

Ovipositional preferences and larval cannibalism in the Neotropical mosquito *Trichoprosopon digitatum* (Diptera: Culicidae)

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Abstract. The effects of age, size, food availability and relatedness on larval cannibalism in the Neotropical mosquito *Trichoprosopon digitatum* were investigated. The eggs of this mosquito are laid in small water receptacles and guarded by females until they hatch. No significant differences in the median level of cannibalism were detected between larvae of the same age derived from the same and from different clutches. Only 4-day-old larvae showed a significantly higher median level of cannibalism at low than at high food levels. When larvae of different ages were placed together, cannibalism was highly size-dependent. A parallel series of experiments was conducted in the field to determine the ovipositional preferences of *T. digitatum* for pots that contained particular developmental stages of the mosquito. Adult females preferentially laid their eggs in (1) pots that contained high levels of food and (2) pots that already contained an adult female guarding its clutch. Adult females avoided laying into pots that contained 8-day-old larvae. The data suggest that the oviposition decisions of the mosquito reduce the chances of its offspring being consumed by conspecifics. It is unclear precisely why ovipositing females should prefer to lay where there are other recently laid eggs although there appears to be little fitness cost in terms of cannibalism.

The oviposition site preferences of mosquitoes are based on a complex array of environmental factors (Bentley & Day 1989). Abiotic factors such as colour, water surface reflectance, humidity, temperature and water salinity all influence the oviposition preferences of certain mosquito species (Wilton 1968; Frank 1985). Chemical substances associated with mosquito eggs also elicit either preferential oviposition (Osgood 1971; Bruno & Laurence 1979) or avoidance by conspecifics (Chadee et al. 1990). Similarly, a number of mosquito species preferentially oviposit in water that has previously held either conspecific larvae (Trimble & Wellington 1980; Maire 1985) or conspecific pupae (Hudson & McLintock 1967; Soman & Reuben 1970). The functional significance of these responses to chemicals produced by conspecifics has typically been explained in fairly vague terms, such as 'assembling females for oviposition' in suitable breeding sites (Osgood 1971), and little work has been done to test or refine such explanations.

Animals should select oviposition sites that maximize their fitness. Factors affecting the choice of oviposition site may include the availability of food for the development of offspring, the

abundance of competitors and the abundance of predators (Blaustein & Kotler 1993). One factor that may represent a strong selective force in influencing the ovipositional preferences of some species of mosquito is larval cannibalism (Seifert & Barrera 1981). Cannibalism appears to be relatively common among mosquito larvae (e.g. Koenekoop & Livdahl 1986; Annis 1990) and it is conceivable that for those species of mosquito that lay a single or few clutches in their lifetime, the ability to avoid cannibalism might be an important determinant of lifetime reproductive success. Furthermore, the degree of cannibalism experienced in a population is generally not constant, but can vary with factors such as food levels, density, relatedness between individuals and the size and age composition of the population (see Fox 1975; Polis 1981 for reviews). Thus, mosquitoes might improve their chances of ovipositing in a suitable site if they possess a more sophisticated discriminatory ability than simply detecting the presence or absence of conspecifics.

In this paper we present the results of two parallel studies which investigated larval cannibalism and ovipositional preferences in a

Neotropical mosquito species *Trichoprosopon digitatum* (Rondani) (Diptera: Culicidae). In the first study we examined how food availability, age, relatedness and size differences influenced larval cannibalism. In the second we investigated the ovipositional preferences of adult females in the field. We compare the results of both studies and consider how ovipositional preferences relate to the degree of cannibalism that newly emerged offspring are likely to encounter.

METHODS

Study Species and Site

Trichoprosopon digitatum is a blood-feeding mosquito which breeds in natural and artificial water receptacles such as fallen fruit husks, bamboo internodes and water storage pots. Females lay a clutch of 60–80 eggs in the form of a raft onto the water surface (Chadee et al. 1989) and do not retain any eggs after oviposition (O'Malley 1986). Each female guards her egg-raft for about 24 h after she has laid it by sitting on the water surface and grasping it with her mesothoracic legs (Aitken et al. 1986). This behaviour reduces the probability of the eggs being displaced from the receptacle by heavy rainfall (Lounibos & Machado-Allison 1987).

The larvae pass through four instars before pupation (Aitken et al. 1968) and feed predominantly on micro-organisms and detritus (Seifert & Barrera 1981). To date there has been no published investigation of cannibalism in *T. digitatum*, although Seifert & Barrera (1981) noted that most larval cohorts were of uniform age and suggested that this might be due to a combination of size-dependent cannibalism and ovipositional preferences. The larvae are known to be extremely hardy, being able to survive for several months in the absence of adequate food (Busck 1908, cited in Zavortink et al. 1983) and able to tolerate several days of drying (Galindo et al. 1951).

We conducted laboratory work during the rainy season, July–August, 1992, at Simla Research Station, Arima Valley, Trinidad (10°42'N, 61°17'W) and fieldwork at the same time in the secondary seasonal deciduous forest that surrounds the station.

Egg Collection and Rearing of Larvae

To aid the collection of egg-rafts from the field, we placed numerous water-filled 500 ml plastic

cups, 8.5 cm in diameter (henceforth referred to as 'ovipots') in sheltered areas within the forest. The ovipots were checked for the presence of newly laid egg-rafts twice daily, at 0900 and 1800 hours. Experimental requirements (see below) dictated that eggs from different clutches should not be allowed to become mixed during rearing. To minimize the possibility of this occurring, we placed each egg-raft in its own vial as it was collected and we discarded any egg-rafts that were irregularly shaped or larger than usual.

In the laboratory, individual rafts were placed in small, plastic cups containing approximately 120 ml of local spring water. Approximately 0.1 g of dried, finely grated white breadcrumbs was added to the water for the larvae to feed on as they hatched. The rearing cups were kept close to a window in natural light (12:12 h light:dark) and at ambient temperature (which varied from 20 to 30°C externally during the experimental period).

Cannibalism Experiments

Experiment 1

We looked at the effect of four different food/relatedness treatments on the degree of larval cannibalism in each of four larval age classes (1, 2, 4 and 8 days old). The treatments were: (1) high food, single clutch; (2) high food, mixed clutches; (3) low food, single clutch; and (4) low food, mixed clutches. It is unclear whether the eggs within a given clutch are full or half siblings (as a result of multiple mating or sperm storage), but eggs from different clutches are very unlikely to be so closely related.

For all treatments, replicates consisted of 48 larvae placed into a plastic cup containing approximately 180 ml of local spring water. In 'single clutch' treatments, all 48 larvae were taken from the same egg-raft (and were therefore closely related to each other), while the 'mixed clutch' treatments consisted of 12 individuals taken from each of four different (unrelated) egg-rafts. In the 'high food' treatment, we added a small quantity (approximately 0.05 g) of finely grated, dried white breadcrumbs to the water at the start of the trial. In the 'low food' treatments, no food was present other than that occurring naturally in the spring water. The age classes used were as follows: day 1 (less than 24 h post-hatching), day 2 (1–3 days post-hatching, consisting of second and third

instars), day 4 (3–5 days post-hatching, consisting of third and fourth instars) and day 8 (fourth instars between 7 and 9 days post-hatching). We found it necessary to use age class rather than instar class because of the difficulty of accurately classifying lower instars.

Cups containing larvae according to a particular treatment were left under conditions of ambient light and temperature for exactly 24 h, after which the total number of larvae remaining were counted. All treatments were replicated 6–10 times for each age class.

Experiment 2

In this experiment, we investigated whether between-clutch differences in larval size could promote cannibalism. As in experiment 1, replicates consisted of 48 larvae in 180 ml of water. In this experiment, however, the 48 larvae were obtained by randomly selecting 24 larvae from each of two different source clutches. Clutches were chosen so that they differed in their age (and, therefore, size). We carried out nine or 10 replicates for each of three combinations of age class: day 8 versus day 1, day 4 versus day 1 and day 8 versus day 4. No food was added to the experimental cups.

For each replicate we placed the required number of larvae into the experimental cup and simply counted the numbers of each age class remaining after exactly 24 h. Different age classes could be easily distinguished by eye since older larvae were both thicker and longer than younger individuals.

During the 24-h duration of each replicate, we measured the lengths of 10 additional individuals from each of the source clutches. Size was estimated by measuring the length from the tip of the head to the base of the respiratory siphon under a microscope at 10 × magnification.

Ovipositional Preferences

We examined the ovipositional preferences of females in the field by simultaneously presenting them with choices of ovipots of different composition. The ovipots contained 500 ml of local spring water, 1.5 g of dried breadcrumbs and a certain number of larvae or pupae of known age (with the exception of experiment 4 below). Each pot was also provided with a transparent petri dish roof raised 4 cm above the lip of the cup to

protect the contents during heavy rainfall. We carried out four separate experiments, in which preferences were measured for the following choices of ovipot: (1) one adult guarding egg-raft versus no adult or egg-raft; (2) 40 day-8 larvae versus 40 pupae; (3) 40 day-8 larvae versus 40 day-2 larvae versus no larvae; and (4) no food versus low food versus high food.

The two or three types of ovipot in each experiment were placed into clusters, with about 5 cm separating each pot. These clusters of ovipots were placed in a linear transect about 3–5 m apart. Generally, 20 clusters were put out each day (i.e. a total of 40 or 60 ovipots) between 1230 and 1300 hours, local time. Trials were replicated at least three times for each experiment, with only one trial being carried out per day. Although the same transect was used for all four experiments, we rotated the relative positions of alternative ovipots in each cluster systematically on successive days.

We monitored the ovipots every hour from 1300 to 1800 hours and recorded the type of pot in each cluster that attracted the first ovipositing *T. digitatum*. Occasionally, *T. digitatum* alighted on the water surface in a pot without laying any eggs, but only when females had begun to lay their eggs was it considered an oviposition event.

Prior to each trial, all ovipots were thoroughly cleaned and prepared before adding the food, water and required number of *T. digitatum*. All pupae and larval instars came from our controlled laboratory culture. In experiment 1, the adults and their clutches were very carefully transferred from ovipots in the field that had been cleared the night before of all adults. Sometimes this resulted in a very small amount (1–2 ml) of ovipot water also being transferred, which was unavoidable. Because every adult had only recently begun guarding its eggs, no case of an adult deserting a transferred clutch was recorded during the experiment. In experiment 4, the weights of breadcrumbs added to the low food and high food treatments were approximately 1.5 and 6 g, respectively.

RESULTS

Cannibalism Experiments

During the study, we frequently observed cannibalistic interactions between conspecifics of all

Table I. Median number and range (in parentheses) of *T. digitatum* larvae missing per replicate per 24 h for each treatment and age class in experiment 1

Age class	Treatment			
	Single clutch, low food	Mixed clutches, low food	Single clutch, high food	Mixed clutches, high food
Day 1	1 (0-3) <i>N</i> =6	0.5 (0-4) <i>N</i> =6	0 (0-2) <i>N</i> =7	0 (0-3) <i>N</i> =7
Day 2	0 (0-1) <i>N</i> =6	1.5 (0-3) <i>N</i> =6	0 (0-3) <i>N</i> =7	0 (0-1) <i>N</i> =7
Day 4	3 (0-10) <i>N</i> =7	1 (0-3) <i>N</i> =7	0 (0-2) <i>N</i> =8	0.5 (0-1) <i>N</i> =8
Day 8	2 (0-8) <i>N</i> =8	1 (0-5) <i>N</i> =8	2 (0-8) <i>N</i> =10	2 (0-9) <i>N</i> =10

There were 48 larvae present at the start of each replicate.

sizes, both in experimental and rearing containers. Monitoring of fourth instar larvae for 30 min every 2 h during the day from 0900 to 1700 hours for 4 days revealed that cannibalism was intense and widespread. Since *T. digitatum* larvae are also extremely hardy (see Study Species and Site), we conclude that cannibalism was the primary source of larval mortality in our experiments. We assumed that all larvae missing at the end of each replicated trial were cannibalized, but, to allow for other sources of mortality, the occasional intact individual that was found dead was not counted as a cannibalism victim.

Experiment 1

The numbers missing from each replicate were generally very low (Table I) and the data contain a large number of zeros. No simple transformation was found that produced a normal distribution, so we analysed the effects of food availability, relatedness and their interaction using a two-way non-parametric analysis of variance, based on the Mann-Whitney *U*-test (Bradley 1968).

Relatedness had no effect on the level of cannibalism; there were no significant differences in the median level of cannibalism between single and mixed-clutch treatments for any of the age classes examined (day 1: $U=20.5$; day 2: $U=24.5$; day 4: $U=34$; day 8: $U=35$; all $P_s>0.1$, see Table I for sample sizes). For food treatments, only 4-day-old larvae showed a significantly higher level of cannibalism when food levels were low (day 1: $U=24.5$; day 2: $U=22$; day 8: $U=34.5$; all $P_s>0.1$ but day 4: $U=43$, $P<0.025$). There was only one significant interaction between food and relatedness, which occurred with 2-day-old instars (day

1: $U=18.5$; day 4: $U=30$; day 8: $U=34.5$; all $P_s>0.1$ but day 2: $U=30$, $P<0.05$).

Experiment 2

For each of the three age-class combinations, significantly more individuals from the younger age class were missing after 24 h than from the older age class (Mann-Whitney *U*-test, day 8 versus day 1: $U=100$, $N=20$, $P<0.001$; day 8 versus day 4: $U=81$, $N=19$, $P<0.001$; day 4 versus day 1: $U=95$, $N=20$, $P<0.001$). There was also a strong positive correlation between mean size ratio (the ratio of the mean size of the larger clutch divided by the mean size of the smaller clutch) and number of smaller individuals missing when data from all replicates of all age-class comparisons were combined (Fig. 1a; Spearman rank correlation: $r_s=0.575$, $N=29$, $P=0.002$). No correlation was found between mean size ratio and number of larger individuals missing (Fig. 1b; Spearman rank correlation: $r_s=0.139$, $N=29$, $P>0.05$).

Ovipositional Preferences

Figure 2 shows how often *T. digitatum* were observed to lay first in each type of pot. We analysed each of these data sets using a replicated goodness-of-fit test (*G*-test), to determine whether *T. digitatum* had an even chance of laying in all of the types of ovipot that were presented. Ambiguous results occurred when mosquitoes laid their eggs in more than one of the alternative ovipots in between successive monitoring and all of these results were ignored. In all four experiments there was no significant heterogeneity in preference between days (experiment 1, $G_{\text{HET}}=13.198$, $N=8$,

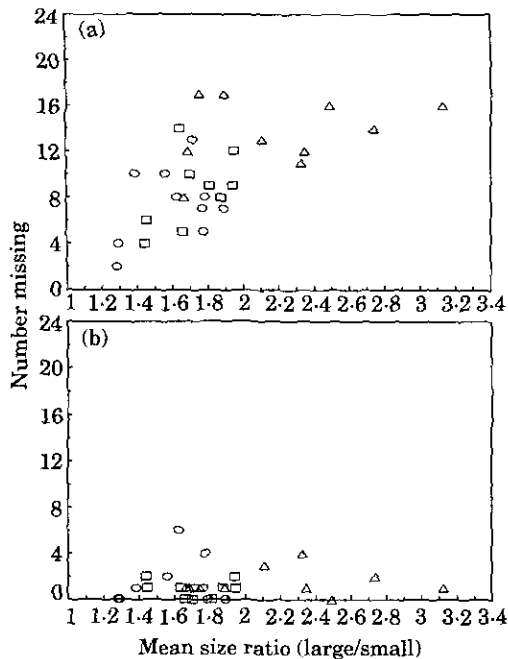


Figure 1. The effect of inter-clutch size difference on the number of (a) smaller instars and (b) larger instars missing per replicate (Δ : day 1 versus day 8, \circ : day 1 versus day 4, \square : day 4 versus day 8). There were 24 large and 24 small larvae present at the beginning of each replicate.

$df=8$; experiment 2, $G_{HET}=1.406$, $N=4$, $df=3$; experiment 3, $G_{HET}=13.096$, $N=6$, $df=10$; experiment 4, $G_{HET}=2.208$, $N=3$, $P>0.05$ in all cases, although in some cases expected values were less than 5). When the data were pooled, highly significant overall preferences for particular types of ovipot were found in all cases (Fig. 2). Females preferred to oviposit in: (1) pots that already contained a female and its clutch; (2) pots with pupae rather than 8-day-old larvae; (3) pots with water and 2-day-old larvae rather than 8-day-old larvae and (4) pots with high food rather than low food or water.

DISCUSSION

Our results indicate that *T. digitatum* larvae engage in a degree of cannibalism which is dependent on the size distribution of individuals within the breeding water receptacle. Individuals of the same age rarely cannibalize each other, whereas

large size differences between larvae can result in an extremely high rate of cannibalism of the smaller individuals. Size-dependent larval cannibalism has been observed in a number of other mosquito species, both detritus feeders (Koenekoop & Livdahl 1986) and predatory species (Jenkins & Carpenter 1946), although cannibalism does not prevail in all species (Kendal et al. 1991). Size-dependent cannibalistic preferences are not likely to incur costs in terms of inclusive fitness because larvae of very different sizes are more likely to be non-relatives than relatives. However, since larvae from mixed clutches of the same age showed no more cannibalism than larvae from single clutches, it is unlikely that non-relatives are selectively cannibalized on any other basis besides size.

We did not detect any consistent changes in cannibalism as we changed the amount of food in the water. Only 4-day-old larvae showed a significantly higher level of cannibalism when food levels were low and only 2-day-old larvae showed a significant interaction between food levels and relatedness. While we should not dismiss these significant effects, it is possible that they represent type I errors which arise out of the 12 statistical tests carried out for this experiment. Other workers have found an increased prevalence of cannibalism in mosquito larvae as food levels are lowered (e.g. Koenekoop & Livdahl 1986) but these workers used larvae of different size classes. We have not investigated here the effects of food availability on size-dependent cannibalism. The local spring water appeared to have a relatively high organic content and this may be another reason why food levels did not generally influence the prevalence of cannibalism.

The occurrence of size-dependent cannibalism clearly has important implications for ovipositional preferences. The egg-rafts are laid directly onto the water surface so it is important that the medium is immediately habitable by the larvae. Eight-day-old fourth instar larvae were highly predatory on 1-day-old instars of the same species, to the extent that more than two-thirds of the young instars were consumed in 24 h. This obviously represents a very strong selective force, so it is perhaps not surprising to see that *T. digitatum* has evolved the ability to discriminate between pots containing 8-day-old larvae and pots containing 2-day-old larvae, water or pupae. In contrast, 2-day-old larvae pose a lesser threat as

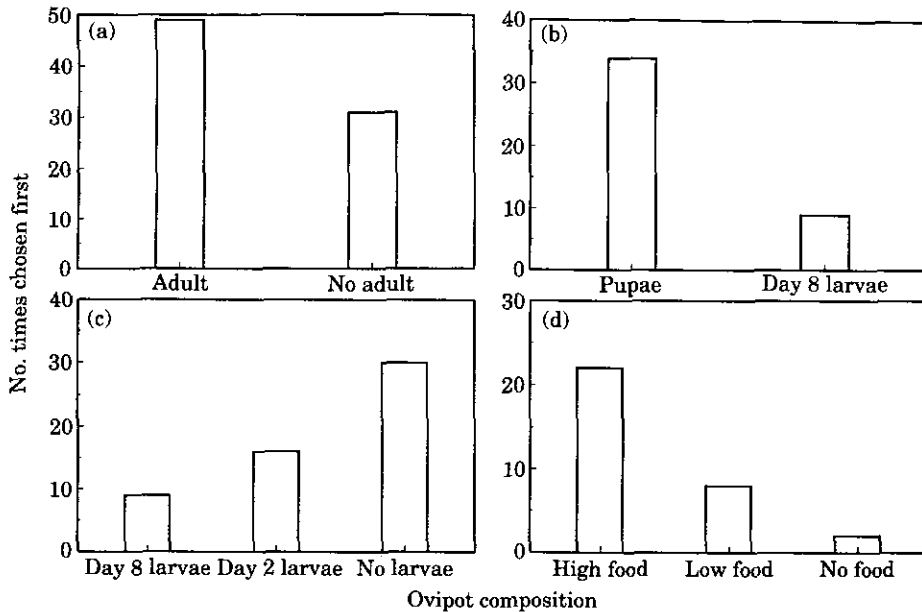


Figure 2. Ovipot preferences of *T. digitatum*. Ordinate represents the number of times a particular ovipot in a cluster was chosen first by *T. digitatum*. (a) Adult guarding egg-raft versus no adult or egg-raft (G -test on pooled data: $G_{\text{pool}}=4.089$, $df=1$, $P<0.05$), (b) 40 day-8 larvae versus 40 pupae ($G_{\text{pool}}=15.489$, $df=1$, $P<0.01$), (c) 40 day-8 larvae versus 40 day-2 larvae versus no larvae ($G_{\text{pool}}=12.386$, $df=2$, $P<0.01$), (d) no food versus low food versus high food ($G_{\text{pool}}=20.553$, $df=2$, $P<0.01$).

potential cannibals of 1-day-old instars and the presence of pupae may indicate a stable and sufficiently rich site, capable of supporting immature stages to adulthood. These findings provide evidence for Seifert & Barrera's (1981) conjecture that cohorts of a uniform age in this species form as a result of both size-dependent cannibalism and ovipositional preferences. In general, though, the relationship between choice of oviposition site and cannibalism has rarely been explored, although Baur (1988) found that the oviposition site of the land snail *Arianta* was not influenced by the risk of egg cannibalism. Other mechanisms may also operate to lower the risk of being cannibalized; Livdahl & Edgerly (1987) found that hatching rates of the mosquito *Aedes triseriatus* were suppressed when pots contained high densities of larvae and argued that cannibalism is a strong selective force in influencing the timing of egg hatch.

In our experiments, females also showed a significant preference for ovipositing where there are relatively high levels of breadcrumbs. The larvae feed predominantly on organic matter so it is not surprising that females should oviposit

where this resource is relatively high. The observed preference of females to oviposit in containers where other females are present with their egg-rafts is, however, more difficult to explain. Our data suggest a low risk of cannibalism amongst larvae of the same age, although one might expect that a high density of larvae within a container might lower the fitness of offspring (Fisher et al. 1990). We suggest two adaptive explanations as to why *T. digitatum* females appear to copy each other when laying their eggs. First, *T. digitatum* is a protandrous species and it is possible that an aggregative oviposition response might reduce the cost of an individual offspring finding a mate (particularly a non-relative) soon after emergence. Second, *T. digitatum* is known to be capable of living in nutrient-rich, near-anoxic conditions (Galindo et al. 1951). We have some evidence (T. Sherratt, unpublished data) to suggest that the survival rate of individual offspring laid in nutrient-rich containers is slightly higher when many clutches (approximately seven) are laid compared with a few clutches (approximately three), although generation times are also longer. One alternative

explanation for the behaviour is that the ovipositing females are responding to chemicals in the small amount of water used to transfer the egg-laying female and its clutch (and subsequently massively diluted), rather than stimuli from the adult or clutch itself. While a functional explanation of the behaviour would seem most likely, it is worth stressing that non-functional explanations are also possible (e.g. Gould & Lewontin 1979). Indeed, it is notable that some artificial attractants have even been found to have larvicidal properties (Maw 1970). Future studies should rigorously test the above explanations.

The way in which ovipositing *T. digitatum* detect the presence of conspecifics has not been elucidated but it is likely to be one or a combination of visual, tactile and chemical cues. It is difficult to say on the basis of this study whether the particular cues provided by conspecifics within the ovipots are of value to both the producers of the cue (conspecifics within the pot) and the recipients (ovipositing females). The results clearly indicate, however, that females of this species oviposit in a way that reduces the chances of their larvae being consumed by conspecifics.

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