J. Med. Entomol. Vol. 21, no. 4: 366–378 26 July 1984

SEASONAL DEVELOPMENT OF TREE-HOLE MOSQUITOES (DIPTERA: CULICIDAE) AND CHAOBORIDS IN RELATION TO WEATHER AND PREDATION[1]

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Abstract. Four species of tree-hole mosquitoes (Diptera: Culicidae) and 1 species of Chaoboridae in temperate north Florida commence their vernal development as embryos or larvae. Except for *Toxorhynchites rutilus*, all species overwinter in various prepupal stages. Overwintering populations of *Orthopodomyia signifera*, *Aedes triseriatus*, and *Anopheles barberi* are sparser and younger in the presence of *Tx. rutilus* than in its absence. Vernal pupation occurs first among *Tx. rutilus*, followed by *Or. signifera–Ae. triseriatus–An. barberi*, and then the chaoborid *Corethrella appendiculata*. *Toxorhynchites rutilus*, *Ae. triseriatus*, and *An. barberi* all pupate over a brief period, while *C. appendiculata* and *Or. signifera* pupate over a period of several weeks. The overwintering stages and the timing and variability of vernal development are interpreted as adaptations to seasonal harshness and to varying degrees of predation. The pattern of seasonal development is reviewed in the context of vector control.

Seasonal development in arthropods is generally considered with respect to its physiological mechanisms and environmental controls and in relation to variable seasonal harshness (Andrewartha 1952, Lees 1955, Danilevskii 1965, Levins 1969, Cohen 1970, Dingle 1978, Beck 1980, Taylor 1980), yet most species are members of more diverse communities and must interact with potential predators and competitors. These community interactions may then combine with weather to shape a given species' pattern of seasonal development. In this study, we consider seasonality of 4 species of temperate mosquitoes and 1 species of Chaoboridae whose immature stages must coexist in a confined habitat.

The community of tree-hole mosquitoes commonly found in southeastern North America usually contains 4 species (Bradshaw & Holzapfel 1983). One species, *Toxorhynchites rutilus* (Coq.), is a predator; two, *Aedes triseriatus* (Say) and *Orthopodomyia signifera* (Coq.), are limnetic and benthic filter-feeders/browsers; and one, *Anopheles barberi* (Coq.), is a specialized surface-feeder and facultative carnivore. The chaoborid *Corethrella appendiculata* Grabham is associated with this community of tree-hole mosquitoes as a predator. *Toxorhynchites rutilus* and *C. appendiculata* are the largest and smallest members of the community, respectively, and exploit distinct size-classes of prey. *Orthopodomyia signifera* is predator-resistant but drought-prone; it coexists in the larger, more permanent holes with *Tx. rutilus*, *C. appendiculata*, and *An. barberi*. *Aedes triseriatus* is predator-prone but drought-resistant; it predominates in the smaller, more transient holes. Despite this partitioning of resources along trophic and spatial lines, both drought and predation affect all species in the community.

No diapause is known in *C. appendiculata* but the 4 mosquito species may, among them, diapause in various stages from embryos to 4th instars (Table 1) and have been recorded as overwintering at any prepupal stage (Table 2). In this paper we describe the seasonal development of these 5 tree-hole species in temperate north Florida, USA, follow the pattern of their vernal development, and examine the factors affecting the age structure of overwintering populations. We then relate these observations to the consequences of community interactions as well as seasonal harshness. Finally, we propose a strategy for vector control that takes these factors into account.

MATERIALS AND METHODS

Details of the study area and sampling techniques are given in Bradhaw & Holzapfel (1983). Briefly, the Tall Timbers Research Station (30.6°N, 84.2°W, 30–60 m elevation) is on a 1200-ha nature preserve along the northern edge of Lake Iamonia, Leon Co., Florida, USA. Between February and December 1978 we made 19 censuses of tree holes at ca. 2-wk intervals. During the censuses, some tree holes dried up permanently and others were located. At the same time, it became clear that we could not continue indefinitely to census every hole. Consequently, we censused all known holes during censuses 4–5 and then reduced our basic number to 44 plus 1 census of any new holes we located. Holes that dried up permanently were considered

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[1] Dedicated to Professor Colin Pittendrigh, a pioneer in quantitative mosquito ecology, on the occasion of his sixty-fifth birthday.

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TABLE 1. Factors controlling development of tree-hole mosquitoes. Stage refers to stage at which diapause or retarded development occurs; onset and term refer to factors controlling the onset and termination of diapause.

	Source*	Stage/ instar	Onset**	Term.**	Temp. & photoper. effects**,***	References
Ae. triseriatus	OH, LR	embryo		LD	LT increases CDL	Kappus & Venard 1967
	OH, LR	IV	SD	LD	LT or low F required for SD effect	Clay & Venard 1972
	IN, LR	embryo	SD			Shroyer & Craig 1980
	IN, LR	embryo		LD	CHL increases rate response to LD	Shroyer & Craig 1983
	30–46°N, LR	embryo	SD		CDL increases 0.24 h/°N	Shroyer & Craig 1983
	s. FL, LR	IV	SD		SD less effective initiating diapause	Sims 1982
	30–40°N, LR	IV	SD	LD	Q_{10} development proportional to PPD; CDL increases 0.43 h/°N, 1.68 h/km elev.	Holzapfel & Bradshaw 1981
	NC, WCW	IV		LD	HT enhances LD effect	Holzapfel & Bradshaw 1981
Or. signifera	NC, WCF	IV		LD	SD may MD, RD, or have no effect	Bradshaw 1973
	NY, WCF	III		LD		Baker 1935
An. barberi	NY, WCF	II		LD		Baker 1935
Tx. rutilus	PA, LR	IV	SD	LD	CHL reduces CDL, AD, and TD; PPDic clock T-compensated 16.5-26.5 °C	Bradshaw & Holzapfel 1975, 1977
	NC, WCF, LR	IV	SD	LD	HT reduces SD effects	Jenner & McCrary 1964; McCrary 1965
	FL, LR	IV	SD	LD		Holzapfel & Bradshaw 1976
	30 & 40°N, LR	IV	SD		CDL does not change with latitude	Trimble & Smith 1979

* LR, laboratory-reared; WCW, wild-caught in the winter. States by U.S. Postal Service zip codes.

** SD, short daylength; LD, long daylength.

*** AD, advances development; CDL, critical daylength; CHL, chilling; F, food level; HT, high temperature; LT, low temperature; MD, maintains diapause; PPD, photoperiod; RD, retards development; T, temperature; TD, terminates diapause.

in the data pool up through the last census in which they contained standing water and were eliminated thereafter. By the 17th census in mid-October, a long drought had dried up all but 1 hole. Apart from spot checks, censusing was then suspended until December, when there was sufficient rain to generate standing water in tree holes.

In addition to actual tree holes, we censused mosquitoes in automobile tires set out in Woodyard Hammock, a beech-magnolia hammock at the southwest corner of the Tall Timbers Research Station. In the northern part of the hammock (WH-N), we had set tires on the ground, leaned them against the base of trees, and added slop from local tree holes during May 1976 and again during January 1977. During dry periods, we maintained standing water of undetermined depth in these tires by the addition of unchlorinated well water. We removed larvae and pupae of *Culex* and *Culiseta* at each census. Starting 15 March 1978 we examined the surface of the tires every 24–72 h, counted the eggs of *Toxorhynchites*, and counted and removed all *Culex/Culiseta* egg rafts. In the southern part of Woodyard Hammock (WH-S), about 100 m from the 1st set of tires, we hung 10 tires 1.5 ± 0.2 m from the ground on trees. On 14 March 1978 we seeded each with slop taken from a single local tree hole and heated to 80 °C to kill the insects present.

TABLE 2. Overwintering stages of tree-hole mosquitoes from sources that make specific reference to stage.*

	LOCALITY**	OVERWINTERING STAGES/INSTAR	REFERENCES
Ae. triseriatus	Canada	embryo	Brust & Kalpage 1967
	NY	embryo	Baker 1935
	IN	embryo	Shroyer & Craig 1983
	PA	embryo	Holzapfel & Bradshaw 1981
	TN	embryo	Breeland et al. 1961
	FL, NC, SC	embryo–IV	Holzapfel & Bradshaw 1981
Or. signifera	MI	III–IV	Bradshaw & Holzapfel, unpubl.
	PA, MD, NC, SC	II–IV	Bradshaw & Holzapfel, unpubl.
	NY	II–III	Baker 1935
An. barberi	NY	II–III	Baker 1935
	NJ	II	Lake 1954
	PA, MD, NC	II	Bradshaw & Holzapfel, unpubl.
	SC	II–III	Bradshaw & Holzapfel, unpubl.
	FL	II–IV	Bradshaw & Holzapfel, unpubl.
Tx. rutilus	PA	IV	Bradshaw & Holzapfel 1975, 1977
	NC	IV	McCrary 1965
	NJ	IV	Lake 1954
	FL	IV	Holzapfel & Bradshaw 1976
	MS	IV	Michener 1947

* This table does not include references that infer overwintering as adults or eggs from the absence of larvae or pupae, or vague references that list mosquitoes overwintering "in all larval instars," "as immature forms," or "as larvae."

** States by U.S. Postal Service zip codes.

The amount of slop was adjusted so that the light of a flashlight could just penetrate to the top of the detritus layer in the tire. During experimental periods covered in this paper, we maintained at least 15 cm of standing water in each tire, either by natural rainfall or, during dry periods, by the addition of unchlorinated well water. We examined these tires every 24–72 h, removed egg rafts of *Culex/Culiseta* from all of them, and eggs and larvae of *Tx. rutilus* from half of them. We used the established WH-N tires to follow vernal development and the new WH-S tires to examine the effects of *Tx. rutilus* on the age structure of the overwintering populations and as surrogate tree holes during a period when all natural holes were dry.

RESULTS

Rainfall and available holes

The year 1978 was characterized by continual rainfall except for 2 dry periods, a short one from late March to early April and a longer one from late September to late November (Fig. 1). The percentage of tree holes containing standing water declined during each dry period, with ⅔ of the holes drying up during the earlier drought and all of the holes during the later one. Modest rainfall during late October and early November was not sufficient to produce standing water in any of the holes.

Seasonal patterns

Toxorhynchites rutilus and *C. appendiculata* occurred at a low frequency in March and early April. Thereafter, the incidence of *Tx. rutilus* generally increased during the year until the long drought. After this drought, we found a single *Tx. rutilus* in only 1 of the 23 wet holes; during the last census, it was absent from this hole. *Corethrella appendiculata* never occurred in more than ⅓ of all holes, reaching peak incidences of 25 and 32% of wet holes in early April and early September, respectively. *Corethrella appendiculata* was absent from the few wet holes immediately before the long drought but was found in 10–25% of the wet holes after the drought.

Initially, *Ae. triseriatus* occurred in more holes than *Or. signifera* and *An. barberi* combined. From early March to late October, the incidence of *Ae. triseriatus* showed a general decline. Rises in the frequency of *Ae. triseriatus*-occupied holes was associated with particularly heavy rains in mid-July and mid-September. As the long drought approached, the incidence of *Ae. triseriatus* declined to zero, but immediately after this drought it rose to its highest level of the year. By contrast, the frequency of *Or. signifera*-occupied holes was low

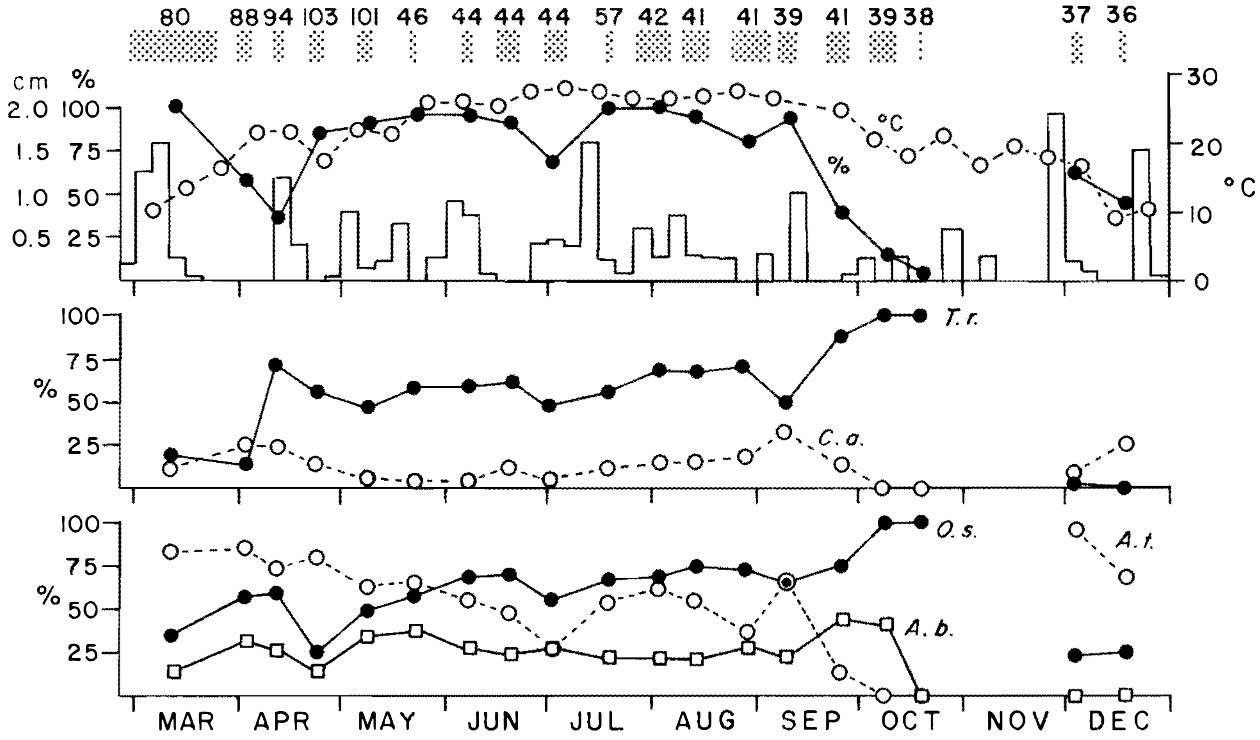

FIG. 1. Seasonal weather patterns and incidence of tree-hole species at Tall Timbers, Florida, in 1978. Top line shows number of holes sampled per census, and time period (screen) during which that census took place. Top graph: histograms show rainfall per day averaged over 5-day periods except for the 26th to last day of each month; dashed lines plot 10-day average air temperatures, which closely approximate tree-hole temperatures (Bradshaw & Holzapfel 1977); solid line plots percentage of holes examined that contained standing water. Bottom 2 graphs plot percentage of wet holes occupied by larvae and pupae of each species; *T.r.*, *Toxorhynchites rutilus*; *O.s.*, *Orthopodomyia signifera*; *A.t.*, *Aedes triseriatus*; *A.b.*, *Anopheles barberi*; *C.a.*, *Corethrella appendiculata*.

at the beginning of March and, except for a decline in late April, rose continually until the long drought. After this drought, *Or. signifera* again appeared but at a low frequency (22–25%). *Anopheles barberi* remained in a relatively low proportion of holes until the long drought, after which we did not find a single individual in any hole.

The above results (Fig. 1) show that *Tx. rutilus* and *Or. signifera* were found with increasing frequency during the year, while populations of *Ae. triseriatus* generally declined. *Anopheles barberi* and *C. appendiculata* occurred in less than 40% of the wet holes throughout the year. After a prolonged autumnal drought, *Ae. triseriatus* reappeared in most wet holes, *Tx. rutilus, Or. signifera*, and *C. appendiculata* in but a few wet holes, and *An. barberi* in none.

Vernal development

During the winter, all tree-hole mosquitoes enter diapause as embryos and/or larvae; a combination of temperature and photoperiod mediates their cessation of development in the fall and their resumption of development in the spring (Table 1). The stages at which temperature and/or photoperiod halt or retard development will determine the starting points for vernal development in each species. To examine the timing and pattern of vernal development, we made parallel censuses in tree holes and tires. We monitored tires starting in January and, when age distributions in tires indicated development tending towards pupation, we commenced censusing tree holes. For tree-hole development, we pooled the census data from sequential 5-day periods through March, April, and May (censuses 1–6). The instar distributions during the 12 resulting time periods are shown in Fig. 2. For development in tires, we censused 7 ground-level tires in Woodyard Hammock (WH-N) in January 1978, and every 10 days to 2 weeks from February through May. The instar distributions during the resulting 10 time periods are shown in Fig. 3.

Toxorhynchites rutilus diapauses as 4th instars: development begins (Fig. 2, 3) in this stage. The first

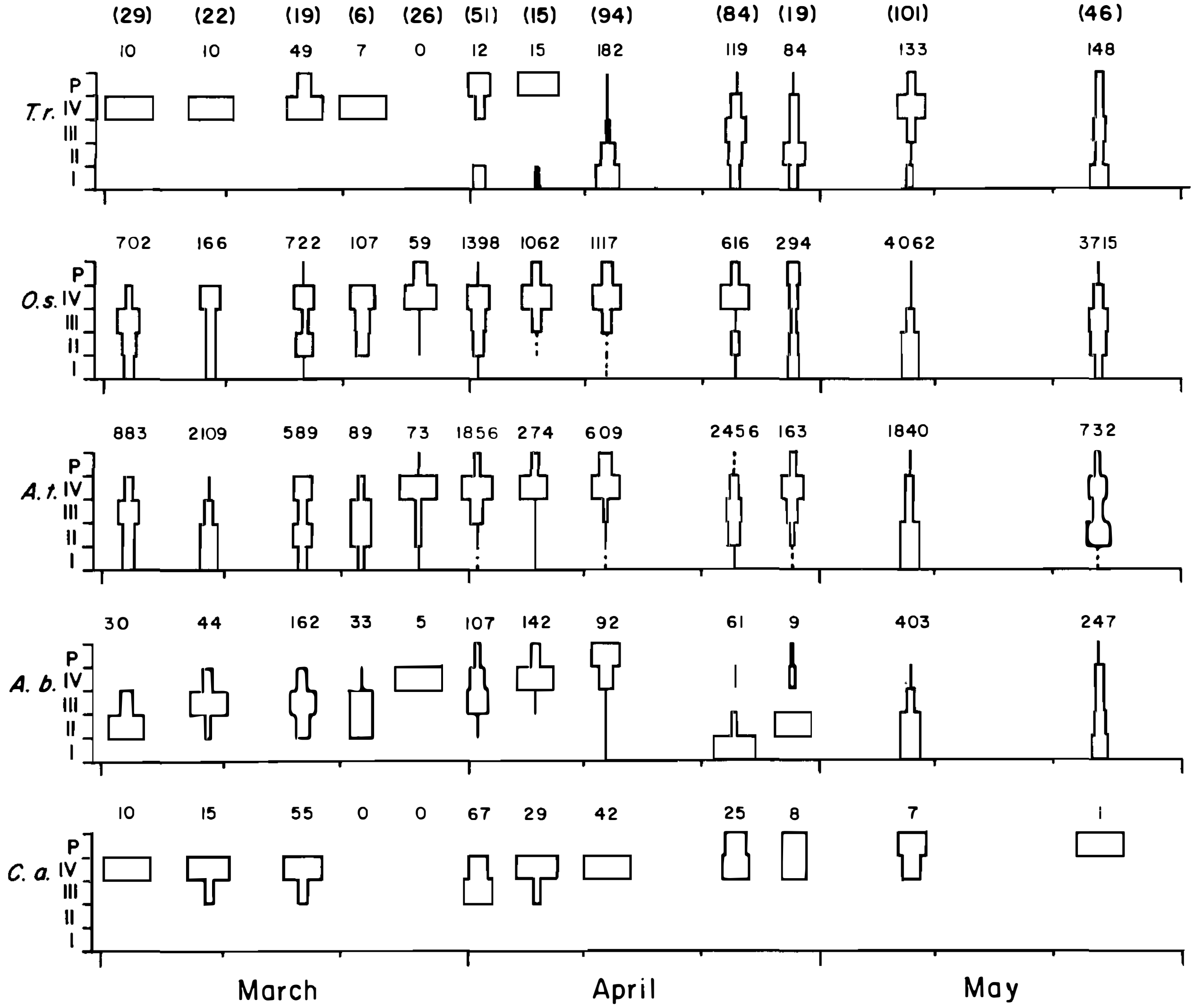

FIG. 2. Instar distribution of mosquitoes and chaoborids in tree holes during sequential 5-day periods in the spring of 1978. Individual histograms are centered on the mean census date. Width of bar indicates percentage of total number of each species in a given stage of development. Number over each individual histogram shows number of mosquitoes of that species contributing to the plot. Numbers in parentheses at the extreme top of figure indicate number of tree holes sampled during that 5-day period.

pupae appeared during early March in tires and during mid-March in tree holes. In both systems, 1st instars appeared during the 1st week in April, and by mid-April the population consisted mainly of 3rd or younger instars. The mean age of the population then increased, pupae again appearing in tires the 1st week in May. In tree holes, pupae of *Tx. rutilus* rise in proportion at the same time. These results suggest that in 1978, overwintering *Tx. rutilus* occupied tree holes or tires exclusively until the 1st week in April; overwintering and 1st summer generations coexisted until mid-April, and the summer generation predominated thereafter. In tires there was a hiatus in the reappearance of 1st instars, suggesting further that the approximate 6-wk interval from early April to mid-May represents the generation time for *Tx. rutilus* at this time of year, when air temperatures averaged about 20 °C.

Orthopodomyia signifera may diapause as 3rd or 4th instars (Table 1) but is found overwintering in all instars (Fig. 2, 3). While embryonic diapause has not been found in this species, the increase in absolute numbers and percentage of 1st instars in tires during February (Fig. 3) suggests that some overwinter in the egg stage. We cannot assess

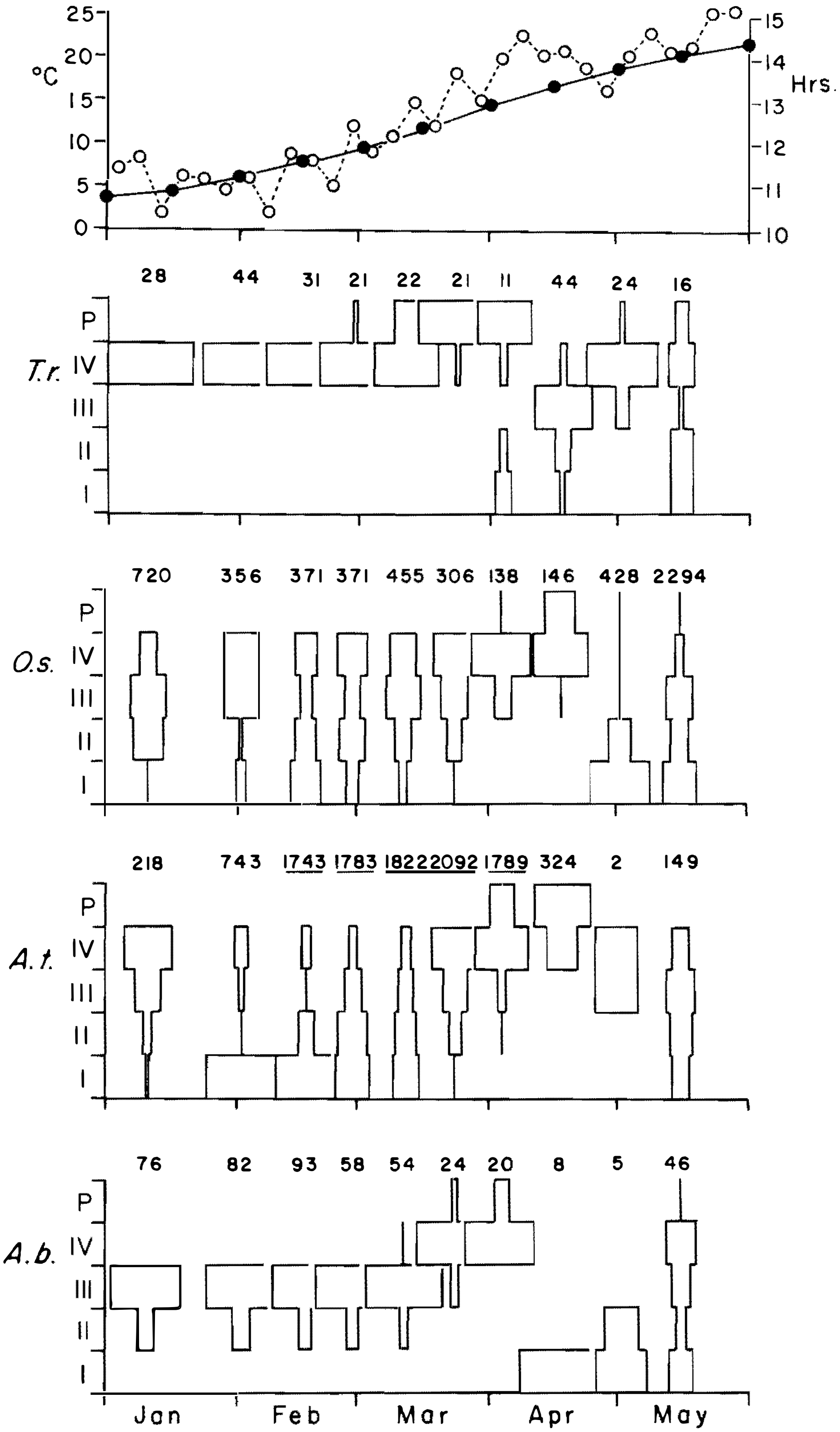

FIG. 3. Instar distribution of mosquitoes in tires (WH-N) during the spring of 1978 with mean 10-day (or 20th to end of month) air temperature and day length (sunrise–sunset + 1 civil twilight). Other conventions as in Fig. 2.

whether these individuals are in a thermally repressed state of embryonation or in an actual embryonic diapause. *Orthopodomyia signifera* mosquitoes then commence their development from various starting points, and it is not surprising that their subsequent pupation spans a longer period—late March to late April—than any other species. In tires the populations of *Or. signifera* became older between early January and early February, but 1st instars increased in both absolute numbers and frequency in mid-February. By early March, the age distribution in tires resembled that in tree holes. We observed the 1st pupae the 3rd week of March in tree holes and the 1st week of April in tires. The population became progressively older during the rest of March and April. A substantial number of 1st instars appeared the last week in April in tree holes and the 1st of May in tires. It would thus appear that the overwintering generation constituted the major proportion of the population through the end of April, that generations were mixed during late April and early May, and that the summer generation predominated thereafter.

Aedes triseriatus diapauses only as embryos or 4th instars (Table 1), but we found all 4 instars in tree holes and tires. In tires 4th instars predominated in smaller populations during January; in early February the populations increased sharply with the appearance of many 1st instars. By mid-March the age distribution of *Ae. triseriatus* in tires and tree holes was similar. The first pupae appeared the last week in March in tree holes and the 1st week in April in tires. Between late March and mid-April, older instars and pupae constituted the bulk of the population. In tree holes, by late April, samples consisted of intermediate and then older instars in 2 sequential 5-day periods. Younger instars then predominated at the next census in early May. Since there was a drought followed by heavy rain at this time (Fig. 1), it is not clear whether the late April pulse of earlier instars constituted a 2nd hatch of the overwintering generation or the initial hatch of the 1st summer generation. Regardless, the 1st and 2nd instars in early May represent a summer generation, and since relatively few older instars are present at this time, there is little overlap between the overwintering and summer generations. In tires, where we maintained water levels, development was delayed compared to that in tree holes. The major pulse of early instars came the first 2 weeks in May. Thus, as in tree holes, there is little overlap between the overwintering and summer generations.

Anopheles barberi mosquitoes overwinter as 2nd instars farther north and probably diapause in that stage (Table 1); we observed them in both 2nd and 3rd instars from January through early March. Thus, at Tall Timbers, *An. barberi* may also diapause as 3rd instars. During mid- to late March, the populations became progressively older, with pupae appearing in late March to early April in both systems. The initial 1st instars appeared in mid-April in tires and in late April in tree holes. Thus, in both tires and tree holes, the transition between overwintering and 1st summer generations of *An. barberi* appears to take place rapidly over a 10-day period, with minimum overlap between the 2 generations.

Corethrella appendiculata is not known to diapause; our only record of it at Tall Timbers in the spring of 1978 comes from tree holes. In tree holes *C. appendiculata* occurred as 3rd or 4th instars until late April when the first pupae appeared.We observed no 3rd instars after early April but did consistently find 4th instars and pupae through the end of May. Since we were not able to census 1st and 2nd instars reliably, it is difficult to assess the degree of overlap between overwintering and 1st summer generations, but these results, particularly the absence of 3rd instars, do indicate that the overwintering generation of *C. appendiculata* persists longer than that of any of the above species.

In sum, these relationships indicate that *Tx. rutilus* overwinters in the oldest, most uniform stage and is the first to pupate and emerge in the spring. It is followed by *Ae. triseriatus, Or. signifera,* and *An. barberi. Aedes triseriatus* and *An. barberi* develop rapidly, and most pupae appear over a 10–15-day period; *Or. signifera* develops gradually and pupation is spread over 5 weeks. *Corethrella appendiculata* pupates the latest of any species. The overlap between overwintering and 1st summer generations is minimal among all species except *Or. signifera,* where 2 generations may coexist for 2 weeks or more.

Age structure of the overwintering population

To examine the establishment of the instar distribution of the overwintering population of tree-hole mosquitoes, we censused 10 tires in Woodyard Hammock (S) every 2–3 weeks during October to December (Fig. 4). We inspected each of these tires

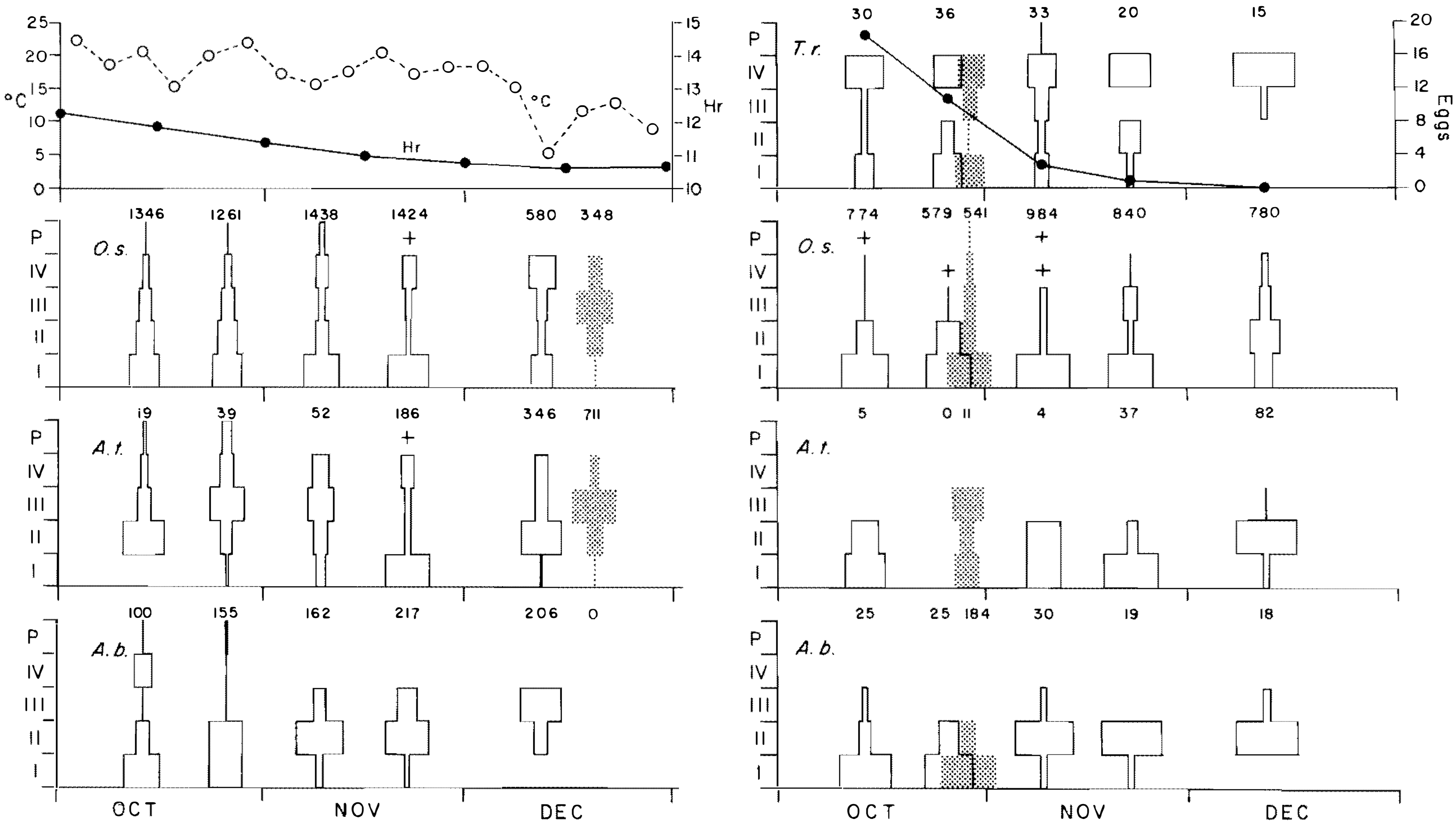

FIG. 4. Instar distribution of mosquitoes in tires (WH-S) during the fall of 1978 with mean 10-day (or 20th to end of month) air temperature and day length (sunrise–sunset + 1 civil twilight). Conventions as in Fig. 2 except that the right-hand graphs plot tires where *Tx. rutilus* was present and the left-hand graphs plot tires where *Tx. rutilus* was removed. The October–November censuses were made when all tree holes were dry; for comparison with a wet fall, the October 1977 (WH-N) pattern is superimposed in screen on the tires where *Tx. rutilus* remained; for comparison with tree holes, the last December 1978 tree-hole census data are superimposed in screen on the December tires where *Tx. rutilus* was absent.

every 24–72 h, removed eggs of *Tx. rutilus* from 5 tires, and, after examination with a flashlight, any larval *Tx. rutilus* that might have escaped as eggs. The other 5 tires retained the eggs and larvae of *Tx. rutilus*. By comparing these 2 sets of tires, we were able to determine the effect of predation on the age structure of overwintering prey.

Toxorhynchites rutilus eggs appeared at a declining frequency during October to December. In early October we observed an average of more than 18 eggs per tire. This number declined to zero by mid-December. As long as there were eggs on the surface, we also found early instars of *Tx. rutilus* in the water. By mid-December 90% of the population consisted of 4th instars. The only pupa of *Tx. rutilus* was found in early November.

Orthopodomyia signifera in tires with *Tx. rutilus* consisted mainly of early instars through December, at which time less than 25% of the population were 3rd and 4th instars. The last pupa in these tires was found in early November. In tires without the predator, older instars and pupae occurred at a consistently higher frequency than in tires with *Tx. rutilus*, and by mid-December most of the population were 3rd and 4th instars. The last pupa in tires without *Tx. rutilus* was found in late November. With the exception of mid-December, the population size of *Or. signifera* was about 1.5 times higher in tires where *Tx. rutilus* was absent, but even in the presence of *Tx. rutilus, Or. signifera* averaged over 150 larvae per tire.

Aedes triseriatus in the presence of *Tx. rutilus* was found exclusively as 1st or 2nd instars until mid-December, when 3% of the population were 3rd instars. We recovered no pupae from these tires. In the absence of *Tx. rutilus*, older instars and/or pupae were always present, so that in mid-December 35% of the population consisted of 3rd and 4th instars. Pupae constituted 7–12% of the population in October and the last pupa was found in late November. In both sets of tires, population size increased with date of census, but over 5 times as many larvae and pupae occurred in tires without *Tx. rutilus*.

Anopheles barberi in tires with *Tx. rutilus* was present only in the first 3 instars, and in mid-December over 85% of the population were 2nd instars. In the absence of *Tx. rutilus, An. barberi* was found in all stages (including pupae) in October, but only as 1st to 3rd instars after that time. By mid-December 60% of the population were 3rd instars and the remainder 2nd instars. The average number of *An. barberi* was over 7 times higher in tires without *Tx. rutilus* than in tires containing the predator.

DISCUSSION

Determinants of seasonal development

The seasonal pattern of tree-hole mosquitoes at Tall Timbers is determined by 3 major factors: desiccation, predation, and seasonal changes in temperature and photoperiod. Throughout the months of favorable weather, *Tx. rutilus* consumes prey to the extent that the latter are not resource-limited (Bradshaw & Holzapfel 1983); however, the net effect of predation impacts on later instars and pupae of the prey so that, even if development is density-independent throughout the year, emergence success is limited by predation (Bradshaw & Holzapfel 1983). During the fall (Fig. 4), there were 1.5 times the number of *Or. signifera*, 5 times the number of *Ae. triseriatus*, and 7 times the number of *An. barberi* in tires without, than in tires with, *Tx. rutilus*. At the same time, and consistent with the earlier observations in tree holes (Bradshaw & Holzapfel 1983), *Tx. rutilus* cropped older instars of prey such that the population entering winter (mid-December) was consistently younger in tires with the predator than without. After the long autumnal drought when *Tx. rutilus* was effectively absent, *Ae. triseriatus* and *Or. signifera* populations in tree holes were older than in tires with *Tx. rutilus* (Fig. 4). Thus, the tendency of predation to alter the age structure of the overwintering population may be moderated or nullified by the timing and extent of seasonal drought.

Both predation and drought interact with physiological mechanisms underlying dormancy or quiescence to determine the actual overwintering stages of each species. *Aedes triseriatus* is highly susceptible to predation but possesses drought-resistant eggs, is among the fastest developing of the tree-hole species, and predominates in the smaller, more transient holes (Bradshaw & Holzapfel 1983). During periods of declining rainfall, its eggs may accumulate on the walls of tree holes and persist through periods of drought that eliminate *Tx. rutilus* from many holes. By hatching in response to heavy rainfall (Fig. 1), *Ae. triseriatus* effectively invades predator-free holes or may, by its large numbers, saturate the predator. Autumnal drought can markedly reduce the number of holes that contain overwintering *Tx. rutilus* and the vernal period may represent the most predator-free time of year for

Ae. triseriatus (Fig. 1). *Aedes triseriatus* thus escapes much predation by virtue of drought-resistant eggs and embryonic dormancy; the 2nd diapause in the 4th instar then relates to development in variable vernal environments (Holzapfel & Bradshaw 1981) rather than developmental compensation for cohabitation with *Tx. rutilus.*

Toxorhynchites rutilus, Or. signifera, and *An. barberi* do not possess drought-resistant eggs. They coexist in the larger, more permanent holes (Bradshaw & Holzapfel 1983). *Anopheles barberi* generally occurs at a low frequency (Fig. 1), $^1/_{10}$ to $^1/_{100}$ the density of *Or. signifera. Anopheles barberi* was the only species totally absent from tree holes after the long drought and the only species not recorded from peninsular Florida (Jenkins & Carpenter 1946, Lounibos 1983). Wet-dry seasons are more characteristic of tropical than temperate zones and there is a latitudinal gradient from continental eastern North America to the tip of the Floridian Peninsula of increasing probability of drought (Fig. 5). The absence of *An. barberi* from southern Florida probably relates to drought-imposed local extinction and the absence of nearby refugia to serve as a reinvasion source. We have proposed earlier (Bradshaw & Holzapfel 1983) that *Tx. rutilus* has its greatest impact on the more common prey (*Or. signifera*) and that *An. barberi,* because of its relative scarcity and habit of feeding from the surface film, may avoid more intense predation. We now also propose that their small overwintering size is an adaptive physiological response to their overwintering coexistence with a large, size-selective predator.

Similarly, the variability in age structure of overwintering *Or. signifera* may be an adaptive response to drought-enforced coexistence with *Tx. rutilus. Orthopodomyia signifera* overwinters at all stages from embryos to 4th instars (Fig. 2, 3). Through mechanisms that are distinct from those of *Ae. triseriatus, Or. signifera* preserves this variability and pupates over a long period. As a result, the overwintering generation grades into the continuous summer generations and there is no optimal time for *Tx. rutilus* to develop in order to maximize the availability of its most prevalent prey. Our data do not provide experimental evidence to demonstrate the role of predation in the evolution of dormancy in these mosquitoes; we can, however, compare the patterns of dormancy described above with those of related European tree-hole mosquitoes where *Toxorhynchites* is absent. *Orthopodomyia pulchripalpis* Rond. overwinters as 4th instars (Tate 1932) and *Anopheles plumbeus* Steph. diapauses in the 3rd and 4th instars (Vinogradova 1962). Thus, in the absence of an overwintering larval predator, *Orthopodomyia* overwinters in an older, more uniform stage and *Anopheles* diapauses in older instars.

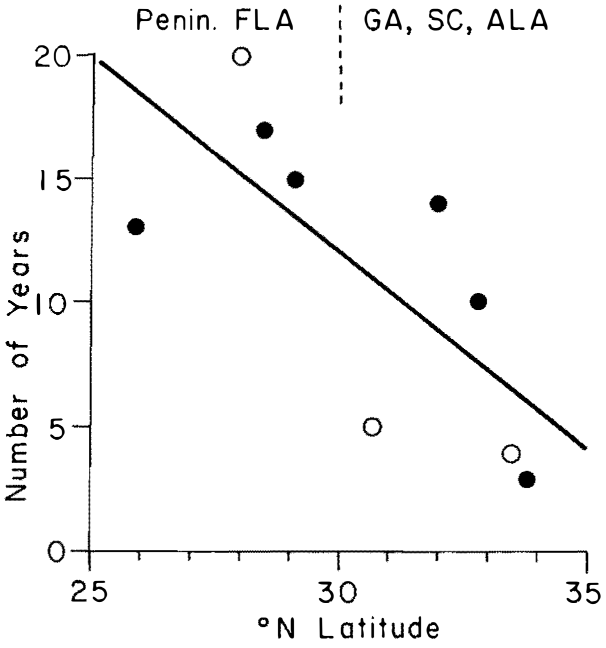

FIG. 5. Number of years from 1936–1975 that a dry month (<2.5 cm rain) was followed by a 2nd dry month, such that the total rain for the 2 months was less than 5.0 cm. Data from Ruffner & Bair (1977) for peninsular Florida (Penin. FLA) and adjacent states. Solid dots show Georgia (GA), South Carolina (SC), and the east coast of Florida; open circles show Alabama (ALA) and west coast of Florida.

Stage of diapause among predators may also be a response to predation. *Toxorhynchites* generally prefers prey its own size or smaller (Steffan & Evenhuis 1981) so that cannibalism among 4th instars is probably less common than by 4th instars on younger ones. A cannibalistic stand-off of 4th instars could provide the selective force maintaining the relatively uniform and advanced age of diapause in *Tx. rutilus* compared to other tree-hole species.

Corethrella appendiculata pupates later and over a longer period than any other Florida tree-hole species (Fig. 2). The first pupae appeared in late April and pupation continued through May. Pupation of this predator is thus delayed until the 1st instars of the mosquito species have started to appear in tree holes. Since *C. appendiculata* preys

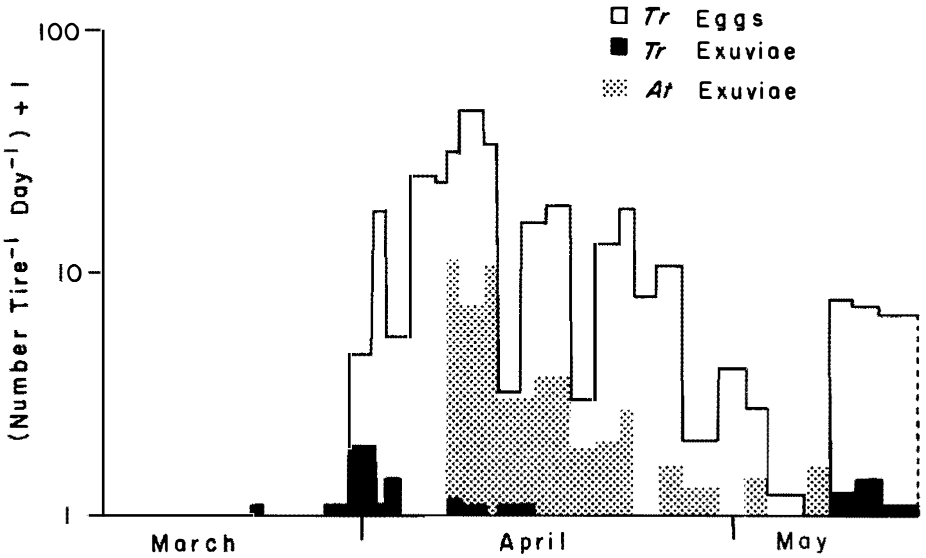

FIG. 6. Vernal eclosion of *Tx. rutilus* and *Ae. triseriatus* from, and oviposition of *Tx. rutilus* into, the same tires as covered in Fig. 3.

preferentially on younger instars (Lounibos 1983), prey availability may contribute to the delay and variation in their vernal development.

Implications for vector control

Further north, *Ae. triseriatus* is the major vector of La Crosse (California group) encephalitis (Pantuwatana et al. 1972, 1974, Thompson et al. 1972, Watts et al. 1972, 1973), and southern populations have the capacity to transmit this virus as well (Grimstad et al. 1977). In the upper Midwest where *Toxorhynchites* is absent, *Ae. triseriatus* is largely univoltine (Shroyer & Craig 1981), and vernal development is largely density-dependent (Durland Fish, pers. commun.). Control measures targeted at killing larvae or adults may then simply eliminate the self-limiting aspects of these populations and result in larger, more fecund adults. At these latitudes, effective control might be effected better through the introduction of a larval competitor than by reducing density-dependent constraints to their development. Further south where *Toxorhynchites* is prevalent, *Ae. triseriatus* is limited by predation and drought (Bradshaw & Holzapfel 1983). At these latitudes, larvicidal or adulticidal measures would remove vectors without contributing to the well-being of the remainder of the population. The problem then lies in eliminating *Ae. triseriatus* without reducing *Tx. rutilus*. The latter involves not only protecting *Tx. rutilus* directly but also its major alternate food supply, *Or. signifera*. A means to effect such differential control lies in the timing of seasonal development among these species.

In the spring (Fig. 6), *Tx. rutilus* is the first to emerge. Not requiring a blood meal, females rapidly disseminate their eggs. By the time of major *Ae. triseriatus* eclosion there are again younger instars of *Tx. rutilus* in tree holes or tires (Fig. 2, 3). Appearance of 1st-instar *Ae. triseriatus* is delayed for several weeks, presumably because the females must locate a host and mature a clutch of eggs before searching for suitable oviposition sites. It is at this precise time that *Ae. triseriatus* is differentially susceptible to aerially disseminated adulticides. Vernal emergence is relatively synchronous and represents the major emergence of *Ae. triseriatus* during the year (Bradshaw & Holzapfel 1983), thus resulting in a maximal effect on the target species. At the same time, the next generation of their principal larval predator is again safe in tree holes and there are still alternate prey (*Or. signifera*) that have not yet developed. Thus, by calculated application of a rapidly biodegradable adulticide, control becomes specific in time, with maximum impact on the vector and minimum effect on its natural, limiting predator. The optimal timing of control measures could be predicted from phenological models (Bradshaw 1974), from monitoring vernal development in easily censused tires, or from a combination of both.

Conclusions

Dormancy and its environmental control are generally considered as adaptations to harsh seasonal weather. However, weather affects species and populations differently so that potential biotic interactions change during the progression of a normal year. To the extent that these changes are predictable from photoperiod and other cues, they too will act as selective forces shaping seasonal development. In the present case, *Ae. triseriatus* has a refugium from predation, and its seasonal development is most easily interpreted as response to winter harshness and unpredictable vernal weather (Holzapfel & Bradshaw 1981). *Toxorhynchites rutilus, Or. signifera,* and *An. barberi* all encounter seasonally changing levels of predation; their stages of dormancy and patterns of seasonal development all reflect this predation as well as seasonal harshness. Understanding the biotic interactions in a community can thus be important to understanding patterns of dormancy and seasonal development and to devising control strategies that effect maximum impact on target species while protecting naturally occurring parasites, predators, and competitors.

Acknowledgments. Much of the background work leading up to the year we spent at Tall Timbers was completed with help and encouragement from Donald Strong, D. Bruce Means, E.V. Komarek, Frances James, Donald Kaufman, Pilar Bradshaw, and Philip Lounibos. Forest Kellog, Gary Doster, Leslie Thrasher, Mel Burns, Louis Beckham, Greg Stewart, Pilar Bradshaw, Philip Lounibos, and Virginia Vail reported many findings of tree holes. We thank Lee Szyska for long hours of assistance in the field and Gregory Daly for his help in data reduction and analysis. We have profited from many long discussions with Bruce Means, Peter Frank, and, especially, Philip Lounibos. Finally, we are very grateful to the Tall Timbers Research Station and the National Science Foundation (DEB 74-00918; DEB 78-22799) for support of this project.

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