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**LABORATORY STUDIES OF LARVAL CANNIBALISM IN
TOXORHYNCHITES AMBOINENSIS (DIPTERA: CULICIDAE)**

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Laboratory Studies of Larval Cannibalism in *Toxorhynchites amboinensis* (Diptera: Culicidae)

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ABSTRACT Rates of cannibalism in *Toxorhynchites amboinensis* (Doleschall) were studied to determine the effect of container volume, container shape, prey density, predator density, starvation, size differences between predators, and the interactions of some of these factors. Although statistically significant effects caused by container volume and prey density were seen, the shape of the container had a stronger influence than did container volume per se. Cannibalism was related inversely to the amount of water surface area in a container, irrespective of the volume contained. Prey density effects were expressed most strongly in containers with relatively large surface areas. No statistically significant differences in cannibalism were caused by starvation or size differences between predators. Cannibalism was most frequent during the second and third stadia. Prepupal killing of conspecific larvae occurred infrequently among pairs of larvae that had not cannibalized within the first 10 d.

KEY WORDS Insecta, *Toxorhynchites amboinensis*, cannibalism, behavior

CANNIBALISM is a common behavioral trait among larvae of the genus *Toxorhynchites* Theobald (Steffan & Evenhuis 1981). It has been observed in the laboratory (Furumizo & Rudnick 1978, Steffan et al. 1980), and its existence in nature has been inferred from the age and spacial distributions of larvae found in field surveys (Trpis 1973, Bradshaw & Holzapfel 1983). The significance of cannibalism in the population dynamics of *Toxorhynchites* spp. is not well understood, but Fox (1975) has stated that cannibalism serves as a regulatory mechanism which limits population size before resources can become limiting.

Several factors are thought to influence the rate of cannibalism by *Toxorhynchites* spp. These include prey density (Rubio & Ayesta 1984), container size (Trpis 1973), water volume, instar (Corbet 1985), and size differences (Lounibos 1985). However, there have been few laboratory studies of the phenomenon. Rubio & Ayesta (1984) suggested that an exponential relationship existed between prey density and cannibalism, and that cannibalism in *Toxorhynchites theobaldi* (Dyar & Knab) approached zero at prey densities above 20 per predator. Norris (1982) concluded that instar and hunger (prey availability) had a strong influence on the frequency of cannibalism in *Toxo-*

rhynchites brevipalpis (Theobald). We conducted the following laboratory experiments to shed further light on the effect of these and other factors on cannibalism in *Toxorhynchites amboinensis* (Doleschall).

Materials and Methods

Colony Maintenance. Specimens used in all experiments were obtained from a colony of *Tx. amboinensis* maintained at the U.S. Naval Medical Research Unit No. 2 Detachment, Jakarta, Indonesia. Mass-rearing methods used for colony maintenance have been described previously (Annis & Rusmiarto 1988). Mass rearing was initiated in December 1985; before that, the colony was maintained using individual rearing methods. The following experiments were initiated in June 1986.

Container Volume. Eggs of *Tx. amboinensis* were placed singly in wells of 24-well tissue culture plates and allowed 48 h to hatch. After hatching, two first instars were placed in each container with 20 first-instar *Ae. aegypti* L. Four different container volumes were used: six-well tissue culture plates with 10 ml of water in each well; 37-ml plastic cups with 20 ml of water in each; 100-ml plastic beakers filled with 100 ml of water, and 550-ml plastic beakers containing 500 ml of water. Each day, the number of *Toxorhynchites* and *Aedes* larvae were counted. *Aedes* larvae were removed and replaced with fresh larvae at the rate of 10 per *Toxorhynchites*. On day 2, 2-d-old *Aedes* larvae were used. On day 3, 3-d-old larvae were added. From day 4 onward, containers were stocked with 4-d-old prey larvae. Water was added as needed

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to maintain the proper levels. Observations continued until cannibalism or pupation occurred. Ten containers of each volume were observed in each replicate, and the experiment was replicated six times.

Container Shape. Eggs were hatched, containers were stocked, and counts were made as described above. The container shapes tested were: tall and thin (graduated cylinder), wide and short (enamel pan), and intermediate (beaker). Two volumes of each container were tested: large, containing 500 ml of water; and small, containing 100 ml of water. Each replicate included five containers of each volume and shape. The experiment was replicated four times.

Prey Density. This experiment was conducted using six-well tissue culture plates with 10 ml of water in each well. The procedures for stocking and counting each well were the same as those previously described; except two prey densities were used. In each replicate, five plates (30 wells) were stocked with 20 first-instar *Ae. aegypti* per well, and five plates were stocked with 40 larvae per well. The experiment was replicated six times.

Interaction of Container Volume, Shape, and Prey Density. Tall and thin (graduated cylinder) and short and wide (enamel pan) containers were tested at two volumes, 100 ml and 500 ml. Containers of each size and shape were stocked with 10 or 30 first-instar *Ae. aegypti* per predator. Five first-instar *Tx. amboinensis* were placed in each container. Procedures for daily counting and restocking of the containers were the same as in previous experiments. Each volume, shape, and density combination was replicated five times.

Predator Density. Cannibalism at different predator densities was evaluated under two different conditions of prey stocking. In one treatment, the number of prey in each container was kept constant at 40. In the other, prey density was maintained at 20 per predator. Two, four, or 10 first-instar predators were placed in beakers with 500 ml of water. Counts were made daily as previously described. The experiment was replicated four times.

Starvation. *Tx. amboinensis* eggs (0–24 h old) were placed singly in wells of 24-well tissue culture plates for hatching. The first group of larvae remained unfed until initiation of the experiment 6 d later. A second group of eggs was set on day 5. On day 7, larvae from both groups were combined in pairs in 37-ml plastic cups containing 20 ml of water. Each container was stocked with 40 *Ae. aegypti* larvae. Counts were made and containers restocked daily as in the above experiments. Ten pairs of starved and unstarved larvae were observed in each of six replicates.

Predator Size. First-instar *Tx. amboinensis* were placed individually in 37-ml plastic cups containing 20 ml of water and fed 10 *Ae. aegypti* larvae daily for 10 d. On the 10th day, wet weights of the larvae were taken. Larvae then were placed in

pairs of similar (same weight) or dissimilar (weights differing by at least 5.0 mg) size. The mean weight of all larvae tested was 17.4 ± 3.1 ($\bar{x} \pm \text{SE}$) mg, and the mean weight difference in dissimilar pairs was 6.6 ± 1.9 mg. Each container was stocked with 20 fourth-instar *Ae. aegypti*. Predators and prey were counted daily until cannibalism or pupation occurred, and prey was restocked as needed to maintain 20 per container. Twenty-one pairs of similar- and dissimilar-sized larvae were studied in replicate 1, 15 pairs in replicate 2, 18 in replicate 3, and 27 in replicate 4.

Statistical Analysis. Results were analyzed by analysis of variance (ANOVA) or *t* test. Duncan's (1955) multiple range test was used to compare means when appropriate. All analyses were performed using SPSS/PC+ (SPSS Inc. 1988).

Results

Container Volume. There were significant differences ($F = 4.25$; $df = 3, 15$; $P < 0.05$) in rates of cannibalism in containers of different volumes (Fig. 1). The mean number of pairs in which both members survived to pupation were 1.2, 0.8, 0.3, and 0.2 per replicate (10 pairs) for volumes of 500, 100, 20, and 10 ml, respectively. Container volume was correlated negatively with the frequency of cannibalism ($r = -0.553$; $df = 22$; $P < 0.005$). However, there was a slightly stronger negative correlation between cannibalism and the surface area of the container ($r = -0.590$; $df = 22$; $P < 0.002$). Increasing container volume also had the effect of delaying cannibalism in the pairs in which it occurred. The mean time to cannibalism was 3.3 d in 10- and 20-ml containers, 4.2 d in 100-ml containers, and 4.6 d in 500-ml containers ($F = 7.24$; $df = 3, 15$; $P < 0.01$).

Container Shape. Container shape had a significant effect on the frequency of cannibalism (Fig. 2). Fewer larvae were cannibalized in short containers having a comparatively large surface area than in tall, thin containers or containers of an intermediate shape. The mean number of pairs per replicate in which cannibalism occurred was 5.0 in cylinders of both volumes, 4.7 and 4.5 in 100- and 500-ml beakers, respectively, and 4.0 and 3.5 in 100- and 500-ml pans. There was no significant difference between container volumes, nor was there a significant interaction effect. As in the container volume experiment, the number of larvae cannibalized was correlated inversely with container surface area ($r = -0.564$; $df = 22$; $P < 0.004$).

Prey Density. Statistically significant differences occurred in the number of pairs in which cannibalism occurred in 10-ml containers at two prey densities. At 10 prey per predator, 29.7 ± 0.33 pairs per replicate of 30 (99%) exhibited cannibalism compared with 28.3 ± 0.92 (94%) at 20 per predator ($F = 4.74$; $df = 1, 48$; $P < 0.05$).

Interaction of Volume, Shape, and Prey Density. There were statistically significant differences

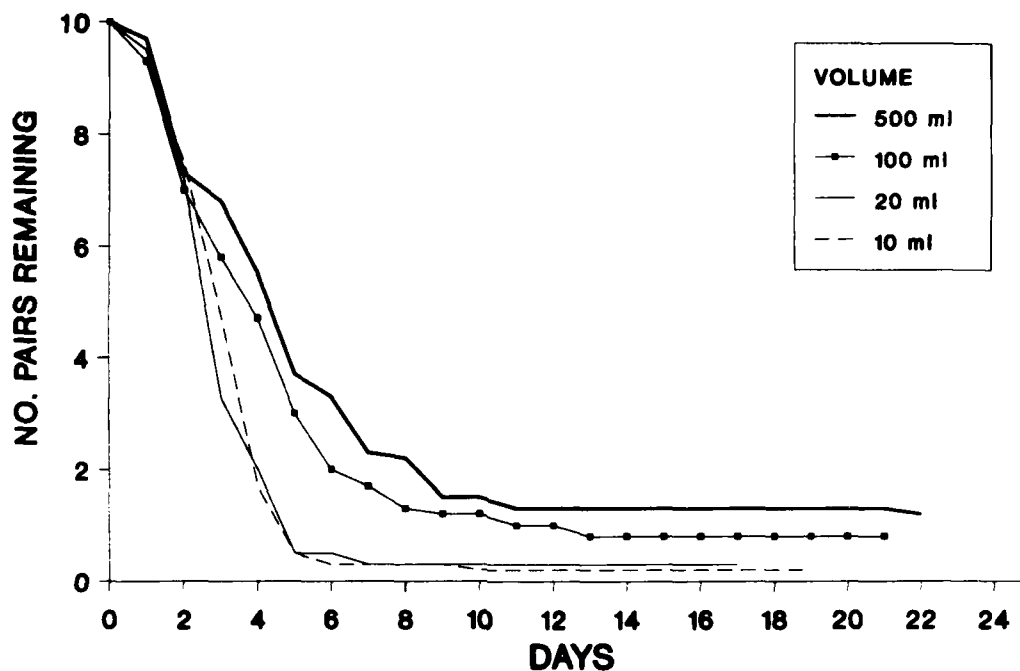


Fig. 1. Number of pairs of *Tx. amboinensis* larvae in which cannibalism had not occurred in containers of different volumes observed daily. Means of six replicates, 10 containers per replicate. Ends of plots represent pupation of last pair.

in the number of larvae cannibalized in containers of different shapes. A mean of 3.95 larvae were cannibalized in cylinders compared with 1.8 in pans. No statistically significant effects because of volume or prey density were seen, nor were any interaction effects significant (Fig. 3). The frequency of cannibalism was nearly equal in cylinders regardless of volume (4.0 and 3.9 larvae cannibalized per replicate in 500- and 100-ml cylinders, respectively) or prey density (4.0 and 3.9 larvae cannibalized at 10 and 30 prey per predator). In pans only, a higher prey density reduced cannibalism from 2.3 larvae per replicate at 10 prey per predator to 1.3 at 20 prey per predator, but means for the two volumes were equal at 1.8 larvae cannibalized.

Predator Density. Increasing predator density in containers caused an increase in cannibalism regardless of prey density (Fig. 4). Maintaining a predator/prey ratio of 1:20 did not significantly reduce cannibalism compared with containers in which prey density remained at 40 per container.

Starvation. Starving first instars for 5 d had no statistically significant effect on the rate of cannibalism. When larvae were starved 5 d before the experiment was initiated, cannibalism occurred in a mean of 9.6 pairs per replicate compared with a mean of 9.2 in pairs that were combined just after hatching ($t = 1.46$; $df = 5$; $P > 0.05$).

Predator Size. When larvae of known weight were placed together in pairs, cannibalism occurred in a mean of 20.25 pairs per replicate of dissimilar size larvae and in 19.5 of the pairs of similar size ($t = 1.3$; $df = 3$; $P > 0.05$). The length of time before cannibalism occurred was slightly (but not significantly) delayed in pairs of similar size (1.25 d in similar pairs, 1.09 d in dissimilar pairs; $t = 1.54$; $df = 3$; $P > 0.05$).

Discussion

Our results may help to explain differing reports on the frequency with which co-occurring *Toxorhynchites* larvae are found in nature. Although we found a significant inverse relationship between container volume and cannibalism, it occurred in 88% of pairs in the largest container (500 ml). In contrast, Norris (1982) reported that the frequency of cannibalism decreased from 82 to 61% as volume increased from 15 to 250 ml. However, Norris's observations were terminated after 24 h; ours were carried out over the entire larval stage. Our results clearly showed that increasing container volume had the dual effect of delaying cannibalism in pairs in which it occurred as well as reducing its occurrence. Thus, short observation periods would tend to magnify the container effect.

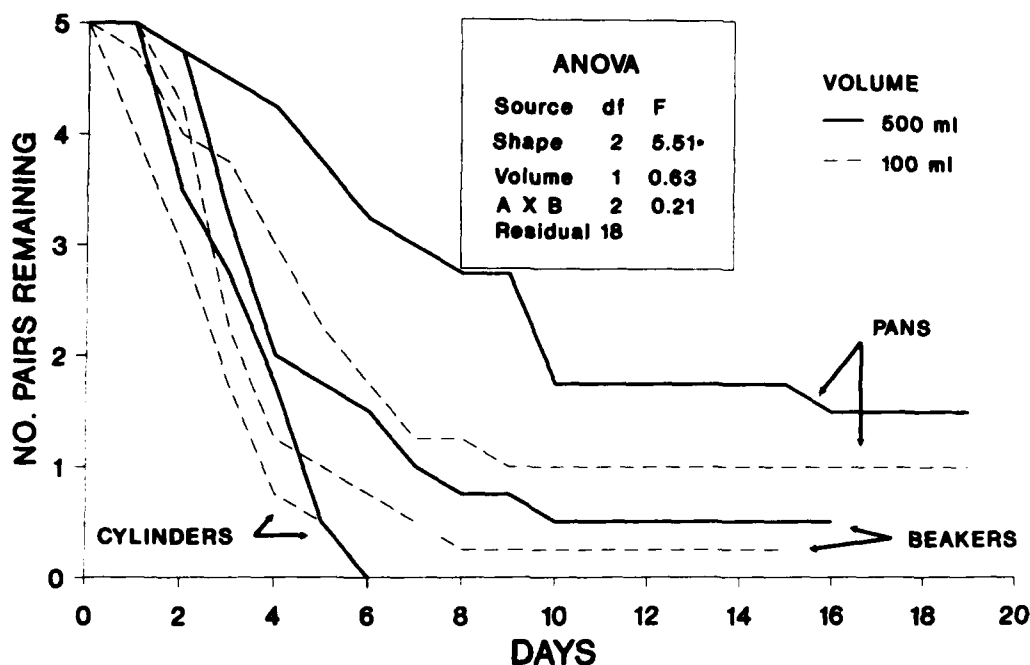


Fig. 2. Number of pairs of *Tx. amboinensis* larvae in which cannibalism had not occurred in containers of two different shapes at two volumes. Means of four replicates, five containers per replicate. *, $P < 0.05$. Ends of plots represent pupation of last pair.

In our experiments, cannibalism was reduced in containers with a relatively large surface area in relation to volume. It seems apparent that the amount of surface area in a container has a greater effect than volume in determining encounter frequency. In containers such as bamboo sections, treeholes (Lounibos 1985) and leaf axils (Mogi et al. 1985) cohabitation by *Toxorhynchites* is relatively rare. However, cohabiting larvae have been found, occasionally in large numbers, in natural *Toxorhynchites* populations in tires. Bailey et al. (1983) reported an average of between three and four *Tx. r. rutilus* (Coquillett) larvae per tire during a 10-wk survey in Florida. Focks et al. (1980) reported similar findings over a period of several months. Trpis (1973) found that multiple *Tx. brevipalpis* larvae occurred in 140 of 244 (57%) positive tires, with as many as 22 larvae in a single tire. In that study, multiple occurrences were twice as frequent in tires as in jars and tins. Similarly, in a study involving releases of *Toxorhynchites* adults for biological control, an accumulation of larvae was seen in tires (Durso et al. 1982). Tires have a large surface area in relation to the volume of water contained, especially when they lie horizontally.

Although statistically significant effects due to prey density were seen, the absolute magnitude of the difference in cannibalism rates at 20 and 40 prey per predator was slight (29.7 versus 28.3 pairs

per replicate of 30, respectively). Although it can be argued that the small size of the experimental containers intensified cannibalism, our container size experiment showed no difference between containers filled with 10 and 100 ml of water. This range of volumes and the prey densities tested are representative of many of those found in natural habitats of *Toxorhynchites* larvae.

Machado-Allison et al. (1985) reported that the largest leaf axils of some species of plants in Venezuela hold only 5–100 ml of water and that most of them contain low numbers of mosquitoes. Mogi et al. (1985), studying aroid axils in the Philippines, found that 90% of the axils surveyed in a farmland area and 70% in a forested area contained 20 or fewer mosquito larvae. Mean water volume was at most 25 ml. Similarly, Rivieri (1985) reported that tree-holes, bamboo, and coconut shells which contained *Toxorhynchites* larvae averaged 8.1, 12.7, and 17.7 *Aedes* larvae per container, respectively. We have found that 10–15 ml of water is a typical volume in bamboo stumps in Jakarta (B.A., unpublished data). Thus, it would seem that the effects of prey density on cannibalism would be minimal in many of the natural habitats of *Toxorhynchites* larvae.

Focks et al. (1982) stated that cannibalism was a significant source of larval mortality in tires and that it was related to prey density. Their obser-

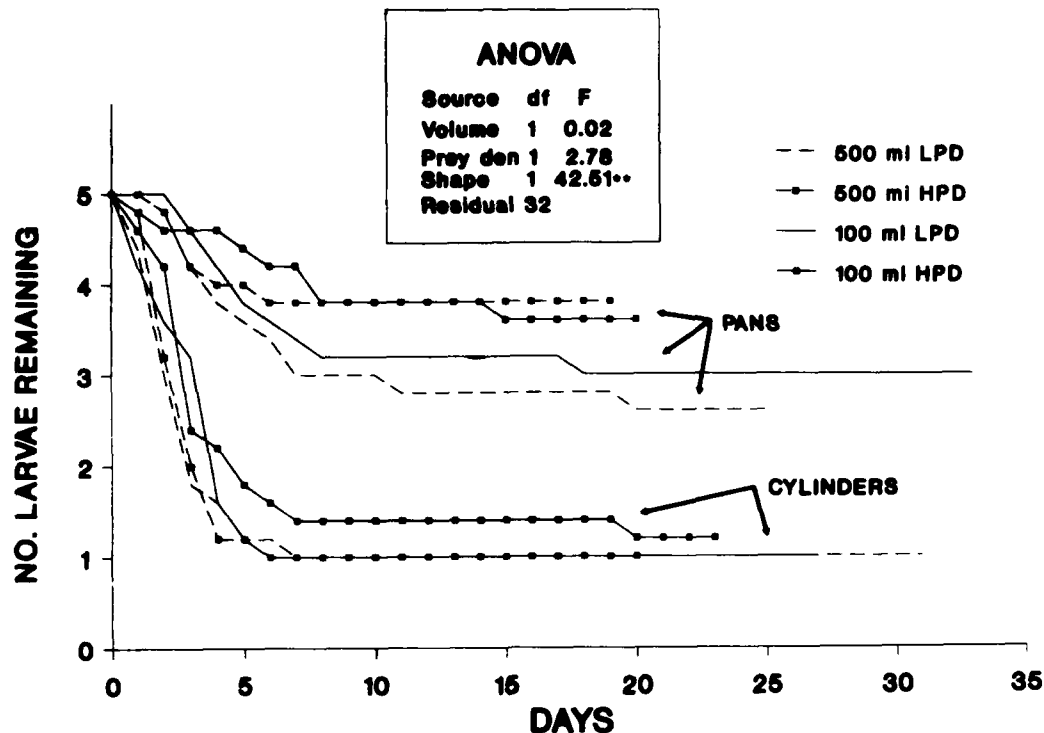


Fig. 3. Numbers of *Tx. splendens* remaining in containers of different shapes at high (HPD) and low (LPD) prey densities. Means of five replicates. **, $P < 0.01$. Ends of plots indicate pupation of last larva.

vation is consistent with the results of our volume $\times$ shape $\times$ prey density experiment. Although not statistically significant, increasing prey density reduced the incidence of cannibalism in containers with a large surface area but had no effect in tall, thin containers. Thus, container shape may influence the degree to which prey density affects cannibalistic behavior. High prey density may reduce cannibalism in tires, but its effect would be limited in containers such as bamboo stumps.

Our data do not support the existence of an inverse exponential relationship between the prey/predator ratio and frequency of cannibalism, as proposed by Rubio & Ayesta (1984). A careful examination of their experimental design reveals that the increasing rates of cannibalism they observed at low prey/predator ratios were caused by increasing predator density rather than the prey/predator ratio. As can be seen in Fig. 4, cannibalism increased with increasing predator density even when the prey/predator ratio was kept constant at 20:1.

Russo (1986) suggested that prepupal killing of prey by fourth-instar *Toxorhynchites* might deprive early-instar competitors of food and cause an increase in cannibalism among this younger group, thereby favoring the older, presumably related co-

hort. We observed a slight increase (4%) in cannibalism in first instars deprived of food for 5 d, but it was not statistically significant when compared with fed cohorts.

Similarity of larval size did not significantly reduce the occurrence of cannibalism in our experiments. This appears contrary to field data collected by Lounibos (1985) and Corbet & Griffiths (1963). However, as Lounibos (1985) suggested, a possible explanation for the similarity of size of cohabiting larvae in nature is that it results from, rather than being a cause of, the failure to cannibalize, because competition for food may limit growth. Alternatively, the ability of larvae to coexist may require their simultaneous presence in a container at some key point during development. In our experiment, larvae were combined after reaching the fourth stadium in isolation.

Evidence for this alternative hypothesis is provided by examination of the data in Fig. 1–3. The great majority of cannibalism occurred before day 10. Although we did not distinguish between cannibalism and "prepupal killing behavior" (i.e., conspecifics killed but not eaten), it is clear that little mortality of either kind occurred among larvae which developed together to the fourth stadium, even though prepupal killing of prey by these lar-

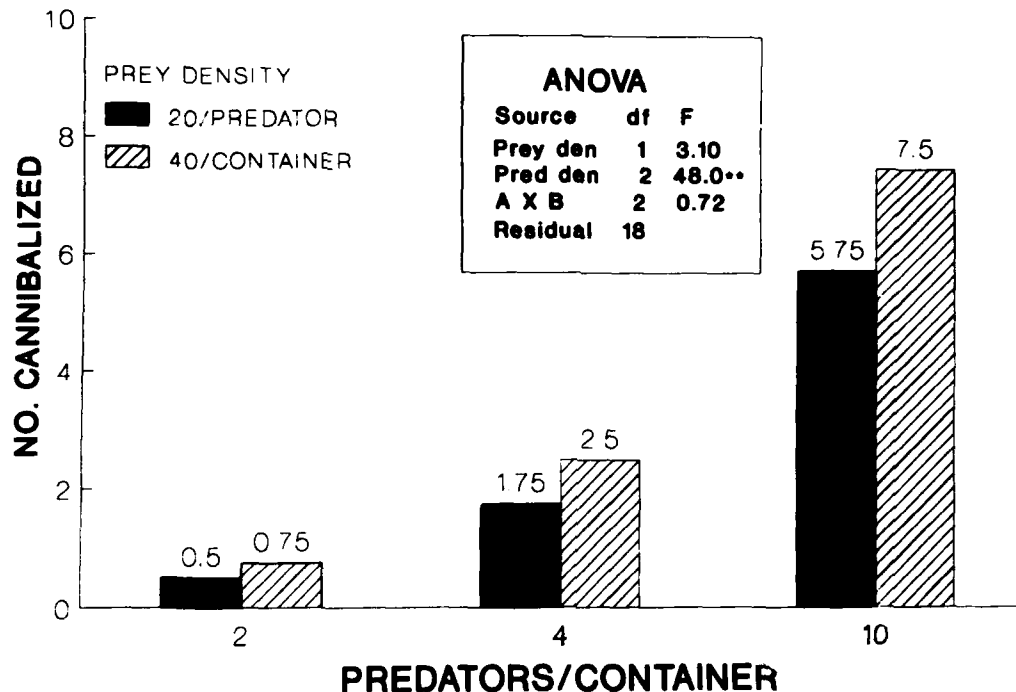


Fig. 4. Numbers of *Tox. splendens* larvae cannibalized at different predator and prey densities. Means of four replicates. **, $P < 0.01$.

vae often was observed. Therefore, the high rate of cannibalism observed in the size difference experiment may have been induced by the highly artificial situation in which larvae were combined in the fourth stadium after being reared in isolation.

Several general conclusions can be drawn from the results of our experiments. The amount of water surface area provided by a container has a greater effect on the occurrence of cannibalism than the volume of water it contains. Variation in prey density appears to have little ameliorating influence on cannibalism in habitats of small size, although the shape of the container may influence the degree to which prey density effects are expressed. Cannibalism is exhibited most frequently by second and third instars, and killing of conspecifics is relatively infrequent among fourth instars that develop to that stadium as a cohort. Therefore, experimental designs that place individually reared larvae together at late stadia or are based on short observation periods probably distort the significance of the factors studied.

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