



①

BIOSYSTEMATICS OF LARVAL MOVEMENT OF CENTRAL AMERICAN MOSQUITOES AND ITS USE FOR FIELD IDENTIFICATION¹

DANIEL STRICKMAN²

Walter Reed Biosystematics Unit, Department of Entomology, Walter Reed Army Institute of Research, Washington, DC 20307-5100

ABSTRACT. Means of locomotion of 48 species of larval mosquitoes was observed using cinematography in Panama, Honduras and neotropical Mexico. General observation led to a classification of movement into path, frequency, position and mechanism. Examination of high speed film sequences (64 frames per second) revealed that all species use the same basic mechanism of flexing, which consists of a power and a recovery phase. The entire flexing cycle is a modification of undulatory propulsion commonly observed in other animals (e.g., snakes, ceratopogonid larvae). Variations on the basic patterns of mosquito larval flexing mainly concern the speed of the power stroke and the degree of sinusoid curvature prior to the power stroke. Four basic patterns of larval flexing were discerned: irregular, sinuous, semisymmetric and anopheline. Some taxonomic groups appear to use one pattern of flexing exclusively or with few exceptions. Examples include *Culex (Melanoconion)* with sporadic irregular flexing, *Cx. (Culex)* with sustained irregular flexing, *Haemagogus* with slow sinuous flexing and *Anopheles* with anopheline flexing. Other groups (e.g., *Aedes (Howardina)*, *Cx. (Carrollia)*, *Deinocerites*, and *Wyeomyia (Wyeomyia)*) use a number of patterns of flexing. Observation of flexing and other aspects of larval movement can be an important addition to geographical, habitat and morphological considerations in field identifications.

INTRODUCTION

Identification of mosquito larvae in the field is useful for operational survey work. Field identification provides the opportunity to seek additional sites during a single trip. Otherwise, mosquitoes must be identified in the laboratory before gaining any idea of exact focal distribution of larvae.

The process of learning field identification of larvae is generally through direct experience. This system functions well in temperate zones where the number of taxa in any one area is limited and skilled persons are available in the form of mosquito control professionals. The problem is more difficult in Central America (and probably other tropical regions) because: (1) the mosquito fauna is much more diverse; (2) the fauna is less studied taxonomically; and (3) mosquito control professionals are often unfamiliar with species outside the genus *Anopheles*.

Written guides to field identification are very scarce. One of the most comprehensive guides (Headlee 1945) provides separate laboratory and field keys for the larval and adult female mosquitoes of New Jersey. Although these field keys do not use larval movement, Headlee discusses the differences between anopheline and culicine

locomotion elsewhere in the text. Other authors have noted the same differences (e.g., Nuttall and Shipley 1901, McDaniel 1935, Hopkins 1952).

From 1985 through 1987 I observed many species of mosquito larvae during field investigations in western Panama, Honduras, and neotropical Mexico (Tapachula area, Chiapas; located on the Pacific coast near the Guatemalan border). This work provided the chance to find larvae in their natural habitats, observe them in a field laboratory and confirm identifications in a museum.

I concentrated on larval movement because other factors (geographic distribution, habitat and morphology) are routinely documented in taxonomic works, but larval movement rarely has been described. Furthermore, no system exists for classifying swimming motions of mosquito larvae. This paper presents an explanation of the basic mechanics of larval movement and classifies the various types observed. Movements of the 48 species examined are associated with their systematic relationships.

MATERIALS AND METHODS

Larval movement was recorded by taking 16 mm, color (ASA 100) motion pictures of fourth-instar larvae collected in the field (except *Sabethes cyaneus*, *Sa. chloropterus* and *Toxorhynchites theobaldi*, which were taken from colonies maintained at the Gorgas Memorial Laboratory, Panama). Photographic equipment included a spring-powered Bolex® camera and lighting from two tungsten bulbs. For side views, larvae were placed in a tissue-culture flask (10 cm

¹ Opinions and assertions contained herein are the private views of the author and are not to be construed as official, nor as reflecting the views of the supporting agencies.

² Current address: Dept. of Entomology, U. S. Army Component, Armed Forces Research Institute of Medical Sciences, APO San Francisco, CA 96346-5000.

91-04163



91 7 05 105

across) set with its cap upwards and about half-filled with water. For top views, larvae were placed in a cup or small pan. Generally, about one minute of film was taken for each species, although this varied with the amount of activity of the larvae. Larvae in Panama (October–November, 1985) were all photographed at 24 frames per second (fps) and usually only from the side. These films were useful but limited because they failed to record sufficient intermediate postures in rapidly swimming species or failed to capture the full range of movement. To correct these deficiencies, filming in Honduras (June–November, 1986) included both lateral and dorsal views at 24 and 64 fps. Only notes were taken in Mexico (August–September, 1987), using experience gained from films taken earlier in Panama and Honduras.

Most filmed larvae were preserved whole for later identification. Identifications were confirmed from larval exuviae, adults or male genitalia from specimens collected at the same site as the larvae filmed. All specimens were deposited at the United States National Museum under accession numbers 1172 for Panamanian, 1179 for Honduran and 1250 for Mexican collections. Sources of all species studied are listed in Table 1.

Films were first studied to gain a general impression of the species' movements. These observations confirmed, for the most part, those already made in the field. Second, short sequences which displayed representative ranges of movement at 24 fps were illustrated by drawing single frames at half-second intervals and every frame in 12 successive sequences. Finally, sequences at 64 fps were studied to understand the basic pattern of movement and how it varied between species.

RESULTS AND DISCUSSION

A description of movement for each species was divided into the components of path, position, frequency and flexing mechanism. Flexing mechanism was the only component that received quantitative analysis. Each component is discussed below, with the classification of movement of each species in Table 1.

Path is the line of movement of the larva as a whole in relation to its external environment. When reduced to a simple scheme, the path was either horizontal, vertical or erratic. Horizontal paths were typical of species which remained principally at the water surface (e.g., *Anopheles*) or near the bottom of the flask (e.g., *Sabethes*), but some species which occupied more of the water column also displayed a tendency to move horizontally. One example was *Deinocerites*

pseudes (Fig. 1a), which often turned from a vertical path to move parallel to the surface and bottom of the container. Many species, such as *Cx. peus* (formerly *thriambus*, Strickman 1988), followed a vertical path during most of their movement, in contrast to the surface and bottom dwellers which restricted their use of vertical paths to ascents and descents. *Culex peus* (Fig. 1b), like other members of the subgenus *Culex*, performed rapid ascents and descents in planes oblique or perpendicular to the surface and bottom. An erratic path (e.g., *Cx. pilosus*, Fig. 1c) was observed most commonly in species which did not make frequent, energetic movements. These species responded to stimuli with a sudden burst of flexing which resulted in a path forming closed curves with sharp changes in direction.

For the purpose of describing movement, position refers to the usual position of the larva in the water column during movement. Although precise determination of position would require lengthy observation, the preference for position was strong enough to provide a general indication even over short time periods. The positions were divided into surface (e.g., *Anopheles*), bottom (e.g., *Sabethes cyaneus*) and middle water column (e.g., *Cx. peus*).

Frequency of movement is another factor which could be studied in considerably more detail than was possible under the conditions of this study. Brief observations allowed a rough categorization of those larvae which moved frequently and those which moved infrequently. The majority of species examined moved frequently, either because of a low threshold of disturbance or in the course of seeking food. Those species which moved infrequently (e.g., *Cx. pilosus*) would become active when stimulated, but otherwise quickly returned to a non-motile state.

The flexing mechanism was the most difficult component of movement to describe. In order to understand why swimming motions appeared different in various species, it was first necessary to understand the mechanics of the motions. The description which follows is based on study of all the species filmed at 64 fps and of the slower-moving species filmed only at 24 fps.

A flexing mosquito larva moved in the direction of its posterior, looping its abdomen in alternate directions. For the purposes of this discussion, the direction toward the posterior of the larva will be designated "forward" and the direction toward the anterior of the larva will be designated "backward." Considering a generalized larva, the swimming motion can be said to begin with the larva in its most flexed posture (Fig. 2a). The body then unflexed relatively

Table 1. Quantification of the flexing mechanisms using cinematography of species of mosquito larvae from Panama, Honduras, and neotropical Mexico.

Species	Collection locality	Position ^a	Power stroke ^b	Sinusoid curve ^c	Flexing form ^d
<i>Aedeomyia squamipennis</i> (Lynch Arribalzaga)	Panama	B/M		0.20	I-Sp
<i>Aedes vexans</i> * (Meigen)	Honduras	M	2/64	0.51 ± 0.14	S-Sl
<i>guerrero</i> Berlin	Honduras	M	1/64	0.17 ± 0.06	I-Su
<i>quadrivittatus</i> (Coquillett)	Honduras	M	2-3/64	0 ± 0	SS
<i>epactius</i> * Dyar and Knab	Honduras	M	2-3/64	0.24 ± 0.06	S-Sl
<i>taeniorhynchus</i> * (Wiedemann)	Honduras	M	1/64	0.39 ± 0.02	S-Fa
<i>Anopheles eiseni</i> Coquillett	Panama	S			A
<i>crucians</i> Wiedemann	Honduras	S			A
<i>hectoris</i> Giaquinto-Mira	Honduras	S	<1/64	0.28 ± 0.040	A
<i>punctimacula</i> Dyar and Knab	Honduras	S			A
<i>neivai</i> Howard, Dyar, and Knab	Panama	S			A
<i>albimanus</i> * Wiedemann	Honduras	S	<1/64	0.31 ± 0.08	A
<i>Culex bihaicola</i> Dyar and Nunez Tovar	Panama	M	2/24	0.17	SS
<i>secundus</i> Bonne-Wepster and Bonne	Panama	M		0	I-Su
<i>coronator</i> Dyar and Knab	Honduras	M	1/64	0.03 ± 0.04	I-Su
<i>declarator</i> gp.*	Honduras	M	1/64	0.20 ± 0.08	I-Su
<i>corniger</i> gp.	Mexico	M			S-Fa(?)
<i>nigripalpus</i> Theobald	Honduras	M	1/64	0.21 ± 0.06	I-Su
<i>quinquefasciatus</i> * Say	Honduras	M	1/64	0.15 ± 0.03	I-Su
<i>peus</i> (former <i>thriambus</i>) Speiser	Panama	M		0.18	I-Su
sp. A*	Honduras	M	1/64	0.11	I-Su
sp. B*	Honduras	M	<1/64	0.04 ± 0.04	I-Su
<i>erraticus</i> (Dyar and Knab)	Mexico	M			I-Sp
<i>garcesi</i> Duret	Panama	B/M			I-Sp
<i>pilosus</i> (Dyar and Knab)	Panama	B/M			I-Sp
<i>imitator</i> Theobald	Honduras	B/M	1/64	0.21 ± 0.06	I-Sp
<i>Culiseta particeps</i> (Adams)	Panama	M		0.45	S-Fa
<i>Deinocerites cancer</i> * Theobald	Honduras	M	2-3/64	0.14 ± 0.07	SS
<i>pseudus</i> Dyar and Knab	Panama	M		0.29	S-Sl
<i>Haemagogus anastasionis</i> Dyar	Honduras	M	2/64	0.33 ± 0.10	S-Sl
<i>equinus</i> Theobald	Panama	M		0.57	S-Sl
<i>mesodentatus</i> Komp and Kumm	Mexico	M			S-Sl
<i>Limatus durhamii</i> Theobald	Mexico	B			SS
<i>Mansonia titillans</i> (Walker)	Honduras	B	2-3/64	0.17 ± 0.17	SS
<i>Orthopodomyia kummi</i> Edwards	Mexico	M			SS
<i>Psorophora confinnis</i> * (Lynch Arribalzaga)	Honduras	M	<1/64	0.25 ± 0.10	S-Fa
<i>ferox</i> * (Von Humboldt)	Honduras	M	<1/64	0.29 ± 0.04	S-Fa
<i>Sabethes cyaneus</i> (Fabricius)	Panama	B	2/24	0	SS
<i>undosus</i> (Coquille t)	Panama	B	2-3/24	0.07	SS
<i>chloropterus</i> (Von Humboldt)	Panama	B	2/24	0.21	SS
<i>Toxorhynchites theobaldi</i> (Dyar and Knab)	Panama	B		0.51	S-Sl
<i>Trichoprosopon digitatum</i> * (Rondani)	All	B	2-3/64	0.11 ± 0.005	SS
<i>Wyeomyia arthro stigma</i> * (Lutz)	Honduras		2/64	0.16 ± 0.05	SS
nr. <i>mitchellii</i> (Theobald)	Mexico	B			SS
<i>pertinans</i> gp.*	Honduras	B	2/64	0.46 ± 0.08	S-Sl

Table 1.—Continued

Species	Collection locality	Position ^a	Power stroke ^b	Sinusoid curve ^c	Flexing form ^d
<i>Uranotaenia lowii</i> Theobald	Honduras	M	1/64	0.15 ± 0.05	I-Su

* Mouth brush movement observed.

^a Position where movement usually occurs: B = bottom of water column, M = middle of water column, S = surface of water column.

^b Range of maximum fraction of a second for completion of power stroke.

^c Mean ± SD of amplitude over half wavelength; where no SD, only one frame measured.

^d I-Sp = irregular, sporadic; I-Su = irregular, sustained; S-Sl = sinuous, slow; S-Fs = sinuous, fast; SS = semisymmetric; A = anopheline.

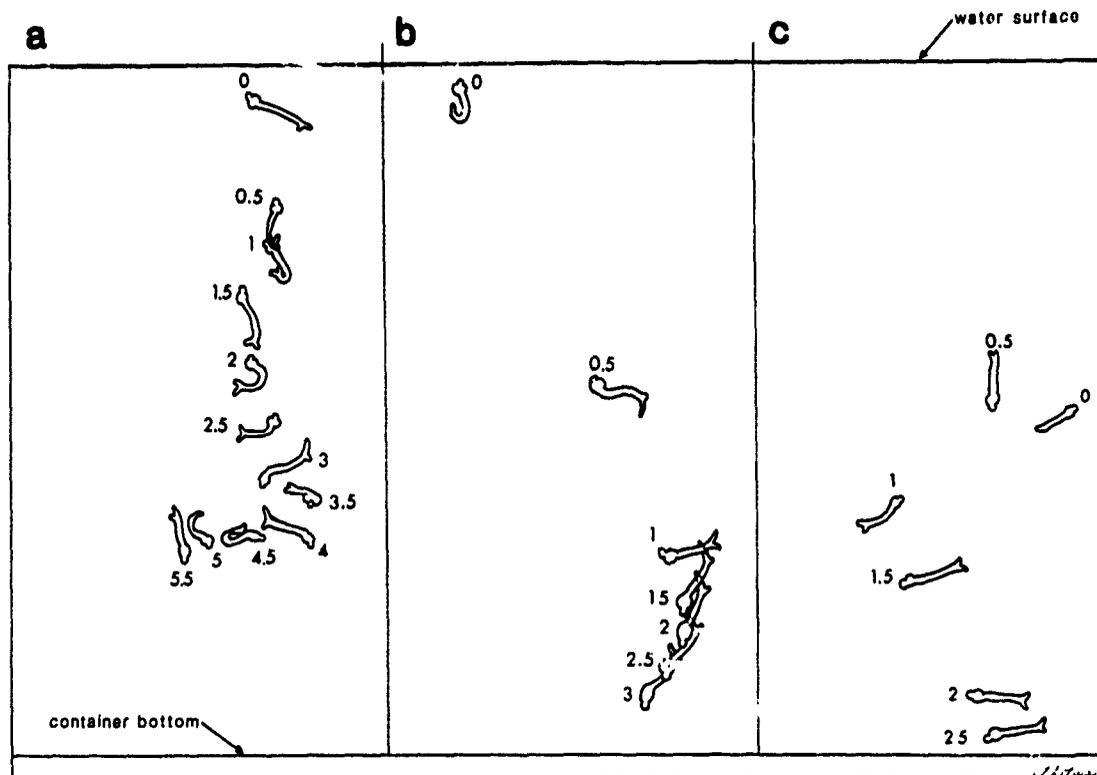


Fig. 1. Representative paths of mosquito larvae. Numbers are time in seconds. The paths and species are: a, vertical turning to horizontal, *Deinocerites pseudes*; b, vertical, *Culex peus* (formerly *thriambus*); c, erratic, *Cx pilosus*.

slowly in a recovery stroke (Figs. 2b-d). Finally, the larva quickly flexed in a power stroke in the opposite direction from the previous flexion (Fig. 2e).

The mechanics of a mosquito larva's pattern of propulsion corresponded to Gray's (1953) model of undulatory motion. Unlike Gray's examples using snakes and ceratopogonid larvae, the mosquito larva's body represents only a portion of the undulatory cycle at any one time. Figure 3a illustrates how the power stroke of a larva corresponds to half of a wavelength of a snake in active movement. The alternating directions of flexion of the larva correspond to the alternating curves of the snake and serve the

same purpose of cancelling lateral deviation from the principle path of the animal. Because the larva uses the entire length of its body in forming a single curve, it is unable to apply power as continuously as a snake. The recovery stroke of the larva represents a single point on the snake where no forward thrust is applied. A possible advantage of this system to the larva is that it maximizes the amplitude of its undulations. According to Gray (1953), the thrust of an undulation is proportional to its amplitude; therefore, the mosquito larval flexing mechanism trades the continuous application of thrust used by snakes or ceratopogonids for a discontinuous, but stronger, series of thrusts.

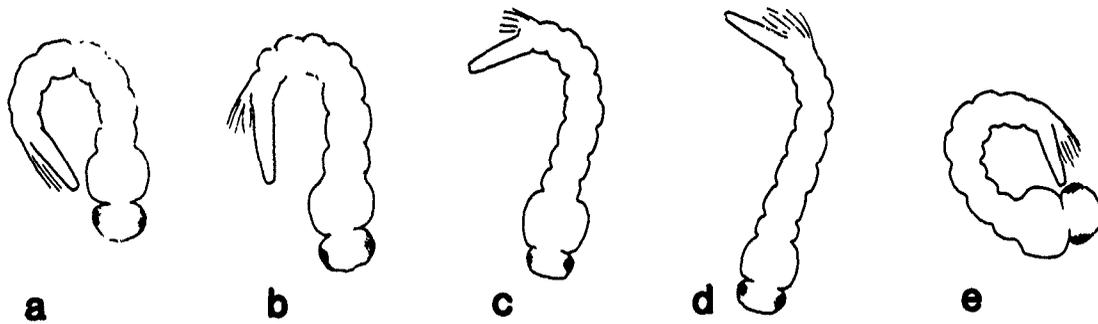


Fig. 2. Stages in flexing movement of mosquito larva (*Aedes vexans*) at 1/32 second intervals; a-d, recovery stroke; e, power stroke.

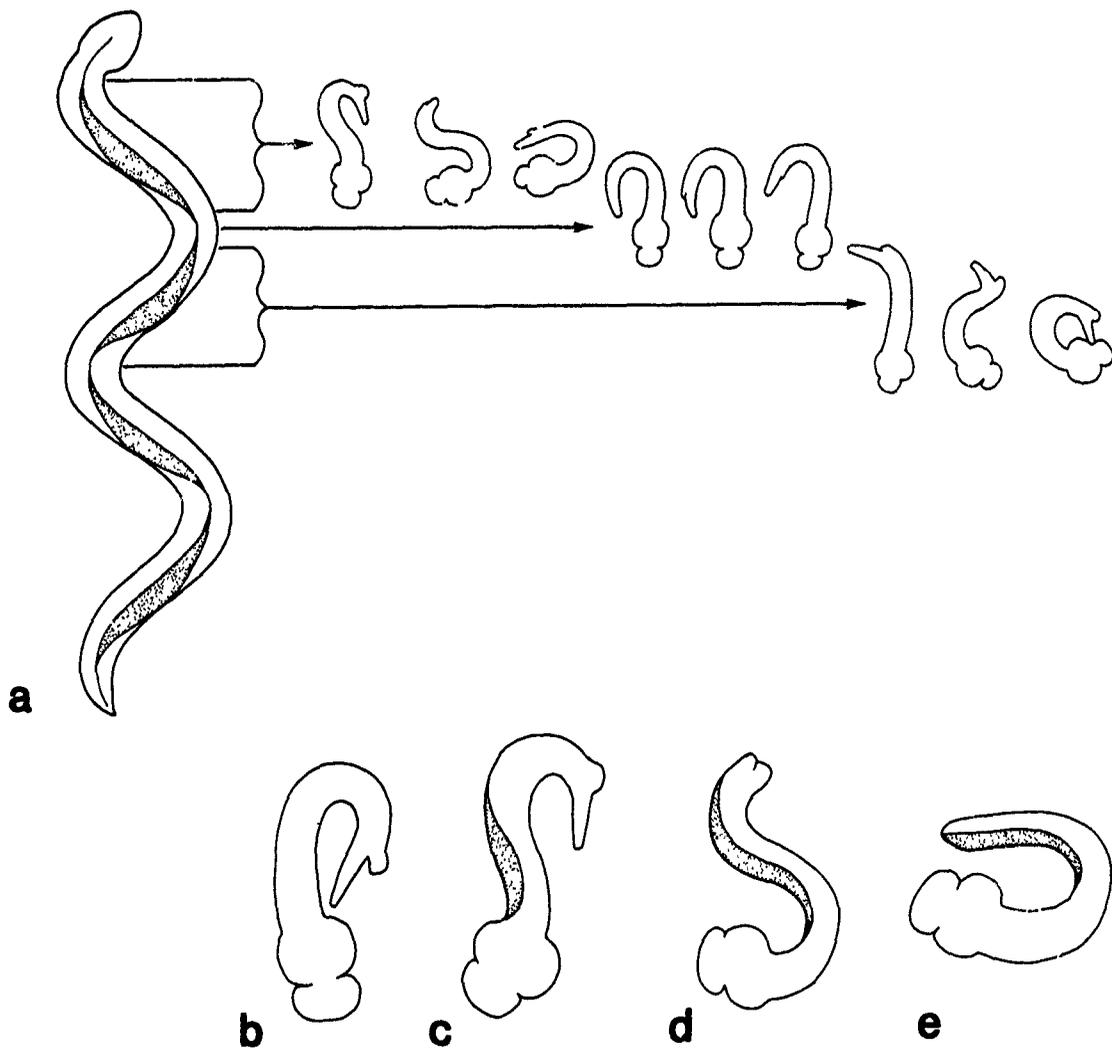


Fig. 3. Comparison of flexing in mosquito larva to undulatory propulsion in a snake (a) and application of propulsive force (b-e) by mosquito larva. Shaded areas are proportional to qualitative assessment of forward force applied at each point of the animals' bodies.

Nachtigall (1965) analyzed larval culicine movement using high speed photography of an unnamed *Aedes* species. He concluded that the larva pulls itself through the water by propulsion

from "fans" at the posterior of the abdomen (probably referring to large branched setae on the siphon and on segments VIII and X), emphasizing that active movement by the anterior

of the larva was important in counterbalancing abdominal motions. Although the propulsion provided by large branched setae at the posterior of the larva may provide the majority of force in many species, Nachtigall's analysis ignored the undulatory component of propulsion that accounts for much of the form observed in flexing motion.

The recovery stroke must be different from the power stroke, otherwise this stroke would push the larva as far backward as the power stroke had pushed it forward. Slower speed and adjustment of the pitch of broad surfaces like the anal brush (seta 4-X) probably contribute to a reduction in backward propulsion during the recovery. A more subtle aspect of the recovery stroke was the formation of a second curve in the anterior of the larval body (Figs. 3c-d). This curve imparted a sinusoid or "S" shape to the larva just before the power stroke. Figures 3b-e illustrate diagrammatically how formation of the sinusoid curve imparted forward propulsive force continuously along most of the length of the larva beginning anteriorly and progressing posteriorly. Formation of the sinusoid curve reduced the amount of the recovery stroke which did not produce forward propulsion and, therefore, reduced the discontinuity of thrust characteristic of mosquito larval flexing mechanisms. Mechanically, the increase of sinusoid curvature would decrease discontinuity of thrust, but also reduce the effective amplitude and power of the final flexion.

The basic flexing mechanism varied among species. The most significant variations were in the speed of the power stroke and the degree of sinusoid curvature before the power stroke. Differences in the speed of the recovery stroke were difficult to analyze because of intraspecific variability. Table 1 lists the speed of the power stroke as a range of fractions of a second corresponding to the frame speed of the motion pictures. Three or four flexing cycles were observed in order to judge the speed. Power stroke speeds for those species filmed at 24 fps were included only when the stroke lasted longer than 1/24 second. Some species were so rapid that the power stroke was less than 1/64 second (i.e., the larva went through more than one flexing cycle in 1/64 second).

The degree of sinusoidal curvature was measured from outlines of projected frames from the film. A line drawn through the center of the outline was taken as the sinusoid curve. The degree of "S" bending was then expressed as the ratio of the amplitude to half of the wavelength (i.e., peak to valley) of the sinusoid curve (Fig. 4). Three or four outlines from different flexing cycles were measured for each species filmed at

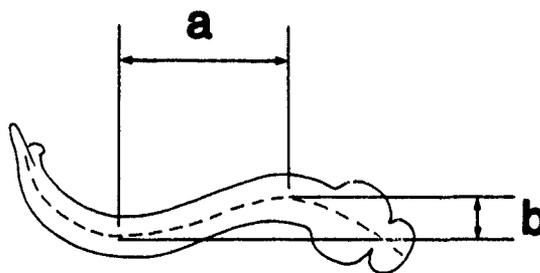


Fig. 4. Measurements made to assess degree of sinusoid curvature on mosquito larvae: a. half wavelength, b. amplitude.

64 fps. Rapid species filmed at 24 fps were not measured because the film failed to capture postures with adequate precision.

The quantitative differences between species corresponded to differences in form observed by the human eye. In terms of form, the flexing mechanism was divided into four types: (1) irregular (both sustained and sporadic), (2) sinuous (both fast and slow), (3) semisymmetric and (4) anopheline. These types are listed for each species in Table 1.

Irregular flexing presented the appearance of rapid movement with little repetition of postures, particularly when viewed from the side. The overall impression was one of ungraceful, energetic flexing. Much of the irregularity was due to frequent changes of perspective as the larva rotated its axis with respect to the observer. Also contributing to this impression was a rapid power stroke which prevented the eye from seeing more than a blur and the weak development of a sinusoid curve during the cycle (Fig. 5a). The shallow sinusoid curve forced the posterior of the larva to travel through a greater arc and created the impression of a series of C-shapes rather than S-shapes. Sporadic irregular flexion occurred as a short burst of activity which tended to propel the larva in an erratic path. Sustained irregular flexion was of greater duration, moving the larva along a straighter path.

Sinuous motion was observed in fast and slow varieties. Fast sinuous flexing combined a rapid power stroke with strong development of a sinusoid curve (Fig. 5b). This type of flexing did not appear graceful, but it did leave the impression of a series of S-shapes in the body of the larva. Slow sinuous flexing (Fig. 5c) included a slow power stroke which contributed to a regular and graceful impression.

Semisymmetric flexing was characterized by a slow power stroke, poor development of a sinusoid curve and greater movement of the anterior portion of the larva during each flexion (Fig. 5d). The relative speed of the power and

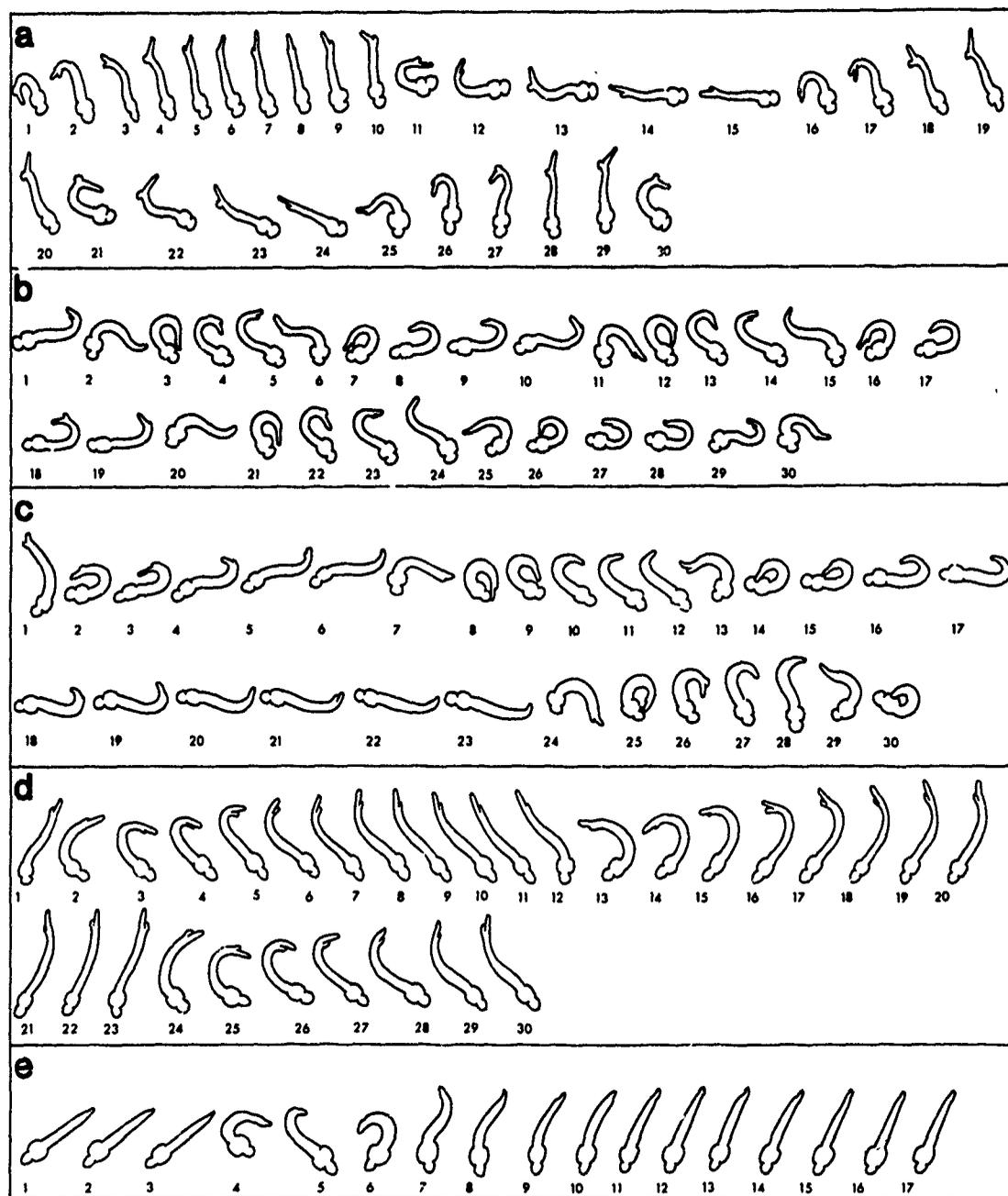


Fig. 5. Top views of mosquito larvae illustrating flexing mechanisms with outlines of larvae filmed at 64 fps. Each number represents a successive frame of the film. Flexing mechanisms and species are: a. sustained irregular, *Culex nigripalpus*; b. fast sinuous, *Aedes taeniorhynchus*; c. slow sinuous, *Haemagogus anastasionis*; d. semisymmetric, *Trichoprosopon digitatum*; e. anopheline, *Anopheles hectoris*.

recovery strokes was similar so that progression of the larva appeared as a series of reversing C-shapes, often blending into a sinusoid track. Progression in these species was usually slow, and their movement presented a very graceful appearance.

Anopheline movement was the most distinctive of the types of flexing (Fig. 5e). Movement was extremely rapid, sometimes completing at

least two flexion cycles in 1/64 second. When possible to observe it, the development of a sinusoid curve in *Anopheles* was strong. Flexing usually lasted for only one or two cycles, providing adequate propulsion for considerable forward travel.

Although undulatory movement was most conspicuous, mosquito larvae also employed mouth brush movement. In mouth brush move-

ment the larva's head was forward (i.e., the opposite from undulatory movement) and propulsion was provided by the rapid action of the mouth brushes against a substrate or the water. Those species for which mouth brush movement was observed are indicated in Table 1. The absence of mouth brush movement was difficult to determine because of the short duration of the films.

Other forms of movement were observed, some of which were unusual. *Culex erraticus* and *Cx. educator* Dyar and Knab were able to progress horizontally by pushing against the water surface tension with their siphons. The siphon would detach from the surface, move forward (anteriorly in relation to the larva), reattach, then push the larva a short distance forward. *Shannoniana moralesi* (Dyar and Knab) moved forward using its head against the substrate. The larva's head would rock forward, contact the substrate, then pull the body of the larva forward. This species was able to move in this way on vertical as well as horizontal surfaces. The manner in which it adhered to a vertical surface was not apparent. Although not as unusual, movement by *Orthopodomyia kummi* was distinctive. This species spent most of its time hanging from the surface. When disturbed, the larva would slowly drift down, only occasionally flexing to accelerate its progress.

Although not the principle focus of this study, posture of larvae at rest appeared to be characteristic of each species studied. Figure 6 illustrates examples of the various postures observed. These postures were traced from single frames of movie sequences which included a larva at rest. Although difficult to assess how typical each posture was for the species, the illustrations are representative of observations in this study. No attempt was made to systematize the variety of postures, but certainly angle to the surface and the orientation of the dorsum to the container bottom were important elements.

Particular flexing mechanisms were associated with certain taxonomic groups (Table 2). All *Anopheles* shared anopheline movement; and all *Culex* (*Culex*), except *Cx. corniger* gp., shared sustained irregular flexing. All sabethines, except *Wyeomyia*, displayed semisymmetric flexing. *Culex* (*Melanoconion*) used only sporadic irregular flexing, *Haemagogus* (*Haemagogus*) used only slow sinuous flexing and *Psorophora* used only fast sinuous flexing. *Aedes* (*Ochlerotatus*), *Aedes* (*Howardina*), *Culex* (*Carrollia*), *Deinocerites* and *Wyeomyia* used more than one mechanism.

Literature on the mechanics of flexing movement varies from simple comments on flexing as a series of alternate lashing movements of the

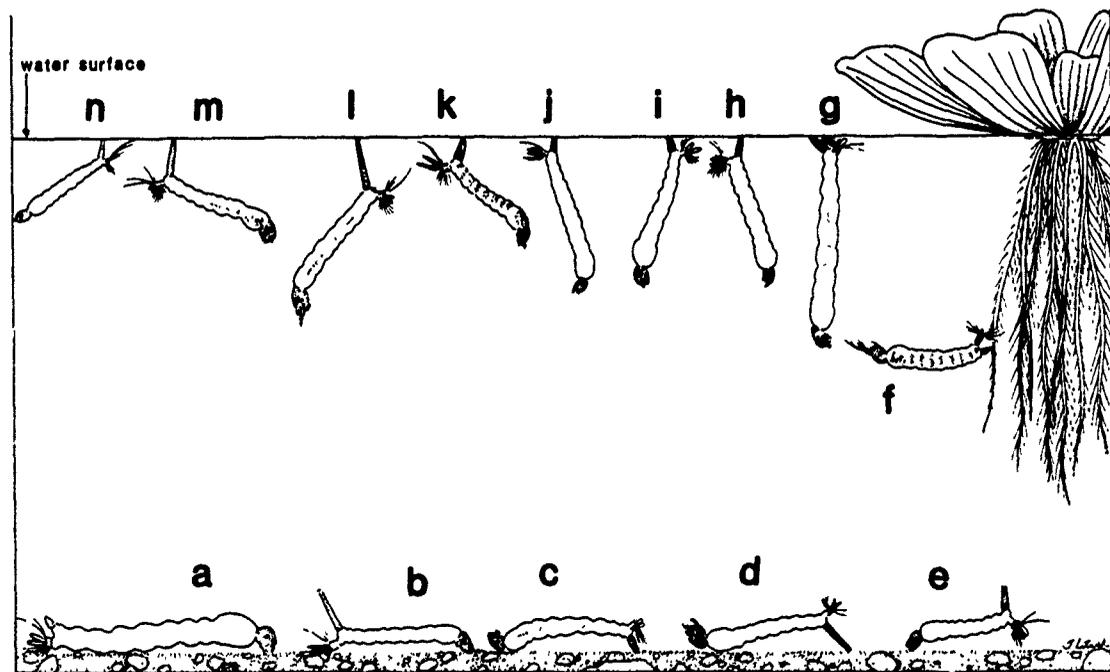


Fig. 6. Postures of representative culicine mosquito larvae while not swimming, illustrated in an artificial composite of species. Species are: a. *Trichoprosopon digitatum*; b. *Culex* (*Cux.*) sp. B; c. *Wyeomyia arthrostigma*; d. *Cx. imitator*; e. *Cx. quinquefasciatus*; f. *Mansonia titillans*; g. *Wy. arthrostigma*; h. *Aedes taeniorhynchus*; i. *Ae. epactius*; j. *Ae. guerrero*; k. *Psorophora confinnis*; l. *Cx. coronator*; m. *Cx. nigripalpus*; n. *Uranotaenia lowii*.

Table 2. Flexing mechanisms among taxonomic groups.

Group	No. of species using flexing mechanism*					
	I-Sp	I-Su	S-Sl	S-Fa	SS	A
<i>Aedeomyia</i>	1					
<i>Aedes</i> (<i>Howardina</i>)		1				1
<i>Aedes</i> (<i>Ochlerotatus</i>)			2	1		
<i>Anopheles</i>						6
<i>Culiseta</i>				1		
<i>Culex</i> (<i>Carrollia</i>)		1				1
<i>Culex</i> (<i>Culex</i>)		7		1		
<i>Culex</i> (<i>Melanoconion</i>)	1					
<i>Culex</i> (<i>Microculex</i>)	1					
<i>Deinocerites</i>			1			1
<i>Haemagogus</i> (<i>Haemagogus</i>)			3			
<i>Mansonia</i>						1
<i>Psorophora</i>				2		
<i>Toxorhynchites</i>			1			
<i>Uranotaenia</i>		1				
<i>Sabethes</i> , <i>Limatus</i> , <i>Trichoprosopon</i>						5
<i>Wyeomyia</i> (<i>Wyeomyia</i>)			1			2

* I-Sp = irregular, sporadic; I-Su = irregular, sustained; S-Sl = sinuous, slow; S-Fa = sinuous, fast; SS = semisymmetric; A = anopheline.

abdomen or formation of S-shapes (McDaniel 1935, Hopkins 1952, Maslov 1964, Sirota 1975, Van Pletzen 1981) to the detailed analysis of Nachtigall (1965). Mouth brush movement has been described repeatedly (e.g., Sirota 1975, Van Pletzen 1981). Brief descriptions of unusual patterns of movement include Nikolsky (1924) on movement by *An. maculipennis* Meigen over dry surfaces, Mattingly (1969) on "shimmying" movement by *Armigeres* and *Eretmapodites*, and Lounibos (1983) on "sinuous crawling" by *Armigeres*, *Eretmapodites* and *Trichoprosopon*.

The purposes of movement have been studied by a number of authors. The most comprehensive categorizations of larval behavior include Jones (1954) for *An. quadrimaculatus* Say, Maslov (1964) for *Cs. bergrothi* (Edwards) and Van Pletzen (1981) for *Cs. longiareolata* (Macquart). These studies attribute flexing movement to alarm reactions and to food seeking. Other studies also associate flexing movement with alarm, especially in response to the passage of a shadow (Mast 1911, Bates 1949, Thomas 1950, Hocking 1953, Leftwich 1954). Larvae have also been observed to swim towards a favorable or optimal temperature (Fernald and Burger 1980), toward shade (Muirhead Thomson 1940) or away from parasitic mites (Smith and McIver 1984).

Except for the differences between culicine and anopheline movement, few comments have been made on the differences between move-

ment and posture of taxonomic groups. Shannon (1931) discussed the differences in movement and behavior of *Ae. aegypti* (Linnaeus), *Culex*, *Anopheles* and sabethines, including comments on their overall levels of activity and usual positions in the water column. He described the flexing of *Ae. aegypti* as more "looping" than *Culex*. Peyton (1977) described general appearance and posture of 11 species in his revision of *Uranotaenia* (*Pseudoficalbia*). Lounibos (1983) proposed that the sinuous movement of *Armigeres*, *Eretmapodites* and *Trichoprosopon* is evolutionarily convergent in the three groups as a result of selection in the viscous fruit husk habitat.

Outside the family Culicidae, Nachtigall's (1965) study compared flexing movement in *Ceratopogon* (Diptera: Ceratopogonidae), *Chironomus* (Diptera: Chironomidae) and *Chaoborus* (Diptera: Chaoboridae), as well as in *Aedes*. The movement of *Ceratopogon* is completely undulatory with progression toward the head. *Chironomus* also moves in the direction of its head, but with a series of looping postures. *Chaoborus* moves similarly to *Aedes*, but with greater movement of the head, resulting in lateral progression of the larva. Linley's (1986) excellent analysis of movement in *Culicoides variipennis* (Coquillett) confirmed undulatory movement in another ceratopogonid and described a change in mechanism when the larva enters a viscous medium.

Results of the current study and observations scattered in the literature demonstrate that larval movement and posture vary among species in visible ways. This variation is not always consistent within groups, but some trends are certainly apparent. The presence of exceptional forms of movement within groups would suggest that the pattern of movement is very plastic evolutionarily and/or that differences within groups indicate the presence of subgroups. Some of the examples recorded in this study suggest the latter possibility: *Cx. corniger* gp. is part of a group of species which are morphologically distinct from other members of the subgenus *Culex* in the New World; the subgenus *Howardina* of *Aedes* is distinct from *Ochlerotatus*; and *Wyeomyia* might be more distinct from the other sabethine genera than is generally supposed. On the other hand, variation within the genera *Deinocerites*, *Culex* (*Carrollia*) and *Aedes* (*Howardina*) suggest that pattern of movement is not fixed in phyletic lines.

Observations of movement can be an important aid to field identification, which must begin by delimiting the potential fauna of a site by geographic area and habitat characteristics. Morphology and movement patterns can then contribute to selection of probable genus,

subgenus or even species from the narrowed list of possibilities. An example of this process would be a ground pool in Central America. Such pools might commonly contain larvae lying parallel to the surface which use anopheline movement, dark larvae with siphons of short to moderate length which use fast sinuous movement, light larvae with prominent antennal tufts and siphons of moderate to long length which use sustained irregular movement, and small larvae with dark markings and long siphons which use sporadic irregular movement. From these observations, one would infer the presence of *Anopheles*, *Aedes* (*Ochlerotatus*) (more rarely *Aedimorphus* at higher elevations), *Culex* (*Culex*) (more rarely *Neoculex*) and *Culex* (*Melanoconion*). Such a scheme for field identification presupposes knowledge of distribution, habitat and morphology, which is available in the literature. Comparison of living larvae and categorization of their patterns of movement should provide experience necessary to recognize types of movement in the field without the aid of cinematography.

ACKNOWLEDGMENTS

This study would not have been possible without initial instruction and continuing encouragement by E. L. Peyton, Walter Reed Biosystematics Unit. I also wish to thank John Petersen and Norberto Guerrero of the Gorgas Memorial Laboratory for support in Panama, Jonathan Pratt and Ronald Koinzan of Medical Element, JTF-Bravo for technical assistance in Honduras, Donald Roberts of the Uniformed Services University of the Health Sciences (USUHS), Bethesda, MD, for assistance in Mexico, Bruce Harrison for organizational support and Taina Litwak for preparing the figures for analysis and publication. National Aeronautics and Space Administration (NASA) contract W-16,306 to USUHS, entitled Application of Remote Sensing and Predictive Modeling to Malaria Transmission and Vector Ecology, funded field work in Mexico. My special thanks go to Imre Toth, Charles Whieldon, David Balaban and Kamaran Halmat of Motion Picture Production, Division of Medical Audio-visual Services, Walter Reed Army Institute of Research, for generous assistance in production of the films.

REFERENCES CITED

- Bates, M. 1949. The natural history of mosquitoes. Harper and Row Publishers, New York.
- Fernald, G. P. and J. F. Burger. 1980. Effect of temperature and light on aggregation behavior of *Aedes stimulans* larvae (Diptera: Culicidae) in a woodland pool. J. N. Y. Entomol. Soc. 88:47.
- Gray, J. 1953. Undulatory propulsion. Quarterly J. Microsc. Sci. 94: 551-578.
- Headlee, T. J. 1945. The mosquitoes of New Jersey and their control. Rutgers Univ. Press, New Brunswick.
- Hocking, B. 1953. Notes on the activities of *Aedes* larvae. Mosq. News 13:62-64.
- Hopkins, G. H. E. 1952. Mosquitoes of the Ethiopian Region. I. Larval bionomics of mosquitoes and taxonomy of culicine larvae. British Museum of Natural History, London.
- Jones, J. C. 1954. Some notes on the behavior of fourth instar *Anopheles quadrimaculatus* Say (Diptera, Culicidae). Mosq. News 14:186-191.
- Leftwich, A. W. 1954. Vision and blindness in mosquito larvae as indicated by the submerging reflex. Proc. R. Entomol. Soc. A29(10), 12:156-162.
- Linley, J. R. 1986. Swimming behavior of the larva of *Culicoides variipennis* (Diptera: Ceratopogonidae) and its relationship to temperature and viscosity. J. Med. Entomol. 23:473-483.
- Lounibos, L. P. 1983. Behavioral convergences among fruit-husk mosquitoes. Fl. Entomol. 66:32-41.
- Maslov, A. V. 1964. On the conditions of life and normal behavior of mosquitoes *Culiseta bergrothi* Edw. (Diptera, Culicidae). Zool. Zh. 43:849-871. (In Russian).
- Mast, S. O. 1911. Light and behavior of organisms. First edition. John Wiley and Sons, New York.
- Mattingly, P. F. 1969. The biology of mosquito-borne disease. George Allen and Unwin Ltd., London.
- McDaniel, E. I. 1935. Flies and mosquitoes commonly found about Michigan homes. Agric. Exp. Stn. Mich. State College, Circ. Bull. 144, Revised. 27 pp.
- Muirhead-Thomson, R. C. 1940. Studies on the behaviour of *Anopheles minimus*. Part II. The influence of water movement on the selection of the breeding place. J. Malaria Inst. India 3:295-322.
- Nachtigall, W. 1965. Locomotion: swimming (hydrodynamics) of aquatic insects, pp. 255-281. In: M. Rockstein (ed.), The physiology of insects, Vol. 2, Academic Press, New York.
- Nikolsky, V. V. 1924. Observations on the ability of larvae of *Anopheles maculipennis* Mg. to crawl. Bull. Entomol. Res. 15:177-178.
- Nutall, G. H. F. and A. E. Shipley. 1901. Studies in relation to malaria. II. The structure and biology of *Anopheles* (*Anopheles maculipennis*). The egg and larva. J. Hyg. 1:45-77.
- Peyton, E. L. 1977. Medical entomology studies. X. A revision of the subgenus *Pseudoficalbia* of the genus *Uranotaenia* in Southeast Asia (Diptera: Culicidae). Contrib. Am. Entomol. Inst. (Ann Arbor) 14:1-273.
- Shannon, R. C. 1931. The environment and behaviour of some Brazilian mosquitoes. Proc. Entomol. Soc. Wash. 33:1-27.
- Sirota, Y. 1975. Population density and rate of dispersal of larvae of *Culex pipiens molestus* (Diptera, Culicidae) (Experimental studies on the dispersal of insects, I). Kontyû, Tokyo 43:233-241.
- Smith, B. P. and S. B. McIver. 1984. Factors influenc-

- ing host selection and successful parasitism of *Aedes* spp. mosquitoes by *Arrenurus* spp. mites. Can. J. Zool. 62:1114-1120.
- Strickman, D. 1988. Redescription of the holotype of *Culex* (*Culex*) *peus* Speiser and taxonomy of *Culex* (*Culex*) *stigmatosoma* Dyar and *thriambus* Dyar (Diptera: Culicidae). Proc. Entomol. Soc. Wash. 90:484-494.
- Thomas, I. M. 1950. The reactions of mosquito larvae to regular repetitions of shadows as stimuli. Aust. J. Sci. Res. 3B:113-123.
- Van Pletzen R. 1981. Larval and pupal behaviour in *Culiseta longiareolata* (Macquart, 1838) (Culicidae, Diptera). J. Limnol. Soc. S. Africa 7:24-28.

DTIC
ELECTE
JUL 08 1991
S C D

Accession For	
NTIS GRA&I	<input checked="" type="checkbox"/>
DTIC TAB	<input type="checkbox"/>
Unannounced	<input type="checkbox"/>
Justification	
By _____	
Distribution/	
Availability Codes	
Dist	Avail and/or Special
A-1	20

