

FACTORS AFFECTING FEEDING RATES OF BLACK FLY LARVAE<sup>1, 2</sup>LAWRENCE A. LACEY<sup>3</sup> AND MIR S. MULLA

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**ABSTRACT.** The effects of current velocity, food particle density and water temperature on the feeding rate of ultimate instars of *Simulium vittatum* Zetterstedt were studied in the laboratory utilizing an aerated jar rearing system and a particulate fluorescent dye. Feeding rates increased with increase in current up to a point, but a curvilinear relationship between current velocity and feeding rate was observed over the whole range. After 50 min of feeding on dye particles at 26 and 39 cm/sec (19°C, 75 ppm) the dye filled 42 and 52% of the gut respectively. When the velocity was raised to 53 cm/sec only 30% of the gut was filled.

When a wide range of particulate densities

Several investigators have presented information on the feeding behavior and functional morphology of simuliid larvae. Anatomy and morphology have been treated and pertinent literature on this subject reviewed by Crosskey (1960), Chance (1970), Craig (1974, 1977), and Davies (1974). Various modes of ingestion have been observed for the family. Although several species graze vegetation (Burton 1973) and some species are capable of both grazing and filter feeding (Craig 1977), the majority of simuliid larvae apparently feed solely by filtering particulates from the water. According to most recent authors black fly larvae are not selective for particle size, but may be restricted to a particular size range or food type due to its relative availability in the lotic environment (Moore 1977a, Wotton 1977). Kurtak (1978), however, conducted detailed studies on the size of particles and the proportion ingested. He

was employed, a significant difference in feeding rate was observed between larvae feeding at high and low particulate concentrations (19°C, 26 cm/sec). The dye in larvae feeding at 1 and 10 ppm filled only 31 and 32% of the gut respectively. At concentrations between 50 and 100 ppm the average filling was 44% of the gut.

Temperature of the medium affected feeding rates in larvae exposed to dye particulates (75 ppm, 26 cm/sec) at 4, 10, 15, 19, 24, and 28°C. The feeding rates at 4 and 10°C were significantly lower than those at 15–28°C.

There was no evidence that peristalsis aids in the posterior movement of the food column in developing larvae.

determined that a greater percentage of larger particles (150  $\mu\text{m}$ ) were ingested than that of smaller particles (5–10  $\mu\text{m}$ ). Particles smaller than the spaces of rays of the fan were ingested in lower proportion to particles with diameters greater than spaces between rays of the cephalic fan. The maximum particle size is apparently governed by the dimensions that can be taken into the mouth (Wotton 1977) and the minimum may approach colloidal size (Wotton 1976).

Various factors can govern the feeding rates of invertebrates. Monakov (1972) reported that the amount of food consumed is influenced by the food concentration, temperature and the size of the consumer. In a previous paper we studied the feeding rates of 3 species of *Simulium* under natural conditions and observed differences in gut clearance times attributable to species, larval age, and stream temperature (Mulla and Lacey 1976).

In this paper we present data on the effects of current velocity, food concentration, and temperature on feeding rates of *Simulium vittatum* larvae. Observations on effects of peristalsis on food column movement are also presented.

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## MATERIALS AND METHODS

Ultimate instar larvae of *Simulium vittatum* Zetterstedt were collected from the Mojave River located on the high desert near Victorville, California and transported to the laboratory at the University of California, Riverside. After allowing the larvae to acclimatize for 24 hr under laboratory conditions, they were exposed to a suspension of 50% fluorescent particulate dye and 50% finely ground lab chow in the modified jar system described by Lacey and Mulla (1977).

The % gut filled, and thus relative feeding rate, was determined in the manner described by Mulla and Lacey (1976), i.e., by measuring the posterior displacement of the dye plug in the gut and expressing this distance as a percentage of the length of the larva. Complete information on the fluorescent dye utilized was presented by Mulla and Lacey (1976). In each experiment the larvae were exposed to the particulates, food and dye, for 50 min. Afterward, 15 larvae from each velocity, concentration or temperature regimen were killed and stored in 70% ethanol for future measurement.

The effect of current velocity on the feeding rate was studied by exposing several dozen larvae to 75 ppm of the food and dye mixture at 19°C at 3 different velocities. Current in each jar was produced by circulating air through an air stone in the jar with a Silent Giant® aquarium air pump. The output of the pump was 3.3 l/min as determined with a flowmeter. Water velocity was varied by running variable numbers of jars per pump. The velocity in each jar was determined by timing the travel of small paper disks (5 mm diam) over a specific distance with a digital stop watch. Ten observations were made for each velocity. The average current produced in 3 jars run on one pump was  $26.18 \pm 4.8$  cm/sec; and for 1 jar was  $52.76 \pm 2.49$  cm/sec.

The effect of particulate concentration on feeding rate was determined by varying the concentration of particulates in a current of 26 cm/sec at 19°C. After expo-

sure to 1, 10, 50, 75, or 100 ppm of particulates, 15 larvae per jar were removed and placed in alcohol.

The feeding rates of larvae exposed to 75 ppm of the dye in a current of 26 cm/sec at 4, 10, 15, 19, 24, or 28°C were studied utilizing a walk-in temperature cabinet. The temperatures varied less than  $\pm 1^\circ\text{C}$  during the course of the study. The larvae were placed in 19°C water initially and gradually cooled or warmed to the experimental temperature at least for 24 hr prior to the addition of the dye particles.

To determine the role of peristalsis on the posterior displacement of the food column, larvae were exposed to 75 ppm of the particulates at 19°C in a 39 cm/sec current for 50 min then left in static water. Ten larvae were removed 0, 1, 3, 6, and 12 hr after the cessation of current and placed in alcohol.

The data for each experiment were analyzed with Duncan's Multiple range test after arcsin transformation and analysis of variance.

## RESULTS AND DISCUSSION

The results of feeding larvae of *S. vittatum* on dye particles in 3 different current velocities are presented in Table 1. Although the feeding rates for all 3 of the velocities differed significantly, there was no significant positive linear correlation between velocity and feeding rate. The observed increase in feeding rate going from the slowest current (26 cm/sec) to the 39 cm/sec velocity was highly significant ( $P < 0.01$ ), but at the highest velocity

Table 1. Proportion of gut filled by dye at 19°C in various current velocities after 50 min of exposure to 75 ppm of dye particles.

Current cm/sec	Mean % gut filled $\pm$ S. E. <sup>a</sup>	Range
26.18 $\pm$ 3.16	42 $\pm$ 2.43 b	29-64
39.24 $\pm$ 4.80	52 $\pm$ 2.51 c	37-71
52.76 $\pm$ 2.49	30 $\pm$ 0.99 a	24-38

<sup>a</sup> Means followed by the same letter are not significantly different at the .05 level.

(53 cm/sec) the feeding rate was the slowest. The relationship between current velocity and feeding rate appears to be curvilinear i.e., once an optimum velocity is reached, increased current only interferes with the feeding process. In the study utilizing 53 cm/sec velocity, the increased airflow through the airstone created rather turbulent conditions for the larvae. The work of Fredeen (1964) Kurtak (1978) and Moore (1977b) tend to support our observations. Fredeen (1964) postulated that slower feeding rates in his study were due to the location of larvae in slower current. In field studies, Kurtak (1978) found that feeding efficiency (ratio of number of particles ingested to those offered) varied inversely with stream velocity and Moore (1977b) observed that black fly feeding was adversely affected by increased stream velocity. Elouard and Elsin (1977) found that the transit rate of particles through the gut of various instars of *S. damnosum* larvae was a function of stream velocity and particulate concentration. Apparently, larvae were not observed in stream velocities that were sufficiently high enough to reduce the rate of intake of particulates. Reisen (1974), however, found that the number of particles removed from stream water by *Simulium* spp. in his study was independent of stream velocity.

Table 2 presents the effects of particle concentration on feeding rate. As particle density increased an increase in feeding rate was noted ( $r = 0.87$ ) up to 50 ppm.

Table 2. Proportion of gut filled by dye at 19°C in a current of 26 cm/sec after 50 min of exposure to variable concn of dye particles.

Concn (ppm)	Mean % gut filled $\pm$ S. E. <sup>a</sup>	Range
1	31 $\pm$ 2.79 a	21-48
10	32 $\pm$ 1.54 a	22-42
50	45 $\pm$ 3.64 b	23-74
75	42 $\pm$ 2.43 b	29-64
100	44 $\pm$ 2.83 b	25-64

<sup>a</sup> Means followed by the same letter are not significantly different from each other at the 0.05 level.

The relationship however, does not appear to be strictly a linear one over the entire range of concentration. At a concentration of < 50 ppm the filtering process is operating at maximum efficiency, i.e. increase in particulate density beyond this point will not result in increased feeding rate. Similarly, Kurtak (1978) found that feeding efficiency of *Simulium* spp. varied inversely with particle concentration. Speir (1975) observed that "feeding actions" appeared to be independent of food density or temperature. If an increased amount of food were proffered to *Simulium* larvae and the fans were closed and cleaned periodically regardless of the food density, one could expect an increase in feeding rate, provided that the particulate density ranged from very low to optimum density. Perhaps Speir (1975) did not observe an increase in feeding rate with an increase in food concentration because the larvae were already feeding at maximum efficiency with the optimum particulate density prevailing in the habitat. After the optimal plateau of particulate concentration is passed an inhibitory effect would undoubtedly be noted with the addition of more particulate matter.

The relationship between temperature and feeding rates is presented in Table 3. As the water temperature increased from 4 to 15°C, so did feeding to the maximum level ( $r = 0.84$ ). The 4° and 10°C feeding rates were not significantly different from

Table 3. Proportion of gut filled by dye at 4, 10, 15, 19, 24 and 28°C in a 26 cm/sec current after 50 min of exposure to 75 ppm of dye particles.

Temperature °C	Mean % gut filled $\pm$ S. E. <sup>a</sup>	Range
4	22 $\pm$ 1.56 a	16-31
10	24 $\pm$ 1.31 a	19-32
15	45 $\pm$ 3.42 b	32-58
19	48 $\pm$ 3.53 b	33-66
24	49 $\pm$ 5.12 b	31-77
28	44 $\pm$ 2.75 b	27-72

<sup>a</sup> Means followed by the same letter are not significantly different from each other at the 0.01 level.

one another but differed significantly from the 4 higher temperatures ( $P < 0.01$ ). All of the feeding rates at the higher temperatures do not differ significantly from one another.

Our findings differ slightly from those of Webster (1973) in that the stepup increase in "filtering rate" in his study was observed at 20°C instead of 15°C. The increase in feeding rate of *S. vittatum* at higher temperatures may be due to the eurythermous nature and ecological plasticity of this species. Becker (1973) found that *S. vittatum* developed at an increased rate and without apparent ill-effect when reared in water at 17–27°C and Webster (1973) observed feeding at 2°C. Another species exhibiting increased feeding rates at higher temperatures, *S. tescorum* Stone and Boreham (Mulla and Lacey 1976) is also found in a broad thermal range, 10–32°C (Lacey and Mulla 1979). Other authors (Ladle et al. 1972, Reisen, 1974, Spier 1975) have found no correlation between increased temperature and feeding rates. This could be due in part to the narrower thermal range where the species studied were found.

Larvae that were removed from lentic water and placed in alcohol 0, 1, 3, 6, and 12 hrs after cessation of a 50 min feeding exposure (39 cm/sec, 19°C) to the dye particles (75 ppm) had displaced the dye  $56 \pm 4.51$ ,  $56 \pm 6.44$ ,  $62 \pm 6.47$ ,  $59 \pm 4.27$ , and  $57 \pm 4.19\%$  of the body length respectively. There was no significant difference in the movement of dye through the gut between larvae that were killed immediately after the feeding period and larvae that were left alive in lentic water but without particles for up to 12 hr following the feeding period. Apparently during the developmental period peristalsis plays no role in the passage of food through the gut, movement only being affected by the continued ingestion of food particles. However, observations in the laboratory indicated that pre-pupae (larvae in the process of cocoon construction) had emptied their gut contents. Since no feeding movements are ob-

served during this period, ostensibly the clearing process is due to peristalsis.

Obviously the dynamics of larval feeding *in situ* are more complex than those presented here owing to the interaction of many factors. However, based on our observations, one could expect the slowest feeding rates in winter, in those species that continue to feed in near freezing water, both due to the decreased amount of seston available and the slower feeding activity induced by the very low temperatures. In species found in a habitat subject to broad seasonal thermal fluctuations, the fastest feeding rates could be expected in warm weather, due to increased stream productivity and the effects of elevated temperatures on the larvae themselves. The differences in feeding rate of various species of simuliids studied would of course modify this hypothesis. For example, the very rapid gut clearance time observed for *S. ornatum* (20–30 min) by Ladle et al. (1972) throughout the year at temperatures above 8°C is much faster than that observed for *S. vittatum* at 28°C in the laboratory and at 13–18°C in the field (Mulla and Lacey 1976).

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## BOOK REVIEW

ANNUAL REVIEW OF ENTOMOLOGY, Vol. 24, 1979. T. E. Mittler, F. J. Radovsky, and V. C. Resh, Editors. Annual Reviews Inc. Palo Alto, CA 94306. 579 pp. \$17.00 from the Entomological Society of America.

Unlike most volumes in this series, Vol 24 has little to interest culicidologists. Last year there was a noteworthy review of "Mosquito-Virus Relationships of American Encephalitides" by J. McLintock. This year there

is a review of tangential interest by K. H. Rothfels entitled "Cytotaxonomy of Black Flies (Simuliidae)." Studies of the salivary gland chromosomes have revealed the existence of taxonomically unresolved sibling species and have contributed to a more complete understanding of phylogenetic relationships. To a considerable extent the close cooperation between cytologists and taxonomists has resulted from the fact that black flies are very resistant to laboratory culture.—W. E. Bickley