that tires and treeholes showed very different mortality profiles in the absence, but not in the presence, of a large conspecific (Table 7).

Discussion

The life tables presented here are the first for a species of *Toxorhynchites* in nature. However, stage-specific life tables have been constructed for the immature stages of mosquitoes from many other genera. The majority of life tables constructed for the familiar species of *Aedes, Anopheles,* and *Culex* (Service 1973, Lakhani and Service 1974, Reisen and Siddiqui 1979, Sempala 1981, Mogi et al. 1986) have revealed type III mortality curves in which the risk of death is approximately constant with age (Slobodkin 1962).

By contrast, it appears that the mortality curves for *Tx. rutilus* (Figs. 1 and 2) are more similar to Slobod-

kin's (1962) type IV, in which the risk of mortality is concentrated in the younger stages. This impression is confirmed by the occurrence of the highest Pd_i values in the egg and first instar (Tables 1 and 2). However, comparisons with previously published mosquito life tables may be misleading because previous studies rarely included the egg stage. Furthermore, the unusually long fourth instar of *Tx. rutilus* exaggerates the concave shape of its stage-specifc survivorship curve.

The range of egg-adult survivorship values for *Tx. rutilus* (1.8–5.6%) falls within, but is on the low side of, averages for other field populations of mosquitoes, such as *Aedes cantans* (Meigen) (6.2%), *Aedes africanus* (Theobald) (9–17%), rice-field *Anopheles* (2%), *Anopheles gambiae* Giles (2.9–3.4%), or *Culex tritaeniorhynchus* Giles (0–31%) (Service 1973, Lakhani and Service 1974, Reisen and Siddiqui 1979, Sempala 1981, Mogi et al. 1986). Our inclusion of the egg in life tables adds an extra stage with a relatively high and consistent proportion dying (0.23–0.38) (Tables 1 and 2). Thus, higher total mortality may be expected because of the additional life stage.

Our results demonstrate significant heterogeneity in survivorship patterns between seasons and habitats (Table 4), a characteristic that is also evident in life

Table 6. First-instar mortality partitioned into two conditions, and maximum-likelihood ANOVA for pooled data, segregated by season

	Presence of large (≥2nd) *Tx. rutilus*		Absence of large (≥2nd) *Tx. rutilus*	
	Present	Missing	Present	Missing
Summer treeholes	12	24	15	12
Summer tires	26	34	10	24
Fall treeholes	8	7	3	6
Fall tires	20	58	12	4
Totals	66	123	40	46

Source	χ^2	df	P
Season	0.4	1	0.541
Conditions	5.2	1	0.023
Season × Conditions	4.3	1	0.038

Table 7. Fourth-instar mortality partitioned into two conditions and maximum-likelihood ANOVA for pooled data, segregated by microhabitat (tires versus treeholes)

	Co-occurrence of another 4th *Tx. rutilus*		Absence of another 4th *Tx. rutilus*	
	Present	Missing	Present	Missing
Summer treeholes	0	7	28	0
Summer tires	3	3	3	3
Fall treeholes	10	3	0	1
Fall tires	8	10	0	2
Totals	23	23	31	6

Source	χ^2	df	P
Microhabitat	8.3	1	0.004
Conditions	4.6	1	0.032
Habitat × Conditions	7.0	1	0.008

tables of other mosquito species (Lakhani and Service 1974, Reisen and Siddiqui 1979, Sempala 1981, Mogi et al. 1986). The survival of *Toxorhynchites haemorrhoidalis* (F.) was shown to be significantly different between wet and dry seasons and among phytotelm microhabitats in Venezuelan rain forest, although life tables for this species were not constructed (Lounibos et al. 1987).

Laboratory studies have shown that prey consumption by *Tx. rutilus* depends on prey abundance and container size, being less in larger vessels (Padgett and Focks 1980). In our studies, the larger tires harbored markedly fewer culicid and chironomid prey per census (mean ± SE, 146 ± 114.6) than the smaller treeholes (414.8 ± 350.1), so both the smaller size and higher prey abundance may contribute to the generally higher survival of predators in treeholes (Tables 1 and 2; Fig. 4). Cannibalism was generally higher in tires than in treeholes (Tables 6 and 7), perhaps because of the lower densities of alternative prey in tires. Survival was lower and developmental time longer in the fall, when colder temperatures may have retarded development compared with summer. Further, short autumnal daylengths are known to induce a fourth instar diapause in subtropical *Tx. rutilus*, which reduces prey consumption and slows growth (Lounibos et al. 1998).

Previous studies of *Tx. rutilus* in Florida treeholes have shown that this species is highly sensitive to drought (Bradshaw and Holzapfel 1988), and that extended dry periods lead to local extinctions (Lounibos et al. 1997). However, tires always held liquid and treeholes rarely dried out during the course of the current study, and larval deaths attributable to habitat drying occurred only in the summer, when drought accounted for only a small proportion of the total mortality in treeholes.

The buoyant eggs of *Toxorhynchites* spp. are susceptible to being swept out of phytotelmata (Lounibos et al. 1987) or water-holding tires (Focks and Sackett 1985) by rainfall. Although some egg mortality occurred in intercensus periods with rainfall, most mortality (62.7–93.7%) of eggs occurred in the absence of rain (Table 5).

By contrast, we present strong inferential evidence that cannibalism is an important mortality factor in the egg and first and fourth instars (Tables 5–7). Cannibalism by *Toxorhynchites* spp. larvae has been documented or inferred from many previous field and laboratory studies (Steffan and Evenhuis 1981, Corbet 1985). Our own research has frequently encountered the exoskeletal remains of *Tx. rutilus* larvae in the dissected midguts of all instars (unpublished data). Additional experiments have confirmed that *Tx. rutilus* larvae in tires may cannibalize eggs (L.P.L. and R. L. Escher, unpublished data), as was demonstrated in laboratory containers for this species and *Toxorhynchites amboinensis* (Doleschall) (Linley and Darling 1993). *Toxorhynchites* released for the biological control of mosquitoes would be cannibalized less if alternative prey were abundant.

It is known that cannibalism is strongly size-dependent in *Toxorhynchites* spp., larger individuals preferentially consuming smaller ones even within the fourth instar (Corbet 1985, Lounibos 1985, Lounibos et al. 1996). On the strength of these past observations and current results, we suggest that a large proportion of egg and larval mortality in our study may be ascribable to cannibalism, because no other natural enemies of *Tx. rutilus* immatures were detected in treeholes or tires.

In all but fall tires, the 'k' factors were highest for first and fourth instars (Tables 1 and 2), which identifies these as key stages (sensu Yamamura 1999) in the life table of this species. Recognition of key stages can be useful in biological control programs that are directed toward increasing the impact of predation on pest or disease-transmitting mosquitoes. To reduce key stage mortality, *Toxorhynchites* should be released at times when the potential impact of cannibalism is least, for instance when alternative prey are abundant or when predator fourth instars are uncommon.

Acknowledgments

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