

SUGAR-FEEDING BEHAVIOR OF *LUTZOMYIA TRAPIDOI* (DIPTERA: PSYCHODIDAE) UNDER EXPERIMENTAL CONDITIONS¹By Byron N. Chaniotis²

Abstract: Phlebotomine sandflies, like many other hematophagous Diptera, require a source of carbohydrate for sustenance. This paper is an attempt to establish useful criteria for sugar feeding of these flies. Utilizing the Panamanian *Lutzomyia trapidoi* (Fairchild & Hertig), a number of parameters associated with experimental feeding were investigated. Of 11 sugars tested, 5 were preferred: sucrose, fructose, maltose, raffinose and glucose. These 5 sugars are primary constituents of nectar, probably the most important energy source in nature for hematophagous flies. Honey was less acceptable than fructose

or corn syrup (Karo). Rate of sugar acceptance was unaffected by concentration, pH, NaCl content, color of the solution or temperature. Concentration of sugar solution had no appreciable effect on fly longevity. Higher feeding rates were obtained utilizing a new holding vessel (styrofoam cup).

The sugar feeding habits of nematoceros biting flies have been well established (Downes 1958). In nature, both sexes obtain sugars from nectar, honeydew, plant juices, or ripe fruit, and in the laboratory, they feed on a wide variety of sweet substances, such as pure sugar solutions, raisins, fresh fruit, and solutions of various commercially available syrups and honey. However, optimal

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laboratory feeding conditions have not been established.

While the blood meal enters the midgut directly and serves principally for ovarian development, sugar solutions are diverted into the esophageal diverticulum and serve as an energy source for the insect's normal activities. Without the provision of sugar, laboratory-reared mosquitoes do not survive more than a few days (Galun & Fraenkel 1957), and I had similar experiences with phlebotomine sandflies.

The present work attempts to define a number of parameters associated with the practical aspects of sugar feeding in laboratory colonies of phlebotomine sandflies in order to achieve maximum longevity and facilitate their maintenance.

MATERIALS AND METHODS

Laboratory-reared *Lutzomyia trapidoi* (Fairchild & Hertig) were utilized to test the effect of various sugar concentrations on longevity of males and females. All other tests used wild-caught *L. trapidoi* which were captured by aspirators at night, transported to the laboratory the following morning, and used within 24 hr after capture.

In the laboratory, the flies were released into a screened cage and randomly divided into 2 or more (up to 11) groups, depending on the size of the catch and nature of the test. Flies were aspirated from the release cage, anesthetized lightly with CO₂ and placed into 0.24-liter (8-oz.) styrofoam cups (No. H08-01, American Can Co., Easton, Pa.). The cups were 8 cm high and 8 cm in diameter at the top; the bottoms and about 80% of their interior walls were coated with plaster of paris, allowing a volume of about 200 ml. Cups containing sandflies were placed in a pan containing water to about 2 cm in depth. A small perforation (4-5 mm diam.) at the bottom of the cup permitted entry of water to wet the interior coat of plaster. Each cup had a plastic lid with a 5-cm diam. window covered with stretched nylon marquisette (35-40 meshes per linear cm).

Reagent grade sugars were used in all tests and were obtained as follows: fructose, mannose, L-glucose, xylose, D- and L-arabinose sucrose and raffinose (General Biochemicals, Chagrin Falls, Ohio); galactose (Difco, Detroit, Mich.); dextrose (Allied Chemical, Morristown, N. J.), and maltose (Fisher Sci. Co., Fair Lawn, N. J.). Solutions were made by weight (w/v) in distilled water. To obtain saturated solutions, powdered sugar was added to a small volume of water until an undissolved residue remained at the bottom of the vial. In testing the

influence of pH on feeding behavior, solutions of sugar with pH 7.1 and 8.4 were made with TRIS buffer, and solutions with pH 4.2 were made with acetate buffer. Solutions of Karo and honey were prepared by volume (v/v). Sugar solutions were made fresh weekly and were kept in screw-cap vials in a refrigerator (5°C). To determine the volume intake of sugar by the flies, as well as the degree of satiation, 1 drop of green food coloring (McCormick & Co., Baltimore, Md.) was added to each 2.5 ml of sugar solution. Red color was used only once in a test for color preference.

Ten small drops of sugar solution were placed on the stretched nylon mesh of the lid and flies were allowed to feed for 24 hr at 25.5°C to 27.5°C, with dark-light photoperiod of approximately 12:12 hr. At the end of this period, the surviving flies were aspirated, killed with CO₂ or cold, and examined while fresh with a stereoscopic microscope for the presence or absence of green-dyed sugar, as well as for the degree of satiation. Sugar-fed flies were classified into 3 categories based on the volume of sugar imbibed: S, with traces of sugar in abdomen; L, with large amount of sugar filling and distending the abdomen; and M with sugar filling a good part or all of the abdomen but producing no distention.

To determine the volume of a sugar meal, flies were allowed to feed on chromium 51-labeled fructose. Each fly was then placed in a 1.18-g (1-dram) vial, and its radioactivity was measured with a radiation counter (Model 181A, Nuclear Chicago, Chicago, Ill.) and compared with radioactivity emitted by a number of control sugar solutions in 1-, 5- and 10-lambda capillary tubes. These flies had been previously classified as S, M, L as described above.

The localization of the sugar solution in the insect was determined by dissection and bloating. Flies to be dissected were washed in 1% detergent solution in water for 1 min. and dissected in a drop of physiological saline with a pair of fine needles. First the head was snipped off, and then the alimentary tract and associated structures were pulled out along with the last abdominal segments. In the 2nd method, flies were washed in detergent solution, as before, and then allowed to bloat in distilled water at 5°C for several days. The highly distended abdominal wall permitted good visibility of the internal organs, including the ventral diverticulum with the colored sugar solution.

RESULTS AND DISCUSSION

Sugar acceptance. It is clear from the data in

TABLE 1. Acceptability of various sugars to wild-caught *L. trapidoi* females.

SUGAR SOLUTION 20%	REPLICATES					Mean	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
Sucrose	83.2(65)*	97.6(47)	93.4(61)	93.3(60)	94.4(54)	93.4(267)	18-70-12
Fructose	85.5(55)	95.2(42)	100.0(61)	84.1(44)	86.4(59)	90.4(261)	18-69-15
Maltose	77.1(83)	95.7(32)	89.8(59)	74.5(51)	75.7(66)	80.1(301)	40-57-3
Raffinose	75.9(34)	86.5(52)	68.9(45)	75.0(56)	72.9(59)	75.9(266)	42-53-5
D-glucose	45.5(61)	83.3(48)	71.9(64)	62.1(58)	72.7(55)	68.4(295)	50-43-7
D-arabinose	30.2(53)	34.8(46)	50.4(52)	56.2(32)	46.7(54)	43.7(233)	78-21-1
Xylose	0.0(57)	15.6(46)	31.9(47)	39.5(43)	6.5(77)	17.0(270)	85-15-0
L-arabinose	5.1(59)	18.2(44)	43.5(46)	3.9(34)	4.8(63)	14.2(246)	83-17-0
Galactose	7.8(77)	0.0(49)	12.3(57)	14.3(42)	15.4(52)	9.7(277)	100-0-0
Mannose	0.0(54)	7.5(40)	13.4(67)	12.8(47)	10.0(63)	8.9(268)	100-0-0
L-glucose	0.0(55)	0.0(42)	3.0(44)	0.0(49)	0.0(60)	0.0(250)	—

*% feeding (number of flies tested).

TABLE 1 that female *L. trapidoi* accepted some sugars and rejected others, indicating a capacity to discriminate among a variety of possible carbohydrate energy sources. The order of acceptance among the 5 most preferred sugars was sucrose, fructose, maltose, raffinose, and D-glucose (dextrose). Sugars accepted included 2 monosaccharides (fructose, dextrose), 2 disaccharides (sucrose, maltose), and 1 trisaccharide (raffinose), an aldohexose (dextrose) and a ketohexose (fructose), as well as dextro and levorotatory sugars (dextrose, fructose). Of the monosaccharides, hexoses elicited the strongest (fructose, dextrose) and the weakest (mannose, galactose) feeding response, while the 2 pentoses (arabinose, xylose) elicited a moderate one. The only discernible association between sugar acceptance and structural properties was in the case of glucose and arabinose, where the D-isomer appeared more attractive than the L-isomer. It appears more likely that the basic underlying relationship among the 5 accepted sugars is the fact that they are the principal constituents of nectar (Wykes 1952), probably the most important carbohydrate source for hematophagous flies in nature. Furthermore, fructose and glucose are abundantly found in a wide variety of fruits which are also potential

energy sources for insects. The sugar feeding behavior of sandflies under experimental conditions seems thus to reflect their natural propensity to feed on nectar, sweet plant exudates and ripe fruits. The experimental results are consistent with the studies of Lewis & Domoney (1966) who detected by chromatographic analysis fructose, glucose, maltose, sucrose and raffinose in the diverticulum of wild-caught paleotomine sandflies, precisely the same sugars *L. trapidoi* took in the laboratory.

Sucrose and fructose provided the strongest feeding stimulus, inducing more than 90% of flies to imbibe predominantly large and moderate volumes of sugar solution (TABLE 1). In some instances, the sugar solution filled and distended the abdomen in its entirety by the expansion of the ventral diverticulum which, even in the most highly satiated specimens, was found to contain the entire volume of ingested sugar.

D-arabinose, an aldopentose, has no nutritive value for mosquitoes and certain flies (Dethier et al. 1956, Galun & Fraenkel 1957). However, 43.7% of sandflies fed upon it, mostly in low-volume feedings. To test its nutritive value, D-arabinose was offered as a 20% solution to newly emerged, laboratory-reared *L. trapidoi* females. Maximum

TABLE 2. Effect of concentration on acceptability of fructose solution to wild-caught *L. trapidoi* females.

FRUCTOSE (% CONC.)	REPLICATES					MEAN	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
0*	1.7(60)**	0.0(34)	7.8(51)	3.1(64)	0.0(58)	2.6(267)	100-0-0
10	85.5(62)	89.2(65)	92.7(55)	92.4(53)	83.3(48)	88.7(283)	22-67-11
20	86.2(58)	86.0(50)	90.0(60)	88.2(51)	88.5(52)	88.2(271)	26-66-8
30	87.3(55)	87.7(57)	94.3(53)	95.4(44)	80.4(51)	88.6(260)	22-70-8
40	82.8(70)	87.5(48)	88.3(77)	89.4(47)	94.0(33)	87.6(275)	24-67-9
50	83.3(66)	87.8(74)	81.2(48)	94.3(53)	85.2(27)	86.6(268)	26-64-8
Satur.	76.6(64)	89.6(77)	84.3(70)	90.6(53)	85.1(47)	85.2(311)	27-65-13

*Distilled water.

**% feeding (number of flies tested).

TABLE 3. Effect of pH on acceptability of sugar solution to wild-caught *L. hepessi* females.

SUCROSE 20%	REPLICATES					MEAN	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
pH 4.1	91.1(99)*	90.6(92)	79.4(63)	73.1(93)	77.8(36)	81.8(314)	24-72-4
pH 7.1	85.5(32)	91.9(99)	65.2(46)	82.8(122)	100.0(19)	87.2(339)	8-71-28
pH 8.4	89.6(26)	80.0(70)	63.8(47)	78.4(83)	100.0(15)	81.0(316)	10-77-13

*% feeding (number of flies tested).

survival time of 29 females on D-arabinose was 4 days (at 27°C), which does not differ from the longevity of flies fed only distilled water or no water. The maximal survival time of flies fed on 10% and 30% sucrose solution was 35 days (TABLE 9).

Galactose (hexose), mannose (hexose), xylose (pentose), and L-arabinose (pentose) were accepted by relatively few flies; in the majority of feedings the volume of sugar solution imbibed was barely traceable in the abdomen. Galun & Fraenkel (1957) reported arabinose, xylose and mannose to be totally devoid of nutritional value and galactose to be considerably inferior to sucrose for the mosquito *Aedes aegypti* (L.).

The only sugar which was totally unacceptable to sandflies was L-glucose; this is in contrast to the relatively high feeding rate on the related D-glucose. Considering the tendency of sandflies to imbibe pure water (TABLE 2), the total rejection of L-glucose by the flies indicates that this compound may be toxic.

Concentration. Following selection of the proper sugar, the next obvious step is to determine the optimal concentration. A simple criterion to do this is the rate of acceptance as well as the volume of intake. Ideally, consideration should also be given to the effects of various sugar concentrations on longevity, blood-feeding and mating of adult flies.

The test for optimal concentration included solutions varying from 10% to saturation, with distilled water as a control. The results summarized in TABLE 2 show little difference in rate of acceptance among the various solutions. It must be concluded that viscosity and osmotic pressure are not vital factors in sugar feeding in sandflies.

It must be pointed out that the method of providing sugar to the flies in the form of drops on the stretched nylon mesh over a 24-hr period may have resulted in an upward change in concentration of the sugar solution by the evaporation of water. However, the proximity of the sugar solution to the constantly wet interior of the holding vessel and the generally prevailing high ambient relative humidity (85-95%) in the insectary room probably retarded evaporation. On many occasions, I noted no ap-

preciable change in the size of the drops at the end of the feeding period, indicating a negligible evaporation rate.

The acceptance of highly concentrated sugar solutions by sandflies is an interesting revelation. First, it suggests the type of sugar solution which biting flies may take in nature when feeding on nectar and other sweet liquids. Hocking (1953), for instance, estimated that floral nectar contained up to 77% by weight of sugars, and crops of insects contained concentrations of up to 76%. Second, it emphasizes the need to re-evaluate the common practice among workers (Coluzzi 1964, Hosoi 1958) of providing sugar solutions of relatively low concentration to laboratory colonies of hematophagous flies. Mosquitoes are known to feed on solid, dry sugars (Eliaison 1963). In a recent test in our laboratory, I confirmed that phlebotomine sandflies will also feed on solid sugar cubes (sucrose). In light of this, provision of highly saturated sugar solutions (more than 50%) appears to be sensible and at the same time practical from the standpoint of application and preservation.

Hydrogen-ion concentration. As shown in TABLE 3, pH had little effect on feeding success within the range from 4.1 to 8.4. In general, the sugar solution with pH 7.1 (neutral) gave slightly better overall feeding rates and improved satiation over the acid and alkaline solutions. The addition of electrolytes has been shown by Salama (1966) to cause rejection of sugar solution (sucrose) by *Aedes aegypti*, the rejection threshold being lower for acids and hydroxides than for neutral salts.

Color discrimination. The addition of color to the sugar solution was necessitated from practical considerations. These included the need to test more than 1 sugar in competitive tests and to visually detect ingested sugar without resorting to dissection.

Preliminary tests suggested that green-colored sugar solutions were better in terms of feeding rates than solutions containing red color. Based on this observation, 1 non-competitive and 2 competitive tests were run to ascertain the validity of this hypothesis. In the competitive test, flies were

TABLE 4. Preference for color of sugar solution by wild-caught *L. trapidoi* females.

Fructose 20%	REPLICATES					MEAN	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
<i>Non-competitive</i>							
Red	85.0(80)*	86.4(86)	88.8(81)	87.5(84)	93.5(48)	82.7(307)	17-75-8
Green	94.9(78)	86.8(38)	80.9(70)	78.6(103)	90.2(41)	85.2(336)	13-76-11
<i>Competitive</i>							
Red	27.4(73)	37.6(76)	25.0(32)	45.9(37)	37.5(56)	31.7(274)	15-80-5
Green	43.6	22.4	28.1	45.9	57.1	39.1	16-71-13
Red	46.3(54)	31.3(67)	43.1(58)	26.7(45)	41.5(65)	38.1(289)	32-57-11
Green	91.5	43.3	31.0	35.5	30.8	34.6	34-54-12

*% Feeding (number of flies tested).

offered both red and green solutions in equal volume and on alternate positions on the nylon mesh. Results in TABLE 4 demonstrate that sandflies were unaffected by color in selecting sugar solutions. The degree of satiation of flies fed on green solutions was, however, slightly greater in 2 of the 3 tests. Insects are known to be capable of distinguishing colors in the range of 3000 Å to 7000 Å (ultraviolet to infrared), but their sensitivity is much greater in the shorter wave lengths (Weiss 1943). Thus, the lack of selection of either color by sandflies indicates that visual stimuli played no part in selecting sugars. This is not surprising in view of reports that mosquitoes and certain flies control the ingestion of carbohydrates solely by a system of chemoreceptors located on the tarsi, labella, labrum and cibarium (Dethier et al. 1956, Salama 1966).

Sodium chloride. The work of Hosoi (1959) with the mosquito *Culex pipiens* showed that sugar feeding was unaffected when the sodium chloride content

of the solution was 0.15 M (0.87%) but declines at higher concentrations. The results in the present study (TABLE 5) indicate that 0.85% of sodium chloride in 20% fructose solution resulted in lower overall feeding rates than the same sugar concentration in distilled water, but the difference was not statistically significant (analysis of variance).

Holding vessel. In preliminary tests, the conventional clay pot with plaster-lined interior wall (Hertig & Johnson 1961) was employed to hold and feed the flies. Drops of sugar solution were provided on the nylon mesh stretched tightly over the pot orifice. Under these circumstances, feeding rates were moderate and variable. When the disposable styrofoam plaster-lined cup was introduced as holding vessel, a surprising increase in feeding rates occurred. The results of the first test in TABLE 6 show that in each of the 5 replicates considerably fewer sandflies confined to clay pots fed on the proffered sugar solution. One significant

TABLE 5. Effect of distilled water or physiological saline as solvent upon acceptability of sugar solution by wild-caught *L. trapidoi* females.

Fructose 20%	REPLICATES					MEAN	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
Dist. water	88.0(50)*	84.4(90)	65.0(60)	97.7(44)	96.5(28)	83.9(273)	10-67-23
Saline (0.85% NaCl)	87.2(39)	59.9(37)	66.1(59)	98.0(30)	83.3(42)	72.2(237)	10-74-16

*% feeding (number of flies tested).

TABLE 6. Effect of type of holding vessel on sugar feeding (20% fructose) behavior of wild-caught *L. trapidoi* females.

HOLDING VESSEL	REPLICATES					MEAN	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
Clay pot*	65.0(54)***	63.2(38)	16.1(31)	23.1(52)	73.0(115)	54.8(280)	25-59-16
Styrof. cup**	83.6(61)	89.2(37)	75.0(28)	85.1(47)	62.8(122)	83.4(295)	16-68-16
Clay pot**	62.5(56)	77.6(76)	95.5(88)	78.3(37)	74.5(102)	77.8(339)	23-62-15
Styrof. cup**	91.7(108)	91.3(58)	96.2(53)	87.0(31)	87.2(78)	90.8(328)	17-71-12

*Volume: 325-350 ml.

**Volume: 200 ml.

***% feeding (number of flies tested).

TABLE 7. Comparative acceptance of pure sugar (fructose), natural product (honey) and a commercial compound (Karo) by wild-caught *L. tritoides* females.

SUGARS 20%	REPLICATES					MEAN	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
Fructose	93.1(56)*	89.5(19)	82.7(58)	87.4(38)	56.0(50)	82.5(223)	27-59-14
Honey	87.3(55)	51.5(33)	61.7(60)	77.1(35)	25.7(35)	63.3(218)	18-51-1
Karo	96.2(53)	87.5(16)	82.2(62)	90.3(31)	76.2(65)	85.3(225)	49-49-2

*% feeding (number of flies tested).

TABLE 8. Effect of temperature on sugar-feeding (20% fructose) in wild-caught *L. tritoides* females.

TEMPERATURE °C	REPLICATES					MEAN	DEGREE OF SATIATION S-M-L (%)
	#1	#2	#3	#4	#5		
24-25	95.1(61)*	79.2(52)	80.3(61)	75.0(43)	95.2(63)	85.4(291)	21-72-7
29	91.7(36)	77.0(51)	70.8(55)	83.1(71)	85.3(52)	80.7(295)	16-76-8

*% feeding (number of flies tested).

difference between the 2 types of vessels was their volume, the clay pot being considerably larger. A 2nd test was performed utilizing smaller clay pots with volume capacity equalling that of the styrofoam cup. The results in this case, shown at the bottom of TABLE 6, demonstrate once more a significant difference (no overlap in any of the 5 replicates) between the 2 vessels, although less pronounced this time. The reasons for this difference are obscure.

Pure sugars vs natural or commercial products. A variety of carbohydrate sources have been used to feed colonies of hematophagous flies (Coluzzi 1964). The rationale for selecting one sugar over another is not clear, and there are instances where the only reference to the sugar solution is to its concentration (Jones 1964). In other words, there is a lack of established criteria for the selection and utilization of sugars, both in general and in specific terms. The results in TABLE 7, although limited, emphasize the need for further work of this nature. Honey, a carbohydrate widely used to feed flies, was significantly inferior to both fructose and Karo on the basis of rate of acceptance by sandflies. It is also interesting that although flies fed on fructose and Karo had similar feeding rates, they differed substantially in degree of satiation, suggesting an overall superiority of the former. It is possible that the size of the sugar meal is related to specific behavioral patterns of the adult female, such as blood-feeding, mating, oviposition, etc.

Temperature. The present work was carried out in an insectary room in which the temperature ranged between 25.5°C and 27.5°C. The assumption has been made that humidity was constant in all tests, since the flies were confined to a

small, wet vessel. The effect of temperature on sugar feeding was a matter of practical significance, and a test was designed to determine its effect. The results in TABLE 8 show a slightly better overall feeding rate at lower temperatures.

Longevity. The assessment of various carbohydrates as suitable energy sources for hematophagous flies has been universally based on the criterion of adult longevity. Related to this is the proper concentration of the sugar solution and its effect on insect longevity. The results of such a test with *L. tritoides*, which were computed by the method of Galun & Fraenkel (1957), are presented in TABLE 9. Flies which died within 48 hr after emergence were excluded from tabulation since it appeared that such early mortality was probably the result of mechanical injury incurred during transfer from the rearing to the holding vessels. The results indicate that the concentration of sugar solution had no significant effect on sandfly longevity.

Volume of sugar solution ingested. The volume of sugar solution ingested by *L. tritoides* females varied from traces to a maximum of 0.4 lambda (=0.4 microliter). This is considerably more than the estimated average volume (0.008 microliter) in the crops of wild-caught phlebotomine sandflies from British Honduras (Lewis & Domoney 1966), and approximately 1/10 of the volume of nectar in the crops of wild-caught mosquitoes (Hocking 1953).

TABLE 9. Survival of laboratory-reared *L. tritoides* females on 3 concentrations of sucrose solution.

SUCROSE SOLUTION (% CONC.)	NO. FLIES	DAYS TO MORTALITY OF		MEAN SURVIVAL (DAYS)
		50%	100%	
10	53	20	35	20
30	53	18	33	19
Satur.	48	17	35	18

In addition to *L. trapidoi*, field collections included 3 other anthropophilic species, *L. gomezi* (Nitzulescu), *L. sanguinaria* (Fairchild & Hertig), and *L. ylephiletor* (Fairchild & Hertig). Both sexes of these species fed readily on the test sugars to the same or greater extent than *L. trapidoi*. The volume of ingested meal was related to the size of the species. *L. sanguinaria* and *L. gomezi*, 2 large-bodied species, imbibed about 0.7 lambda as compared to only 0.4 lambda for the smaller *L. trapidoi* and *L. ylephiletor*. Males normally took only about 1/2 to 1/3 of the volume taken by females of the same species.

CONCLUSIONS

The foregoing study was conducted to establish a sound basis of sugar feeding for laboratory colonies of phlebotomine sandflies. The results from the various tests demonstrate that sandflies have preferences for specific sugars but are less fastidious with respect to the concentration and physical state of the sugar solution. However, the conditions of sugar provision can be important to feeding success. In general terms, the optimal sugar meal can be described as a highly concentrated solution of sucrose or fructose in distilled water with or without color.

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DISTRIBUTION OF LARVAL TABANIDAE (DIPTERA) IN A *SPARTINA ALTERNIFLORA* SALT MARSH¹

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Abstract: Larvae of *Cheypsi fuliginatus* Windemann and *Tabanus nigrovittatus* Macquart were recovered from the soil of a regularly flooded salt marsh having *Spartina alterniflora* Loisel (smooth cordgrass) as the dominant vegetation. The larvae were

found throughout the sampling area with no consistently greater abundance adjacent to a natural drainage ditch. The larvae were found about as frequently in areas of "tall" as in "short" *S. alterniflora*.

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Larvae of the salt marsh Tabanidae are most abundant where living plants maintain uniform moisture conditions which favor the free movement of the larvae (Bailey 1948). Although Bailey confirmed the fact that larvae were widely distributed in the marsh soil, he indicated that the Massachusetts salt marshes which were ditched for mosquito control had greater expanses of suitable larval