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THE ECOLOGY AND BEHAVIOR OF *TACHOPTERYX THOREYI* (HAGEN) (ANISOPTERA: PETALURIDAE)

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A Florida colony of *T. thoreyi* was studied throughout the flight season of 25 March - 28 May 1978. Larvae of several instars were found near the uphill edges of permanent seeps in deciduous forest, hiding between or under leaves in thin sheets of flowing water. In captivity they preferred to live above water on wet soil. Transformation occurred on any vertical support 0.2-1.4 m above ground during mid-morning, and sexual maturity was attained in 2-3 weeks. Males searched tree trunks or waited in the seepage areas for females. Males had no day-to-day site fidelity at the seeps. Larger prey taken was about 2/3 Lepidoptera and 1/3 Odonata. The minimum population, based on individual marking and collection data, was 128 males and 46 females. Marked males moved distances of at least 1.1 km, and both sexes shifted locations often. The egg and 3 larval instars are described. Ecological adaptations and ecological relationships with *Cordulegaster* are discussed.

INTRODUCTION

The biology of petalurids is of exceptional interest because this group was a dominant one in Mesozoic times but has now been reduced to only 9 known relict species. *Tachopteryx thoreyi* (Hagen) is the single species of its genus and the only petalurid in eastern North America.

I studied the ecology and behavior of *T. thoreyi* for an entire flight season of 25 March - 28 May 1978 at Gainesville, Alachua County, Florida. Gainesville is the southern known limit of the range of this species, although there are unconfirmed sight records from Lake County 110 km to the southeast. As in all other *T. thoreyi* breeding localities known to me, the habitat studied consisted of permanent, spring-fed, hillside seeps in broad-

-leaved deciduous forest. Near the end of the adult emergence period on 11 April 1978 after nearly a month without rain, these seeps had the following characteristics: Temperature 20°C, pH 5.4, total alkalinity 10 ppm, total acidity 12 ppm. On 17 April several days after rain had fallen 10 measurements of dissolved O_2 were made in the water nearest to where larvae or exuviae had been found. Dissolved O_2 values were 1.8-7.5 ppm or 20-85% saturation at 20°C, $\overline{X} = 52\%$. This habitat is currently being destroyed by a housing development, but 2 other known colonies of *T. thoreyi* in the Gainesville area are protected.

METHODS AND RESULTS

EGGS

Many mature females were placed in separate containers floored with wet paper toweling. Only a few laid eggs, and only one deposited a small clutch (17) of fertile eggs. The eggs were elongate-oval, rounded at both ends, and measured 0.55-0.60 x 1.33-1.40 mm (Fig. 1). The chorion was thickest at both ends, with a short transparent pedicel at the anterior pole. They were a pale yellow at first, becoming orange-brown within a day.

The eggs of *Tachopteryx thoreyi* are similar in size and shape to those of the petalurids *Tanypteryx hageni* (Selys) and *Uropetala carovei* White. The eggs of *U. carovei* are glued to moss, whereas *T. thoreyi* eggs have a non-sticky surface. The incubation time for *Tanypteryx hageni* was 26 days, and for *U. carovei* was 21-25 days (SVIHLA, 1959; WOLFE, 1953), compared with 32 days for *T. thoreyi* at room temperature. The eggs of *Petalura gigantea* Leach are different from the above 3 species in that they are pointed at one end (TILLYARD, 1909).

LARVAE

First instar. — The first instar larva or prolarva was not observed but its exuviae was left attached to the egg chorion after hatching. The first instar larva hatches through a curved slit in the chorion which extends from the anterior pole to slightly more than half the length of the egg (Fig. 1). The hatching slit is jagged in *Uropetala carovei* (WOLFE, 1953).

Second instar. — Total length 2.24-2.38 mm, head width 0.48-0.51 mm, pale brown in life with the head, thorax, and abdominal segments 1-2 a little darker. Head about 2x as wide as long, antennae stout and 3-segmented. Middle antennal segment about as wide as long, ratio of segment lengths from base to tip about 2:3:7. Labial palps with 7-11 sharp teeth on the anterior border and extending onto the medial border (Fig. 1). Labium with a short,

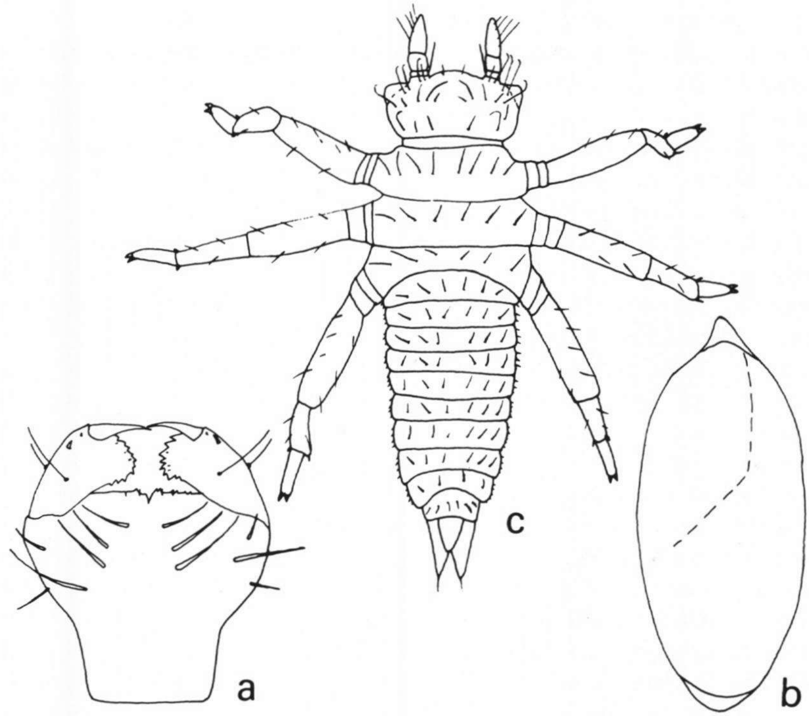

Fig. 1. Egg and second instar larva of *Tachopteryx thoreyi*: (a) Dorsal view of labium, 125x; — (b) egg showing location of hatching slit, 25x (drawn from a photograph); — (c) Dorsal view of second instar larva, 25x (drawn from a photograph).

stout, spine near the base of the movable hook, anterior premental margin with an open V-shaped cleft flanked by a triangular tooth and 2 short setae on each side. Legs stout, with 4 large digging setae at the distal end of each tibia, tarsi 1-segmented. No dorsal or lateral abdominal spines. Body with many long hair-setae to which debris adheres.

Third instar. — Total length 2.50 mm, head width 0.72 mm, all tarsi 2-segmented, 6-7 equal anterior premental teeth on each side of cleft, 11-13 teeth on each palp.

Fourth instar. — Total length 3.30 mm, head width 0.88 mm, antennae 4 or 5 segmented, tarsi 2-segmented, 9 premental teeth on each side, 17 teeth on each palp, small lateral abdominal spine on segment 9. Of the several larvae I attempted to rear, only one became fourth instar before dying. They were reared in separate vials of water and fed brine shrimp nauplii — they obviously require more natural conditions.

Last instar. — WILLIAMSON (1901) described the last instar larva, but missed a few features because mud encrusted his specimen. BYERS (1930) added to the description the spur at the base of the palpal movable hook, lateral spines on segments 2-9 of the abdomen, and a pair of setose dorsal tubercles on segments 2-9 of the abdomen. In life, the body is dark brown with pale brown wing cases, and the abdomen has a narrow white mid-dorsal stripe. The compound eyes are transparent, with scattered black flecks as the only pigmentation. Thus the eyes seem adapted for use in dim light.

Larval behavior. — Four second instars were placed in a chamber made from a petri dish in which a slanted paper towel allowed the choice between water and a moist surface in air. They remained in the water but were often at the edge where they bulged the surface film upward.

Larvae found in the wild were between or under wet leaves near the uphill edges of seeps. They were usually in a thin slowly flowing layer of water, but some were above the water surface. A few were in depressions in the soil, but none were in burrows, nor were there any burrows present like those described for some other petalurids.

Large larvae kept in aquaria with the choice of water or mud seldom went into the water, and could molt in air. Possibly the amount of time spent above or below water depends on the relative abundance of prey in those two habitats. Dissolved O_2 in the aquaria water was 4.2-5.0 ppm, well within the range measured in the field. Given the choice of leaves or bare soil, the larvae hid under the leaves, and given the choice of darkness or light preferred the dark during the daytime. Small cockroaches were avidly eaten, but terrestrial isopods did not seem to be acceptable food. At night the larvae were alert and would turn toward moving prey or stalk it for a few cm. They did not seem to recognize motionless prey. If a roach crawled on the abdomen of a larva, the larva vibrated the abdomen from side to side, which sometimes caused the prey to run over the head of the larva where it could be caught. Small larvae kept with large ones were not cannibalized. The larvae do not swim, a behavior which may help to prevent their being swept out of their habitat during heavy rainstorms.

Adult emergence. — A larva in captivity began transformation at 1116 on 29 March 1978, and 3 larvae were found in transformation in the wild on 1 April at about 0900. Unfortunately the entire emergence sequence was not observed. Transformation occurs on vertical stems of any size from herb stems to tree trunks, and the emergence is similar to that in the Gomphidae and in *Tanypteryx pryeri* (EDA, 1959). The emerging adult supports itself upright on the abdomen with the legs held close to the thorax. The wings expand and become smooth first at the base, then progressively toward the tip. This contrasts with the Aeshnidae in which the wings expand and smooth out at the same rate from base to tip. The wings of teneral *Tachopteryx thoreyi* are tinted pink.

Thirteen exuviae, 8 males and 5 females, were found 0.2-1.4 m, $\overline{X} = 0.6$ m, above ground. None were more than 1.0 m horizontally from seeps or trickles of water. Exuviae are thin and fragile, and would easily be dislodged by rain. They were found over a 23 day period from 25 March - 16 April 1978, with the peak number on 1 April.

ADULTS

The 1978 flight season began with the finding of an exuviae by F. Carle on 25 March, and the first adults were marked on 1 April. Figure 2, curves A and B, shows that the population rapidly rose to a peak about 10-20 April and slowly declined until the last adult was seen 28 May. The 1978 adult season was late in Gainesville, following an exceptionally long and cold winter. The flight season in previous years began as early as 8 March (K. Knopf, pers. comm.). As many adults as possible were individually marked with a 1 or 2 digit number-letter combination written on the underside of the right hindwing of males and the left hindwing of females. Marks were placed on the hindwing instead of the forewing so that the marks would be more out of a marked individual's field of vision during flight. Marking was done with black India ink, black permanent felt-tip pens, and green permanent felt-tip pens. All of these worked equally well, with no evidence that any of the marks wore off, caused mortality, or caused behavioral changes. Females marked with either green or black and released near males were immediately taken in tandem. Unfortunately all such pairs were lost to view in the forest. Perched adults were usually caught in mid-air after touching them at the tip of the abdomen with the net rim to make them fly. Using this technique, none were

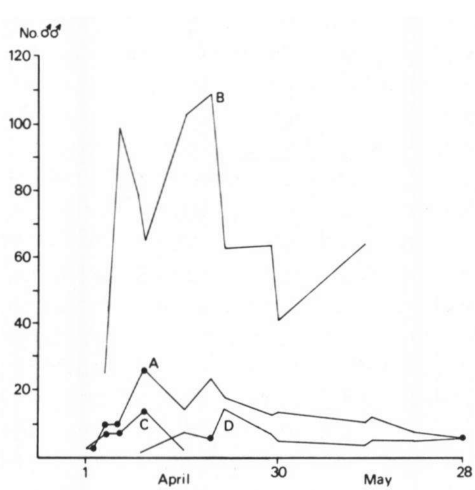

Fig. 2. Number of adult male *Tachopteryx thoreyi* present per day, Gainesville, Florida, 1978. Enlarged points indicate $1/2$ day counts x 2. A: Marked males, both newly marked and sightings of previously marked individuals, — B: Estimated male population, — C: Fresh males caught (brown eyes, soft abdomen), — D: Mature males caught (grey eyes, hard abdomen).

significantly damaged by capture.

Tachopteryx thoreyi adults when away from seepage areas usually perch on sunny tree trunks, sometimes shady tree trunks, occasionally horizontal logs, and rarely weed stems or the ground. The estimated height at which 92 individuals perched on tree trunks was 0.3-5.0 m, $\overline{X} = 1.7$ m. No preference for any particular color or texture of bark was apparent, for the same individual would perch successively on any combination of smooth pale trunks or rough dark barked trees. Perching in the shade was probably done to lower body temperature. On cooler days, when a cloud covered the sun, some males perched near seeps wing-whirred to raise body temperature.

In addition to chance encounters, males had two other methods of finding females. For the first, they investigated a linear sequence of tree trunks, flying up the sunny side of each while facing the trunk several cm from the bark, and gliding downward to the next trunk. They usually flew toward the sunny side of the trunks, and it is interesting to speculate whether the male population drifts west in the morning and east in the afternoon or what would happen if a series of afternoons were cloudy. However, some males flew toward the sun, and in this case had to turn away from the sun while flying up each tree trunk. Since such males continued flying a linear path after repeatedly about-facing, the implication is that they remembered which direction they were flying. I believe such tree trunk searching was for females rather than prey because no prey was seen to be flushed from tree trunks, the behavior appeared when most individuals were mature, and a female was seen to be captured by this method.

Males also waited for mates in the seeps from about 1000-1600. Here they perched in sunspots near the water on anything available but usually something substantial such as vines, saplings, or palmetto fronds. The number of males present in the seeps appeared to be related to vegetation density. The density of the forest canopy determined how many sunspots were present, and the density of the understory determined how far the insects could see each other. Thus the most male *T. thoreyi* were present when the canopy was sparse but the understory dense. Any *T. thoreyi* that came in sight, usually a matter of several m, was vigorously chased, and thus only one male occupied a "territory". There was no day-to-day territorial fidelity. None of 22 marked males engaged in this behavior was seen at the seeps again, though 6 were seen later elsewhere. Unlike many other Anisoptera, *T. thoreyi* males freely caught prey while in their reproductive territories.

Mating and oviposition of *T. thoreyi* are rarely seen. I saw only a few mated pairs and these were lost to view in the forest shade or canopy. J. Daigle (pers. comm.) saw a male fly down from a tree trunk to pick a female off the ground. The pair in tandem but not in copulation was still perched high on a horizontal tree branch when he left after a few minutes. Of two females I saw ovipositing, one was on a low nearly dry vertical surface in a seep at 1355, the other also in the afternoon flat on the ground at the edge of a seep.

T. thoreyi adults tend to take larger prey than most Anisoptera. Prey taken included 12 butterflies, 7 moths, 10 odonates, 1 beetle, and numerous small insects that were rapidly swallowed. The butterflies comprised 7 little Wood Satyrs *Euptychia cymela* Cramer, 1 Tiger Swallowtail *Papilio glaucus* L., 1 Black Swallowtail *P. polyxenes* Fab., 1 Red Spotted Purple *Limenitis astyanax* Fab., 1 Question Mark *Polygonia interrogationis* Fab., and 1 Red Admiral *Vanessa atalanta* L. Among the moths were a Forester *Alypia wittfeldi* Henry Edwards, and a Polyphemus *Telea polyphemus* Cramer. Odonate prey was generally teneral and was 8 *Calopteryx maculata* (P. de Beauvois), 1 *Gomphaeschna antilope* (Hagen), and 1 *Gomphus minutus* Rambur. One cerambycid beetle was eaten but a lycid beetle was rejected after its capture. When attacking prey, *T. thoreyi* commonly flits toward it with wings and abdomen raised, then makes a quick short dash of less than 1 m to secure it. The abdomen is also usually raised while prey is being eaten. Many prospective prey escaped by diving into cover; others including some butterflies, *Pachydiplax longipennis* (Burm.), and *Libellula vibrans* Fab. outflew the predator.

A total of 105 males and 27 females were individually marked and released. In addition, 23 males and 18 females were taken by human collectors and the wings of 1 teneral female were found in a seep. Thus the population contained a minimum of 128 males and 46 females. Assuming an actual sex ratio of 1:1, the population at the study site was about 256, 3-4x more than my subjective estimates made in previous years without marking data. M.J. Parr and G.M. Jolly very kindly co-operated to analyze my capture/resighting data. They found that an assumption of constant probability of capture was justified and assumed that survival was variable. Their population estimates for males are graphed in Figure 2; too little data were available on females for a population estimate to be made. The largest daily population estimate for males of 110 occurred on 20 April, with a standard error of 26.

I subjectively classified the adults I caught as fresh, juvenile, or mature. Fresh adults had brown eyes and an abdomen that felt soft with gentle finger pressure. Mature adults had grey eyes and the abdomen felt hard. Juvenile adults were older than fresh ones but younger than mature. The peak number of mature males was caught 13 days after the peak number of fresh males (Fig. 2, curves C and D); the same interval for females was 14 days. The first mature male was caught 16 days after the first exuviae was found. The first mature males were seen waiting for females at the seeps 23 days after first emergence and a pair was seen in copulation on the same date. Thus *T. thoreyi* adults look mature in 2 weeks and are definitely sexually mature at an age of 3 weeks.

Only 11% (3/27) of the females were seen 1 or more days after marking; the range of intervals was 4-17 days. Of males, 31% (32/105) were seen 1-36 days, $\overline{X} = 14.2$, after marking. One male, classified as mature when marked, survived for at least 35 more days and was probably 7 weeks old when last seen.

The 3 females seen 1 or more days after marking had moved at least 0.08-0.53 km. The 32 comparable males moved 0-1.1 km; i.e. they were seen again where they were marked or moved as far as the full breadth of the area I explored. But these results do not mean that the females traveled less than the males. On the contrary, the females probably scattered even further because so few marked or mature females were seen. The average distance traveled by males between sightings was 0.28 km. For the 17 males seen more than once on the same day, 13 stayed near one place, 3 moved about 0.1 km, and 1 moved 0.96 km. Great mobility is also indicated by the fact that after walking a path for several hundred meters and then retracing the same path, nearly always a different set of individuals would be seen on the return trip.

DISCUSSION

COMPARISON WITH PREVIOUS STUDIES

A few notes on the behavior and ecology of *Tachopteryx thoreyi* have appeared, most of which are consistent with my observations, such as WILLIAMSON (1900, 1901), and FISHER (1940). BYERS (1930) reported on the habits of *T. thoreyi* in the same area where this study was conducted, but some of my conclusions differ from his. He states that *T. thoreyi* was wary and ".... fly with a darting motion for long intervals without rest". I found the species to be generally unwary, even occasionally perching on people. They usually flew only a short distance before perching, and the flight style was smooth, not darting. BYERS (1930) went on to say that "*Tachopteryx* has a peculiar affinity for light colored objects. They will almost invariably settle on trees with the lighter shades of bark". He probably got this impression because most of the tree trunks in some areas of Gainesville have smooth pale grey bark, on which *T. thoreyi* can be more easily seen than when they are perched on rough dark bark. WILLIAMSON (1932) states that he saw a female *T. thoreyi* in Missouri oviposit ".... in the creek ...." He also describes a larva walking with the ".... tarsi turned back almost parallel to the tibiae. When disturbed it threw its abdomen around in stinging motions". Florida *T. thoreyi* displayed none of these traits.

ECOLOGICAL RELATIONSHIP WITH *CORDULEGASTER*

Tachopteryx thoreyi is apparently not in keen competition with any other species of animal at Gainesville with the possible exception of *Cordulegaster sayi* Selys in the larval stage. A few small *C. sayi* larvae were mixed with the *T. thoreyi* larvae in the seeps, but most of the former were further down the seep gradient where the water was deeper, the current greater, and there were less leaves and more silt. Since larvae of the genus *Cordulegaster* are adapted morphologically and behaviorly to submerge themselves in silt, we may envision *C. sayi* evolving to live in seepage trickles to the upper limit of silt deposits. Meanwhile *T. thoreyi* was evolving to live among broad wet leaves at the uphill edge of seeps where the water currents seldom wash leaves away. The flight seasons of *T. thoreyi* and *C. sayi* are almost perfectly juxtaposed. *C. sayi* males end their sexual patrols in the seeps just as male *T. thoreyi* appear at the seeps. On the only occasion when I saw a male of each species close together in the seeps, they ignored each other. These species do not compete in the sexual maturation phase either, for *C. sayi* begins emergence earlier, matures in open fields, and feeds primarily on small Hymenoptera. The present geographical range of *C. sayi* is far more restricted than for *T. thoreyi*. Preliminary observations in northern Georgia indicate that *Cordulegaster diastatops* (Selys) has nearly the same relationship to *T. thoreyi* there as *C. sayi* does in Florida.

EVOLUTION

From the fact that all odonate larvae have a well developed tracheal system we may deduce that the ancestors of Odonata had terrestrial larvae. I visualize that the early odonate larvae were rather thin-skinned, not resistant to dessication, and thus lived in moist or wet places on land. The Anisoptera line evolved an enlarged rectum as a way to absorb additional oxygen from the air through the moist membrane of the hindgut. This rectal chamber could also be used to absorb oxygen underwater, and became more efficient tracheal gills for this purpose with the development of an increased surface area through folding. Perhaps because the early Anisoptera were not well chitinized but were also relatively large, they could compete with other animals best with the support of a liquid medium. The rectal chamber could double as a means of jet propulsion with stronger muscles when a larva was underwater. Thus Anisoptera larvae were able to radiate into many aquatic ecological niches, leaving only a few relict species existing in a semi-terrestrial mode, the latter primarily being the Petaluridae. A few species of other families have secondarily become somewhat terrestrial, such as the aeshnid *Antipodophlebia asthenes* (Till.) (WATSON & THEISCHINGER, 1980).

Tachopteryx thoreyi according to the scheme above has an early Anisoptera larval ecology. But this species also exhibits numerous specializations in both larva and adult. The larvae are leaf-mimics, with a flattened, widened abdomen and well developed lateral abdominal spines. The dorsum of the head and thorax is flat with sharp lateral carinae. Thus the head and thorax can fit closely against a leaf above, forcing prey to go around the larva instead of over it, possibly half the time to within reach of the labium. The thick muscular antennae can be raised in air simultaneously with the labium strike. The legs are strong and allow the larvae to easily walk in air. Second instar larvae are strong enough to crawl under a water surface-tension film which immobilizes most other second instar Anisoptera. The epiproct is truncate and fits together with the paraprocts to form a dorsal respiratory opening. By this means a larva can breathe above water without having to use muscles to separate the anal appendages against water surface tension. The dorsal position of the opening helps to avoid silt intake. GREENE (1977) reported that large larvae of *Uropetala carovei* absorbed O_2 in air relatively much better than small larvae. If this applies also to *Tachopteryx thoreyi*, larger larvae could stay out of water for longer periods of time than small larvae.

The larvae of all the known living petalurids have been described except for *Petalura ingentissima* Till. and *P. pulcherrima* Till. Most of these construct burrows and exhibit some different specializations from *T. thoreyi*. These specializations include better developed digging spines on the tibiae, a sub-cylindrical abdomen, and reduced or absent lateral abdominal spines. The morphology of *Phenes raptor* Rambur is intermediate between *T. thoreyi* and the burrowing species. Probably *P. raptor* is not a burrower, since SVIHLA (1960) found a larva on the wet soil of a hillside seep.

Just as the leaf-like form of the larva suggests a long historical association with broad-leaved deciduous forest, certain adult adjustments of *T. thoreyi* can be seen as adaptations to a deciduous forest habitat. The flight season begins before the trees have fully leafed out, thus more sunny tree trunks are available as perches. Males can find more sunspots in which to wait at the seeps, and are better able to see arriving females. Females can more easily find the seeps for oviposition. Perching on tree trunks may be an adaptation for a cool weather flight season, since other Anisoptera which do not usually perch on tree trunks bask thereon during cool days. In addition, both thermoregulatory ability and the male tree trunk searching behavior must have taken considerable time to evolve.

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