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EFFECTS OF MATING AND SUGAR FEEDING ON THE EXPRESSION OF AUTOGENY IN CRABHOLE MOSQUITOES OF THE GENUS *DEINOCERITES* (DIPTERA: CULICIDAE)[1]

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Abstract. Autogeny was much more prevalent in a temperate than in a tropical population of *Deinocerites pseudes*. Most sugar-fed *De. pseudes* females did not initiate autogenous egg development until after mating. High proportions (>90%) of autogeny were found in tropical, subtropical, and temperate-zone populations of *Deinocerites cancer*. Either sugar feeding or mating triggered egg development in *De. cancer*, but sugar-fed females produced more eggs. Whether sugar-fed or not, unmated *De. cancer* females developed eggs after blood feeding. Thus 3 factors, blood feeding, sugar feeding, or mating, can independently stimulate the production of the initial egg clutch in *De. cancer*.

Most of the 18 recognized species of *Deinocerites* mosquitoes are confined to tropical regions in Central and South America, where their aquatic stages normally develop in burrows made by crabs, particularly land crabs inhabiting tideland areas (Adames 1971). A few species, such as *Deinocerites cancer* Theobald and *Deinocerites pseudes* Dyar & Knab, occur over a wide latitudinal range extending from the Neotropics to the temperate zone of North America. Because they are highly stenogamous, several species of *Deinocerites* mosquitoes can be colonized and maintained readily in the laboratory (Fisk 1941, Komp 1956, Galindo 1967, Provost & Haeger 1967, Gentry et al. 1970).

Autogenous mosquitoes produce their initial egg clutch without blood feeding. This trait is common in female *De. cancer* along the east coast of Florida near the northern limit of the species' range (Haeger & Phinizee 1959, O'Meara 1979). Although mating is a prerequisite for autogeny in some mosquito species (O'Meara & Evans 1976, 1977), sugar-fed *De. cancer* females from Florida are highly autogenous whether mated or not (O'Meara 1979). Sugar feeding influences autogenous reproduction in some species but not in others (Lea 1964, Corbet 1967, O'Meara & Krasnick 1970). One objective of the present study was to reevaluate the role of mating in the expression of autogeny among *Deinocerites* mosquitoes by examining sugar-fed and unfed females.

Within several different groups of closely related species of freshwater mosquitoes, autogeny is much more prevalent or is obligatory in populations or species occurring at higher latitudes (O'Meara & Craig 1970, Spielman 1971, Lounibos et al. 1982). An exception to this pattern is the saltmarsh mosquito, *Aedes taeniorhynchus* (Wiedemann), which does not exhibit a clearly defined pattern of latitudinal variation in the frequency or expression of autogeny, at least not when the total range of the species is considered (O'Meara & Edman 1975). Autogeny is characteristic of a number of mosquito species and other hematophagous Diptera that inhabit tideland areas (Rioux et al. 1975, Lane et al. 1983, Linley 1983). To identify geographical variations in the expression of autogeny among crabhole mosquitoes, especially with regard to sugar feeding and mating requirements, the experiments described herein involved both tropical and temperate-zone populations of *De. cancer* and *De. pseudes*.

MATERIALS AND METHODS

We established and used 3 laboratory colonies of *De. cancer*. Two of these colonies (VERO BEACH and FLAMINGO) were initiated from field collections taken during the summer of 1982 at Vero Beach (27.6°N, 80.3°W) and Flamingo (25.1°N, 80.9°W), Florida, USA. A 3rd colony (BELIZE) was derived from a collection taken near Belize City (17.3°N, 88.1°W), Belize, in February 1981. In addition, some experiments used individuals collected as 4th-instar larvae or pupae from the tidelands adjacent to the Florida Medical Entomology Laboratory in Vero Beach. In the laboratory the mosquitoes were kept at 26.5 ± 0.5 °C and 85 ± 10% RH, and at a photoperiod of 16.5:7.5 h L:D, with a 62-min simulated twilight at each transition. Larvae were reared on a diet of equal parts of brewers yeast, lactalbumin, and rodent lab chow. Approximately 150 larvae were cultured together in enamel pans filled to a depth of 4 cm with ca. 350 ml of 50% sea water. We tried to provide the most

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nutritious diet possible without producing a scum on the water surface. Except for experiments involving unfed females, the mosquitoes had continuous access to a 10% sucrose solution. For all experiments, females were denied an oviposition site. Ovarian condition was assayed by dissection after a holding period of 5 days or more. At this time the spermathecae were examined for the presence of sperm in those females that had been kept with males. A female was considered autogenous when at least 1 ovariole contained a stage V follicle (Clements & Boocock 1984).

Two strains of *De. pseudes* were used: (1) the Gorgas Memorial Laboratory (GML) colony, which had been in the laboratory for several years since its initiation from field collections taken in Gorgona (8.4°N, 79.5°W), Panama; and (2) the TEXAS strain, which was derived from individuals taken from the Brownsville (25.9°N, 97.3°W), Texas, area in June 1982. Some of the experiments involving *De. pseudes* were conducted at the Florida Medical Entomology Laboratory, and here the rearing and experimental conditions applied to *De. pseudes* were similar to those used for *De. cancer*. Other experiments with *De. pseudes* were conducted at the Gorgas Memorial Laboratory, Panama, Republic of Panama, where the mosquitoes were maintained under conditions of natural ambient temperature and light. Consequently, the day–night cycle was ca. 12:12 h L:D and temperature fluctuated daily between 21 and 27 °C with a 70 ± 10% RH. At the Gorgas Memorial Laboratory, larvae were fed on a diet of guinea pig chow, and adult *De. pseudes* were sugar fed on solutions of sucrose or honey. All other experimental conditions were similar to those used at the Florida Medical Entomology Laboratory.

To test for the significance of differences between 2 percentages we used the method of Sokal & Rohlf (1969) based on the arcsine transformation.

RESULTS

Deinocerites pseudes

High rates of autogeny were found in mated, sugar-fed females of the TEXAS strain, whereas only 13.3% of the unmated, sugar-fed females of this strain developed eggs autogenously (Table 1). The mated females from group #7 and the unmated females from group #8 came from the same larval rearing pans, and on average they attained the same adult size based on wing length measurements. Hence, the differences in egg development between the 2 groups would not appear to be the result of larval rearing conditions. The vast majority of *De. pseudes* from GML were anautogenous whether mated or not; however, the few cases of autogeny found in the GML strain were among mated females (group #2, Table 1). Mosquitoes in group #1 were reared at the Florida Medical Entomology Laboratory under the same conditions used for the TEXAS strain (groups #6, #7, and #8). In general, the adult body size was similar for mosquitoes reared at the Gorgas Memorial Laboratory and those reared at Florida Medical Entomology Laboratory. The mean autogenous fecundity of sugar-fed, mated females from TEXAS (gravid females in groups #6, #7, Table 1) was equivalent to that attained by blood-fed females from the GML strain (mean ± SE = 57.8 ± 3.32, $n = 44$; $t_s = -1.63$, df = 136, not significant). These females, which were sugar fed and mated, obtained a blood meal from a guinea pig.

Adults of both the TEXAS and the GML strains mated in the laboratory even when confined to relatively small cages (19 cm high × 19 cm wide × 27 cm deep). At first it appeared that teneral *De. pseudes* females were refractory to insemination during the 1st day following emergence. When 2 groups of 15 young females, one group 16 to 24 h old and the other group 14 to 30 h old, were each exposed to 20 one day older males for 16 to 24 h, only 5 of the 30 females were inseminated. However, in a similar test using 2 groups of older females (30 to 48 h old and 48 to 55 h old), 21 of 30 females were inseminated. In another test, 60 males 5 to 7 days old were placed in a cage (30 × 30 × 30 cm) with a dish containing pupae of *De. pseudes* (GML strain). The males were attracted to the dish containing the pupae and readily mated with newly emerged females. Eleven of 13 females dissected contained sperm in their spermathecae.

Deinocerites cancer

Similar high rates of autogeny were found in sugar-fed, unmated females of the BELIZE, FLAMINGO, and VERO BEACH strains of *De. cancer* (Table 2). Nevertheless, among these 3 strains the mean levels of autogenous fecundity varied considerably. For example, gravid females of the BELIZE strain were more fecund than those of the VERO BEACH strain ($t_s = 14.1$, df = 98, $P < 0.001$).

Among unfed, unmated *De. cancer* females of the VERO BEACH strain, only 5 of 202 developed

TABLE 1. Effects of mating on autogenous ovarian maturation in sugar-fed ♀ *Deinocerites pseudes* from GML (PANAMA) and TEXAS strains.

GROUP NO.*	TREATMENT	NO. ♀♀	% AUTOGENOUS	EGGS/AUTOGENOUS ♀ ($\bar{x}$ ± SE)	WING LENGTH (mm) ($\bar{x}$ ± SE)
GML (PANAMA) strain					
1	mated	55	0.0	—	—
2	mated	44	6.8	23.3 ± 3.7	3.25 ± 0.03
3	mated	21	0.0	—	3.05 ± 0.05
4	unmated	24	0.0	—	3.22 ± 0.03
5	unmated	32	0.0	—	2.81 ± 0.03
TEXAS strain					
6	mated	66	97.0	54.9 ± 0.7	3.23 ± 0.01
7	mated	30	100.0	51.7 ± 0.9	3.07 ± 0.02
8	unmated	30	13.3	38.5 ± 2.8	3.08 ± 0.02

* Females in groups #2, #3, #4, and #5 tested at the Gorgas Memorial Laboratory. Females in groups #2 and #4 provided with sucrose. Females in groups #3 and #5 provided with honey.

eggs autogenously (Table 3, test groups A, B, and C). By contrast, most (145 of 166) of the unfed, mated females of this strain were autogenous (test groups B and C). Nearly all sugar-fed females matured eggs autogenously, whether mated or not. Sugar-fed females produced an average egg clutch twice the size of those found in the unfed females (Table 3). These results were obtained from *De. cancer* that had been field collected as 4th-instar larvae or pupae from crabholes adjacent to the Florida Medical Entomology Laboratory in Vero Beach. For each test group the mosquitoes came from the same collection, and they were randomly selected for the various treatments. Both within and among the test groups, the mean size of the adult females, based on wing length measurements, was similar for each treatment.

In the experiments involving sugar-fed mosquitoes, females had access to a sugar source from the day of adult emergence. To evaluate the effects of delaying sugar feeding on autogenous egg production, sugar was withheld until the females were 3, 5, 7, or 9 days old; 4 to 5 days later, the mosquitoes were dissected to determine the degree of ovarian development. Generally, the longer the delay before the onset of sugar feeding, the greater the reduction in the expression of autogeny (Table 4). Most virgin *De. cancer* females from the VERO BEACH strain that had been starved for 2 or 4 days responded to a sugar meal by producing eggs. Increasing the starvation period to 6 or 8 days drastically reduced the frequency of autogeny.

Newly emerged, teneral *De. cancer* females will mate readily with 1-day-old males, even when confined to 8-dr shell vials. Hence, to obtain virgin females it is necessary to isolate the sexes at the pupal stage. In the present study, pupae were routinely isolated individually in 8-dr shell vials, and sex was determined by observing the emerged adult under a stereomicroscope at low magnification (12×). Once a sexually mature male (i.e., >1 day old) was added to a shell vial containing a virgin female, mating usually began within a few minutes. For experimental treatments that required mated females, a male usually was placed together with a female on the day she emerged. However, in 1 experiment conducted to evaluate the effects of delayed mating on autogeny, unfed virgin females were held in isolation for 2 days before males were added. Most of these 2-day-old females produced eggs after mating (Table 4).

TABLE 2. Autogenous ovarian maturation in sugar-fed, unmated ♀ *Deinocerites cancer* from the BELIZE, FLAMINGO, and VERO BEACH strains.

	NO. ♀♀	% AUTOGENOUS	EGGS/AUTOGENOUS ♀ ($\bar{x}$ ± SE)
BELIZE	36	100.0	98.2 ± 1.6
FLAMINGO	169	94.7	68.8 ± 0.9
VERO BEACH	66	97.0	57.3 ± 1.2

Blood-feeding activity was examined in unmated *De. cancer* females from the VERO BEACH strain. Three age groups (2-, 3-, and 4-day-old females) were tested using both sugar-fed and unfed females. More than 90% of the non-sugar-fed females in each age group took blood when offered a restrained host (chicken) for a period of 16 h (Table 5). Most of the sugar-fed females in each of the 3 age groups also took a blood meal when offered the same type of host, but within each age group significantly fewer sugar-fed females blood fed than did non-sugar-fed females (2-day-old ♀♀, $t_s = 2.56$, $P < 0.05$; 3-day-old ♀♀, $t_s = 3.81$, $P < 0.001$; 4-day-old ♀♀, $t_s = 3.64$, $P < 0.001$).

Sugar feeding enhanced the fecundity of both blood-fed and non-blood-fed *De. cancer* females. Young (1- to 2-day-old), virgin, unfed *De. cancer* females from the VERO BEACH and the FLAMINGO strains were allowed to obtain a blood meal from a chicken; some of these blood-fed females then were provided with sugar, while others were denied a sugar meal. In the case of the VERO BEACH strain, the percentage of gravid females was significantly greater in the group of females that blood and sugar fed than in the group of fe-

TABLE 3. Effects of sugar feeding and mating on the expression of autogeny in ♀ *Deinocerites cancer* from the VERO BEACH population.*

	No. ♀♀	% AUTOG-ENOUS	EGGS/ AUTOG-ENOUS ♀**	WING LENGTH (mm)**
Test group A				
Sugar fed and unmated	61	93.4	59.9 ± 1.4	2.80 ± 0.02
Unfed and unmated	63	0	—	2.81 ± 0.02
Test group B				
Unfed and mated	115	84.3	26.2 ± 1.4	2.78 ± 0.01
Unfed and unmated	80	0	—	2.78 ± 0.01
Test group C				
Sugar fed and mated	50	100.0	58.4 ± 2.3	2.79 ± 0.02
Sugar fed and unmated	58	94.8	53.6 ± 2.3	2.82 ± 0.01
Unfed and mated	51	94.1	26.0 ± 2.2	2.81 ± 0.02
Unfed and unmated	59	8.5	16.4 ± 8.4	2.81 ± 0.01

* All ♀♀ tested were from wild-caught 4th-instar larvae or pupae.

** Mean ± SE.

TABLE 4. Effects of delaying sugar feeding or mating on autogenous egg production in *Deinocerites cancer*.

	No. ♀♀	% AUTOG-ENOUS	AUTOGENOUS FECUNDITY ($\bar{x}$ ± SE)
Virgin ♀ *Deinocerites cancer*, VERO BEACH strain			
Sugar provided from day*			
3	25	80.0	37.8 ± 2.0
5	32	65.6	26.2 ± 1.6
7	28	17.9	17.8 ± 4.0
9	25	12.0	19.3 ± 5.6
Unfed ♀ *Deinocerites cancer*, VERO BEACH strain			
♂♂ present from day*			
1	111	76.6	18.3 ± 1.3
3	108	61.1	15.1 ± 1.2
♂♂ not present	84	1.2	15

* Day 1 = day of adult emergence.

males that blood fed only ($t_s = 4.79$, $P < 0.001$). Moreover, the mean number of eggs per gravid female was also significantly greater among the blood-fed females that had access to sugar ($t_s = 12.04$, df = 44, $P < 0.001$, Table 6). Similar results were obtained with the FLAMINGO strain, i.e., sugar- and blood-fed females were more fecund than blood-fed females that did not sugar feed ($t_s = 7.09$, df = 67, $P < 0.001$). There was, however, no significant difference in percentage gravid between the sugar- and non-sugar-fed *De. cancer* females from the FLAMINGO strain ($t_s = 1.84$, ns, Table 6).

DISCUSSION

Although mating can stimulate the initiation of autogenous egg development in both *De. pseudes* and *De. cancer* (Tables 1, 3), mating seems to be more essential in *De. pseudes*. For *De. cancer*, either sugar feeding or mating will in most cases trigger autogenous egg maturation, whereas in *De. pseudes* autogeny is usually expressed by sugar-fed females only after they have mated. A somewhat similar type of male-induced autogeny, whereby mating triggers egg development in sugar-fed females, occurs in *Aedes taeniorhynchus* and *Wyeomyia vanduzeei* Dyar & Knab (O'Meara & Evans 1977, O'Meara 1979).

A substance from the male accessory gland passed to the females during mating is responsible for stimulating autogenous egg development in both *Ae. taeniorhynchus* and *Wy. vanduzeei* (O'Meara & Evans 1977, O'Meara 1979). Presumably, the same physiological mechanism is operating in *Deinocerites* mosquitoes. Whether or not mating is required for the initiation of autogenous egg development in some *Ae. taeniorhynchus* females is influenced by conditions in the larval stage; the more stressful the condition, the more likely mating will be a prerequisite. Typically the male-induced form of autogeny in *Ae. taeniorhynchus* populations is associated with low levels of autogenous fecundity (<30 eggs/female). However, by blood feeding these mosquitoes can produce a much larger initial egg clutch. Female *Ae. taeniorhynchus* with ovaries in the previtellogenic stage (e.g., stage II) are active blood feeders, but once they reach a more advanced stage of development they become reluctant blood feeders; the few that feed at this time show little or no enhancement of fecundity. In many mosquito species, including *Ae. taeniorhynchus*, females are sexually refractory to insemination for 1 or more days following emergence (Edman et al. 1972). For *Ae. taeniorhynchus* females the combination of a sexually refractory period and required mating for the onset of autogenous egg development increases the possibilities for facultative autogeny. Where autogeny is facultative the mosquito may develop the initial egg clutch with or without a blood meal (Corbet 1967).

Male *De. cancer* display an unusual behavior, "pupal attendance" (Provost & Haeger 1967), and often mate with a female before she is entirely out of the pupal skin. Males of *De. pseudes*, at least older ones, are also attracted to pupae, and freshly emerged *De. pseudes* females will readily mate with these

TABLE 5. Blood feeding by unmated ♀ *Deinocerites cancer* from the VERO BEACH strain.*

AGE GROUP (DAYS OLD)	TREATMENT PRIOR TO BLOOD-FEEDING TEST**	NO. ♀♀ TESTED	% BLOOD FEEDING
2	sugar fed	115	80.0
	unfed	118	91.5
3	sugar fed	32	53.1
	unfed	29	93.1
4	sugar fed	29	62.1
	unfed	29	96.6

* All ♀♀ had access to a restrained host (chicken) for 16 h.
** Sugar-fed mosquitoes had access to 10% sucrose solution from day of adult emergence.

TABLE 6. Effects of sugar feeding on egg production in blood-fed ♀ *Deinocerites cancer*.*

	NO. ♀♀	% GRAVID**	EGGS/GRAVID ♀ ($\bar{x} \pm SE$)
FLAMINGO strain			
Blood fed & sugar fed	44	86.6	77.0 ± 2.1
Blood fed only	41	73.2	49.0 ± 2.3
VERO BEACH strain			
Blood fed & sugar fed	28	100.0	75.3 ± 2.6
Blood fed only	28	64.3	20.6 ± 4.0

* Unmated ♀♀.
** 4 days after blood feeding.

males. Early mating by *Deinocerites* mosquitoes may diminish the chances for facultative autogeny. Of course, instances of facultative autogeny need not be restricted to situations in which egg development is delayed owing to lack of mating or sugar feeding. Under laboratory conditions, most (35 of 61) 3- and 4-day-old, sugar-fed *De. cancer* females took a blood meal (Table 5). Nearly all of these blood-feeding females had ovaries with advanced stages of egg development (stages III and IV). Maybe these *Deinocerites* mosquitoes with vitellogenic ovaries can still increase the size of their initial egg clutch by blood feeding. Under these conditions, early onset of autogenous egg development would not totally preclude a role for blood feeding during the production of the 1st egg clutch. Hence, one of the functions of early mating in *Deinocerites* mosquitoes could be to hasten egg development.

Deinocerites cancer females possess considerable gonotrophic flexibility. When starved and unmated, *De. cancer* females survive for more than a week (Table 4), and during this time they will readily blood feed under laboratory conditions. To a slightly lesser extent, sugar-fed, unmated *De. cancer* females also show a propensity for blood feeding (Table 5). By feeding on blood alone, most *De. cancer* females from the FLAMINGO and VERO BEACH strains became gravid (Table 6). Thus in this crabhole mosquito, 3 factors—mating, sugar feeding, or blood feeding—can independently stimulate the production of the initial egg clutch.

In the mosquito's natural tideland habitats, these factors undoubtedly interact rather than operate independently. Females are most likely mated at or shortly after emergence. Floral and extrafloral nectaries are common in many areas inhabited by crabhole mosquitoes (Van Handel et al. 1972; J.S. Haeger, pers. commun.), and high rates of sugar feeding have been found in other tideland mosquitoes (Bidlingmayer & Hem 1973). Consequently, ample opportunities would seem to exist for sugar feeding by *De. cancer* females. Even if sugar feeding or mating were delayed for a few days following emergence, they could still have an effect on egg production (Table 4).

Edman (1974) detected a blood meal in ca. 5% of the *De. cancer* females aspirated from crabholes in the tidelands near Vero Beach, Florida. These blood meals had been taken from both birds and mammals, indicating that *De. cancer* has a broad host range. It is not known to what extent blood feeding contributes to the initial egg clutches in field populations of *De. cancer*. Based on previous studies (Haeger & Phinizee 1959, O'Meara 1979), *De. cancer* seemed to be obligatorily autogenous for the 1st egg cycle, but the findings of the present study indicate that blood feeding may play a role in the development of the initial egg clutch. In the laboratory, most nulliparous, sugar-fed *De. cancer* females blood fed when offered a host (Table 5).

Interstrain variation in the capacity for autogeny was more pronounced in *De. pseudes* than in *De. cancer* (Tables 1, 2). High rates of autogeny were found in tropical, subtropical, and temperate-zone populations of *De. cancer*. It remains to be determined if a low rate of autogeny is a common feature of *De. pseudes* populations in the tropics. Obviously, additional populations need to be examined to obtain an accurate picture of the geographical variation in autogeny among populations of *De. cancer* and *De. pseudes*. Moreover, it would be informative to examine populations of other species of *Deinocerites*.

St. Louis encephalitis (SLE) and Venezuelan equine encephalitis (VEE) viruses have been isolated from wild-caught *De. pseudes* (Grayson et al. 1967, Tempelis & Galindo 1970), and in laboratory studies this mosquito species has been shown to be

an efficient vector of VEE (Grayson & Galindo 1972). The potential for a mosquito species as an important vector of pathogens would appear to be decreased where autogeny is common, particularly the obligate, 1st-cycle type. In this regard *De. pseudes* would seem to be less affected than *De. cancer,* since in *De. pseudes* autogeny is an uncommon trait in some populations.

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