

EGG CANNIBALISM AND CARNIVORY AMONG THREE SPECIES OF *TOXORHYNCHITES*

J. R. LINLEY AND D. DUZAK

Florida Medical Entomology Laboratory, Institute of Food and Agricultural Sciences, University of Florida, Vero Beach, FL 32962

ABSTRACT. In laboratory experiments, third and early fourth instar larvae of *Toxorhynchites amboinensis*, *Tx. splendens* and *Tx. brevipalpis*, previously starved 24 h, rapidly cannibalized eggs of their own species, or ate the eggs of other species present on the water surface in small containers. *Toxorhynchites amboinensis* and *Tx. splendens* larvae of either instar cannibalized eggs somewhat more rapidly than *Tx. brevipalpis*, probably because *brevipalpis* eggs distributed themselves around the edge of the container and were less accessible. When offered heterospecific eggs, fourth instar larvae of all three species ate them as efficiently as they cannibalized their own except that eggs of *Tx. brevipalpis* were eaten very slowly. *Toxorhynchites amboinensis* larvae were offered conspecific hatched eggs, and these also were consumed.

INTRODUCTION

In a recent study (Linley 1988) of oviposition behavior in *Toxorhynchites amboinensis* (Doleschall), it was observed that when females laid their eggs on water containing 20 third or fourth instar larvae previously starved 24 h, large numbers of eggs were cannibalized. Although this was apparently the first published report of egg cannibalism in *Toxorhynchites*, egg carnivory had been reported previously (Kazana et al. 1983). It has been known for many years (see Steffan and Evenhuis 1981) that the larvae are mutually cannibalistic, probably in all instars (Furumizo and Rudnick 1978, Steffan et al. 1980). The extent to which cannibalism among larvae may regulate populations in nature is not known, but the behavior certainly occurs in natural habitats (Trpis 1973, Kazana et al. 1983). Similarly, if egg cannibalism is widespread and occurs naturally, then it also may play a role in regulating larval populations. This is not only of intrinsic interest, but it is also of practical importance in view of the biological control applications of *Toxorhynchites* (Gerberg 1985).

In experiments reported here, we have tested whether egg cannibalism is exhibited also by *Toxorhynchites splendens* (Wied.) and *Tx. brevipalpis* Theobald. Experiments were also done with *Toxorhynchites amboinensis* for purposes of comparison, as the methods in earlier experiments (Linley 1988) differed from those used here. Additional experiments tested whether larvae of the three species would eat each other's eggs and, in the case of *Tx. amboinensis*, whether fourth instar larvae would eat conspecific hatched eggs.

MATERIALS AND METHODS

Larvae and eggs were obtained from laboratory colonies maintained at 27°C under LD

12:12. Larvae were reared throughout development in the presence of an excess of *Aedes aegypti* (Linn.) prey of the same instar. Adults emerged in cages 38 × 50 × 65 cm in which mating took place and eggs were obtained as needed by allowing the females to oviposit in black, plastic pots 9 cm diam × 7 cm deep containing tap water.

All experiments were done in a laboratory maintained at 27.0 ± 2.0°C under approximately 500 ft-candles illumination. Each experiment consisted of 10 replicates, each of one third or fourth instar larva, starved 24 h, then allowed access to 20 unhatched eggs (with one exception, see below) of either their own or one of the other species, for 6 hours. Only fourth instar larvae were tested with heterospecific eggs. One control pot, containing 20 eggs, but no larva, was set up for each experiment. Second instar larvae were not tested because, in earlier experiments with *Tx. amboinensis* (Linley 1988), they showed no significant ability to cannibalize eggs. Fourth instar larvae were taken in the first 2 days of the instar to ensure that none had yet reached the period of compulsive killing (prey killed but not eaten) that precedes pupation (Trpis 1972, Furumizo and Rudnick 1978, Padgett and Focks 1980).

During the 24-h period of starvation, larvae were confined individually in tap water in wells (3.5 cm diam, 1 cm deep). Experiments were done in small, black plastic pots 4 cm diam × 3 cm deep, filled with tap water to a depth of about 2.5 cm. At the beginning of each experiment, a larva was placed in each of the 10 pots, which already contained 20 eggs of the selected species on the water surface. The numbers of eggs remaining (uneaten) were then counted every 0.5 h for 6 hours. In one experiment, fourth instar *Tx. amboinensis* larvae were tested with hatched eggs. These consisted mainly of entire individual eggs, but also of some large fragments,

since hatched eggs are joined only by a thin strip of chorion, which breaks easily when manipulated.

To facilitate statistical comparison of the rates at which eggs were consumed, the data (e.g. for *Tx. splendens*, Fig. 2) were rectified to linear by log (n + 1) transformation of the time axis (Fig. 1) and tests run for differences between the regression coefficients.

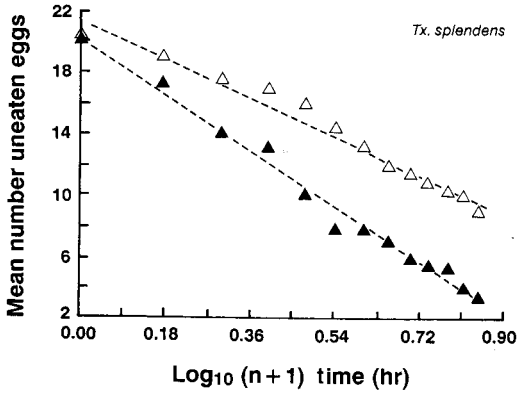


Fig. 1. Transformed data (from Fig. 2) for egg cannibalism by third (open symbols) and fourth (closed symbols) instar *Toxorhynchites splendens* larvae.

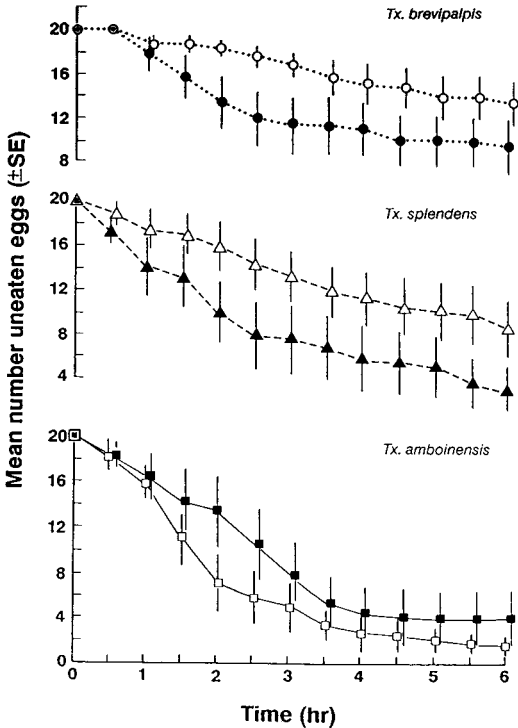


Fig. 2. Egg cannibalism by single third (open symbols) and fourth (closed symbols) instar *Toxorhynchites brevipalpis*, *Tx. splendens* and *Tx. amboinensis* larvae previously starved 24 h.

RESULTS

Controls: Twenty eggs were invariably present on the controls after 6 h; consequently, no further reference is made to control pots.

Egg cannibalism: Starved third and fourth instar larvae of *Tx. amboinensis*, *Tx. splendens* and *Tx. brevipalpis* rapidly cannibalized their eggs (Fig. 2). There was no significant difference in consumption rate between instars in *Tx. amboinensis*, but fourth instars ate the eggs more rapidly in the case of *Tx. splendens* ($P < 0.001$) and *Tx. brevipalpis* ($P < 0.001$). Both instars of *Tx. brevipalpis* consumed conspecific eggs more slowly than either of the other two species ($P < 0.001$ in all instars).

Consumption of heterospecific eggs: Fourth instar *Tx. brevipalpis* larvae ate eggs of *Tx. amboinensis* significantly more rapidly ($P < 0.001$) than eggs of their own species (Fig. 3 cf. Fig. 2), but at about the same rate as *Tx. splendens* larvae ate *Tx. amboinensis* eggs (Fig. 3). Fourth instar larvae of *Tx. amboinensis* consumed *Tx.*

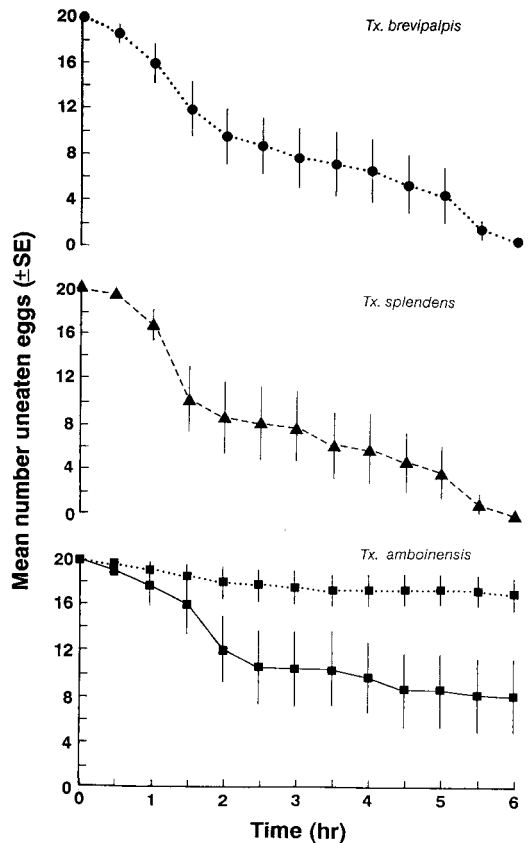


Fig. 3. Consumption of heterospecific eggs by single fourth instar *Toxorhynchites brevipalpis* (eating *amboinensis* eggs), *Tx. splendens* (eating *amboinensis* eggs) and *Tx. amboinensis* (eating *brevipalpis* eggs) (dotted line) and *splendens* eggs (continuous line) larvae previously starved 24 h.

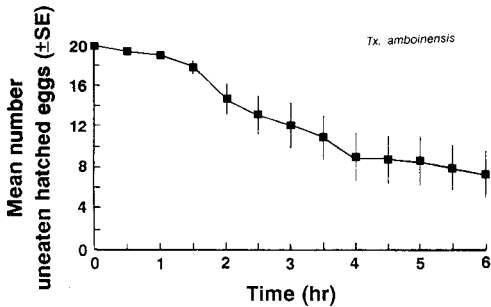


Fig. 4. Consumption of hatched conspecific eggs by single fourth instar *Toxorhynchites amboinensis* larvae previously starved 24 h.

splendens and *Tx. brevipalpis* eggs more slowly ($P < 0.001$ in both instances) than these species had eaten *Tx. amboinensis* eggs. When *Tx. brevipalpis* eggs were the prey, *Tx. amboinensis* larvae found and ate them much more slowly ($P < 0.001$) than *Tx. splendens* eggs (Fig. 3).

Cannibalism of hatched eggs: When 20 hatched *Tx. amboinensis* eggs were placed on water containing conspecific fourth instar larvae, they were eaten somewhat more slowly ($P < 0.02$) than unhatched eggs (Fig. 4), but quite rapidly nonetheless. There may have been some error in these counts inasmuch as it was not always possible to determine whether larvae ate the entire hatched egg, or whether it sometimes separated into one or more additional pieces. Small fragments intermittently appeared on the surface, suggesting that some breakage had taken place. Effectively, this added egg material to the surface and slowed the apparent rate of consumption. To minimize error, however, we did not count very small pieces obviously outside the size range of those initially introduced.

DISCUSSION

Our main objective in these experiments was to determine whether egg cannibalism, as previously noted in *Tx. amboinensis* (Linley 1988), also occurred in other species. The results indicate that hungry third and fourth instar larvae of both *Tx. splendens* and *Tx. brevipalpis* also will eat eggs laid by females of their own species. All three species show a propensity for egg cannibalism and can detect, seize and ingest eggs floating on the water surface.

Among the three species, *Tx. brevipalpis* appeared to be least efficiently cannibalistic. In both instars it disposed of its own eggs at a significantly slower rate than the other two species. This difference was, however, almost certainly caused more by the distribution of *brevipalpis* eggs on the water surface than by differences in behavior. Most eggs of *brevipalpis*

quickly accumulated in the meniscus around the edge of the dish, whereas *amboinensis* and *splendens* eggs invariably floated away from the edges, usually in one or two adherent clumps. Larvae of all three species tended to remain away from the edges. Thus, in the case of *brevipalpis*, larvae simply may not have had comparable access to the eggs. It is noteworthy that when fourth instar *brevipalpis* larvae had access to *amboinensis* eggs, they consumed them far more efficiently (Fig. 3). It should be mentioned also, that every 0.5 h the clumped *amboinensis* and *splendens* eggs were separated to facilitate counting, but they regrouped into clumps almost immediately.

The behavior that enables larvae to find floating eggs merits further study. Larvae were often seen with their bodies parallel to the water surface, with heads and mouthparts touching or very close to the interface. We noticed on a number of occasions that contact by groups of eggs on a larva's siphon would often cause the animal to investigate the contact with its head. Since the pot interiors were black, the behavior at detection and seizure of an egg could not be seen clearly, but disappearance of an egg was instantaneous, suggesting that larvae seize eggs with the same extremely rapid head and mandibular action that accompanies capture of other prey (Breland 1949, Furumizo and Rudnick 1978). Eggs of *amboinensis* and *splendens*, being extremely hydrofuge, float very high on the surface, and presumably can be seized only if the mouthparts are used to strike sharply upwards, with the head inclined.

The experiments described here were done under highly artificial conditions that are undoubtedly at variance with conditions likely to occur in nature. Single larvae might often be found in a natural container and, in the case of some species, for example *Tx. haemorrhoidalis* (Fabricius) occurring in bracts of *Heliconia caribaea* (Lounibos et al. 1987), in one of dimensions similar to those used here. Even though the presence of 20 eggs simultaneously on the surface in such a limited habitat seems improbable, the rate at which eggs are eaten experimentally suggests that egg cannibalism may occur in nature. According to Trpis (1972) and Furumizo and Rudnick (1978), respectively, the egg stage of *Tx. brevipalpis* lasts about 44 h (at 25.0°C) and that of *Tx. splendens* 48–60 h (at 26.5°C). Single fourth instar *splendens* and *brevipalpis* larvae, respectively, ate about 17 and 11 of the initial 20 eggs in 6 h, and *Tx. amboinensis* had eaten about 16 in this time. It is probable, therefore, that some eggs would be eaten in over 40 h, even if egg and larval densities were much lower. The rate of cannibalism would presumably be affected by egg density and also by the amount of other prey present.

ACKNOWLEDGMENTS

This paper is Institute of Food and Agricultural Sciences, University of Florida Experiment Stations Journal Series No. 8985.

REFERENCES CITED

- Breland, O. P. 1949. The biology and the immature stages of the mosquito *Megarhinus septentrionalis* Dyar and Knab. *Ann. Entomol. Soc. Am.* 42:38-47.
- Furumizo, R. T. and A. Rudnick. 1978. Laboratory studies of *Toxorhynchites splendens* (Diptera: Culicidae): biological observations. *Ann. Entomol. Soc. Am.* 71:670-673.
- Gerberg, E. J. 1985. Sequential biocontrol application in the use of *Toxorhynchites* spp. pp. 33-46. In: M. Laird and J. W. Miles (eds.), *Integrated mosquito control methodologies*, Vol. 2, New York: Academic Press.
- Kazana, M., C. E. Machado-Allison and L. A. Bulla. 1983. Preferencias alimentarias de *Toxorhynchites theobaldi* (Diptera: Culicidae). *Acta Cient. Venez.* 34:151-158.
- Linley, J. R. 1988. Laboratory experiments on factors affecting oviposition site selection in *Toxorhynchitesamboinensis* (Diptera: Culicidae), with a report on the occurrence of egg cannibalism. *Med. Vet. Entomol.* 2:271-277.
- Padgett, P. D. and D. A. Focks. 1980. Laboratory observations on the predation of *Toxorhynchites rutilus rutilus* on *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* 17:466-472.
- Steffan, W. A. and N. L. Evenhuis. 1981. Biology of *Toxorhynchites*. *Annu. Rev. Entomol.* 26:159-181.
- Steffan, W. A., R. D. Stoaks and N. L. Evenhuis. 1980. Biological observations of *Toxorhynchitesamboinensis* (Diptera: Culicidae) in the laboratory. *J. Med. Entomol.* 17:515-518.
- Trpis, M. 1972. Development and predatory behavior of *Toxorhynchites brevipalpis* (Diptera: Culicidae) in relation to temperature. *Environ. Entomol.* 1:537-546.
- Trpis, M. 1973. Interaction between the predator *Toxorhynchites brevipalpis* and its prey *Aedes aegypti*. *Bull. W. H. O.* 49:359-365.