Elephant mosquito *Toxorhynchites rutilus* Coquillett, 1896 (Insecta: Diptera: Culicidae)¹

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Introduction

Toxorhynchites rutilus is one of the largest known species of mosquitoes in North America. Larvae of Toxorhynchites are aquatic predators and prey upon aquatic invertebrates with preference under some circumstances for larvae of other mosquitoes, a characteristic that can contribute to the use of Toxorhynchites mosquitoes as potential biological controls against container-inhabiting mosquitoes (Focks 2007). Larvae of *Toxorhynchites* can develop in natural containers (e.g., tree holes, plant leaf bases, bamboo, broken stems and internodes) and in artificial man-made containers (e.g., cans, flowerpot saucers, planters, and discarded tires) (Steffan and Evenhuis 1981). Adult females of Toxorhynchites are autogenous and feed only on carbohydrate-rich sources (e.g., nectar, honeydew, and fruit), but not blood which makes them harmless in terms of serving as a vector of pathogens to humans and animals.

Distribution

Toxorhynchites rutilus has a wide geographical distribution in the eastern half of the United States. There are two subspecies, *Toxorhynchites rutilus rutilus* and *Toxorhynchites rutilus septentrionalis*, where the latter has a wider geographic range (Burkett-Cadena 2013) (Figure 1).



Figure 1. The geographical distribution of *Toxorhynchites rutilus* in the United States. Map is redrawn after Burkett-Cadena 2013. Credits: Abdullah A. Alomar, UF/IFAS

Synonymy

Megarhinus rutilus Coquillett 1896

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Description

Adult

The adults of Toxorhynchites are larger than most other mosquito species (Wilkerson et al. 2021) (Figure 2). The adult body consists of three parts, head (antennae, eyes, proboscis, and palps), thorax (wings and legs), and abdomen (genitalia). The adult proboscis is very long and distinctively downward curved at a 90-degree angle or more (Figure 3). The subspecies can be distinguished based on morphological differences among adult males. Male of *Toxorhynchites rutilus rutilus* has a pale band on the foreleg tarsus, whereas male of Toxorhynchites rutilus septentrionalis has entirely dark scaled tarsi of the forelegs (Burkett-Cadena 2013). The thorax and the entire body are covered dorsally with iridescent scales of various colors, including blue, white, green, and purple (Burkett-Cadena 2013). The scutellum is evenly rounded and has no setae (Wilkerson et al. 2021).



Figure 2. Adult female of *Toxorhynchites rutilusrutilus*. Credits: Nathan D. Burkett-Cadena, UF/IFAS



Figure 3. Proboscis of adult female of *Toxorhynchites rutilus*. Arrow indicates the proboscis exhibiting a downward bend. Credits: Abdullah A. Alomar, UF/IFAS

Egg

Toxorhynchites eggs are creamy white in color, oval in shape (similar to a rugby ball, an elongated ellipsoidal shape), and covered with papilliform ornamentation (Figure 4). Females deposit their eggs individually on the surface of water while in flight (hovering). The surface of the eggs is covered entirely with outer chorionic tubercles, except a small area around the micropyle (Linley 1989). The eggs are hydrophobic which allows them to float horizontally and high on top of the water surface until the emergence of first instar larvae (Steffan and Evenhuis 1981). The hydrophobic surface of the egg enables freedom of movement upon disturbance, which may be an adaptation in response to predation. The incubation period of *Toxorhynchites* eggs ranges from 40 to 60 hours and it is dependent on the temperature (Collins and Blackwell 2000). Since the eggs are not resistant to desiccation, they must remain in contact with water to remain viable (Steffan and Evenhuis 1981).



Figure 4. Eggs of *Toxorhynchites rutilus*. Credits: Abdullah A. Alomar, UF/IFAS

Larva

Larvae of *Toxorhynchites* are larger in size and darker in color than most other mosquito species (Figure 5 and 6). While the dorsal view of the body is dark red, the ventral view of the body is pale grayish white (Burkett-Cadena 2013). The head of larvae are square and contain a pair of compound eyes, mouthparts, and antennae. *Toxorhynchites* larvae are predators and prey upon other aquatic animals, including other mosquito larvae. The heavily chitinized mouthparts of *Toxorhynchites* larvae have comb-like mandibles which are used to grasp and consume aquatic prey. The antennae are shorter than the length of head. The thorax contains many stout spines (Burkett-Cadena 2013).

The abdomen has eight apparent segments. Comb scales are absent. The siphon is short and stout with no pecten (Burkett-Cadena 2013). The anal papillae are extremely short.



Figure 5. Larva of *Toxorhynchites rutilus*. Credits: Nathan D. Burkett-Cadena, UF/IFAS



Figure 6. The size of aquatic larval stage (fourth instar) of *Toxorhynchites rutilus* compared with a U.S. penny. Photo was taken out of water for size comparison. Credits: Abdullah A. Alomar, UF/IFAS

Pupa

Toxorhynchites pupae have a comma-like shape, which is larger than most other mosquito pupae (Figure 7). The body of the pupa consists of head and thorax, which are fused in a cephalothorax, and abdomen. The pupa is a non-feeding, developmental stage. The cephalothorax has a pair of respiratory trumpets located on its dorsal surface, where these trumpets are used to obtain oxygen directly from the air. The abdomen has eight segments with a pair of paddles at the abdomen apex, using for swimming. Newly pupated individuals are light brown and become dark brown to black before adult emergence. The development of pupal stage lasts from 3 to 7 days, but others have observed development times as long as 23 days (Steffan and Evenhuis 1981).



Figure 7. Pupa of *Toxorhynchites rutilus*. Credits: Nathan D. Burkett-Cadena, UF/IFAS

Life History

Toxorhynchites undergoes complete metamorphosis (egg, larva, pupa, and adult). Unlike many mosquito species, Toxorhynchites have been observed to have a unique oviposition behavior, where gravid female exhibit counterclockwise flying for a series of ellipses above the oviposition containers prior to eject an egg during the last ellipse of downward flight (Linley 1987). This aerial mode of oviposition behavior provides females of Toxorhynchites with several advantages, including the ability to deposit their eggs in containers with limited access (e.g., small or obstructed opening) as well as reducing the possibility of females to be captured by predators that are commonly found around mosquito habitats (e.g., spiders) (Steffan and Evenhuis 1981). A female may distribute eggs over several container habitats. The continuous production of mature follicles allows females to continue laying eggs over many days (1.0-3.2 eggs per day with 58.5 eggs total during the adult lifespan, Focks et al. 1977, Focks and Boston 1979). Common oviposition sites include artificial (e.g., flowerpots, discarded tires, earthen pots, and barrels) and natural (e.g., tree hole and hollow internodes of bamboo) container habitats (Steffan and Evenhuis 1981). All larval instars are

predaceous on aquatic animals, generally of their same size or smaller (Steffan 2007). A single larva may consume thousands of prey items during its development (Steffan and Evenhuis 1981, Focks 2007). The predatory behavior is considered opportunistic (ambush predator), and larvae rely on mechanoreceptors to detect prey movement passing by (Sato 1961).

Cannibalism among Toxorhynchites larvae is not uncommon, especially when alternative prey are unavailable, which depends on prey availability and the size of prey relative to larvae of Toxorhynchites (Steffan and Evenhuis 1981). Fourth instar larvae of Toxorhynchites exhibit prepupal compulsive killing behavior, where the larvae kill the prey without consumption (Lounibos 1979, Steffan and Evenhuis 1981). It is likely that prepupal killing evolved in response to the vulnerability of the pupal stage to mortality from predators, including other Toxorhynchites larvae (Collins and Blackwell 2000). The development time of Toxorhynchites larvae are dependent on several factors, such as prey density, prey size, container size, and water temperature (Lounibos 1979, Collins and Blackwell 2000). Density of prey, a measure of availability of nutrition, can strongly affect the development time of *Toxorhynchites* larvae (i.e., increased number of prey consumed daily accelerates development). At the end of last instar of larvae (fourth instar), larvae can molt to pupae and these pupae remain on the water surface for about 3-7 days, after which adults emerge from pupal case. Adults of Toxorhynchites are active during the daytime (Wilkerson et al. 2021). Both males and females of Toxorhynchites feed on nectar and other plant exudates with no need for blood. The females of Toxorhynchites are autogenous and obtain all nutritional requirements for egg development in adulthood from the consumption of prey during larval stages (Focks 2007).

Photoperiodic control of fourth instar diapause

Throughout its range, short daylengths experienced by early instar larvae of this species lead to diapause in the fourth instar (Bradshaw and Holzapfel 1975, Trimble and Smith 1979). Some *Toxorhynchites rutilus* from south Florida also diapause, which condition leads to reduced prey consumption rates (Lounibos et al. 1998). The composite index of performance (r') for diapausing cohorts was $\frac{1}{2}$ to 2/3 that of non-diapausers (Lounibos et al. 1998).

Top predator in Florida treehole community

Bradshaw and Holzapfel (1983) concluded from a yearlong study of natural treeholes in northern Florida that predation by *Toxorhynchites rutilus* reduced abundances of culicid prey and thereby minimized larval competition among mosquito prey. The same authors also concluded that *Toxorhynchites rutilus* larvae preferentially occupied drought-resistant treeholes with a subcommunity that included predator-resistant mosquito prey, such as *Orthopodomyia signifera* (Bradshaw and Holzapfel 1988).

Natural prey of *Toxorhynchites rutilus* larvae in south Florida treeholes and tires

Campos and Lounibos (2000a) dissected wild-caught larvae of *Toxorhynchites rutilus* to determine prey types ingested from exoskeletal remains in midguts. Twenty taxa of aquatic prey were recognized, as well as remains of terrestrial arthropods of nine insect orders and mites. Mosquitoes accounted for only 6% of prey items from treeholes and 5% from tires. Prey choice was estimated, and it was high for *Aedes albopictus* but low for *Orthopodomyia signifera* and *Toxorhynchites rutilus*.

Life tables of *Toxorhynchites rutilus* aquatic stages in south Florida treeholes and tires

A companion paper by Campos and Lounibos (2000b) examined stage-specific survivorships of *Toxorhynchites rutilus* calculated from repeated censuses of treeholes and water-holding tires at the Florida Medical Entomology Laboratory. Survivorship from egg to adult ranged from 1.8-5.6% and varied significantly between seasons and container types. Cannibalism was imputed to be a factor influencing high mortalities in the egg and fourth instar larval stages.

Long term dynamics of *Toxorhynchites rutilus* and prey reduction in south Florida treeholes

The aquatic contents of ten treeholes were censused fortnightly between 1978-93 to examine the population dynamics of aquatic culicid occupants (Lounibos et al. 1997). Time series analyses showed that the presence of *Toxorhynchites rutilus* fourth instar larvae significantly reduced the abundance of late-stage larvae of eastern treehole mosquito *Aedes triseriatus*, with pupae of this prey species depleted relatively more than fourth instar larvae. Overall, this predator-prey pair was temporally decoupled, and *Toxorhynchites rutilus* disappeared from censuses during a 30-month drought.

Use in Biological Control

Adults of Toxorhynchites do not consume blood and so they are incapable of transmitting pathogens to humans or animals by bite. The larvae of Toxorhynchites are voracious predators and have ability to consume thousands of larvae of mosquito vectors. Additionally, late instar larvae of Toxorhynchites show prepupal compulsive killing behavior against prey larvae. Toxorhynchites larvaehave ability to resist starvation and survive weeks without prey, especially at late instars (Focks 2007). Adults of Toxorhynchites has ability to locate cryptic domestic and natural container habitats for oviposition. Rearing and maintenance of Toxorhynchites under laboratory conditions are possible. These aforementioned unique characteristics led many scientists to suggest that Toxorhynchites has potential to be utilized as an alternative mosquito control method against container-inhabiting mosquito vectors of pathogens. For instance, Toxorhynchites rutilus larvae were used for the biological control of container mosquito pests in New Orleans (Focks et al. 1983), until New Orleans Mosquito Control settled on deployment of a tropical predator species (Toxorhynchites amboinensis), which yielded better coverage of both natural and artificial containers (Focks and Sackett 1985). Although the use of Toxorhynchites alone to eradicate mosquito vector populations has limited success, incorporating Toxorhynchites with other integrated mosquito control tools (e.g., insecticidal agents) may enhance the outcomes of control against the populations of mosquito vectors (Collins and Blackwell 2000, Alomar et al. 2020, Alomar and Alto 2021, 2022).

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