

## DISPERSAL BEHAVIOR AND VECTOR POTENTIAL OF *Aedes cantator* (DIPTERA: CULICIDAE) IN SOUTHERN MARYLAND

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**Abstract.** Three *Aedes cantator* broods were monitored in the vicinity of a salt marsh during May–July 1978. Landing rates and parous rates were estimated semiweekly at 4 sites extending 2 km inland from the marsh-upland ecotone. Larval surveys and light-trap data were also used to detect brood emergences. Data indicate that females disperse inland at least 2 km and return to the marsh for oviposition. Parous females return inland for additional blood feeding and no inhibition of dispersal tendency was detected in parous individuals. Parous mosquitoes were present at all sampling sites from 22 May–5 July and no significant difference in parous rates was found at any of the study locations. These data suggest that *Ae. cantator* could act as a biological vector both near the marsh and at inland locations. Initial dispersal behavior appears to be similar to that of *Aedes sollicitans* in that flight is appetential and gradual in nature; however, it differs from true migration exhibited by *Aedes taeniorhynchus*.

Of the salt-marsh mosquitoes common to the eastern United States, *Aedes cantator* (Coquillett) has probably received the least study. This species has been reported along the Atlantic seaboard from southeastern Canada to Virginia, and as far inland as Ohio (Carpenter & LaCasse 1955, Carpenter 1968, 1974). Breeding takes place primarily in coastal marshes flooded by fresh or brackish water, and low salinity is reportedly preferred (Smith 1904). In southern Maryland, larvae are found in salt marshes dominated by *Distichlis spicata* L. (salt grass) and *Spartina patens* (Aiton) (salt-meadow grass).

*Aedes cantator* has been described as an early season salt-marsh mosquito that is replaced by *Aedes sollicitans* (Walker) as the major pest species during the summer and fall (Carpenter & LaCasse 1955, Smith 1904). However, other reports indicate that *Ae. cantator* breeds throughout the season. Davis (1940) reported that *Ae. cantator* breeds throughout the summer in Massachusetts, and Magnarelli (1978) found breeding to occur from April–October in Connecticut. Mosquito surveillance data from Calvert Co., Maryland, indicate that *Ae. cantator* produces broods throughout the

summer when rainfall is adequate. Late season breeding appears to be regulated by the water level in salt marshes rather than by any inherent seasonality of the species.

In many parts of southern Maryland, *Ae. cantator* is the predominant salt-marsh *Aedes* throughout the summer. Broods are produced when salt meadows and peripheral pools flood following rainfall and spring tides. Coastal inhabitants are often severely annoyed by this species, especially during evening hours, and females are often collected over 5 km from the nearest breeding habitat (pers. observ., S.C.W.).

One characteristic common to many salt-marsh *Aedes* is the ability to disperse inland from the larval habitat. Dispersal of *Aedes taeniorhynchus* (Wiedemann) has been extensively studied in Florida (Provost 1952, 1957; Haeger 1955, 1960), and recently dispersal patterns of *Ae. sollicitans* were described by Crans et al. (1976) in New Jersey. Investigations concerning dispersal behavior of *Ae. cantator* were conducted to determine similarities and differences in dispersal patterns among these species. Common characteristics were sought that might be inherent in an adaptive strategy for salt-marsh existence.

*Ae. cantator* is capable of transmitting eastern equine encephalitis (EEE) virus under laboratory conditions (Merrill et al. 1934, Ten Broeck & Merrill 1935, Davis 1940). Although this mosquito species has not often been included in arbovirus surveillance collections, EEE has been isolated from it in New Jersey (Martin Goldfield, N. J.; Dep. Health, pers. commun.). Magnarelli (1977) reported that hosts of *Ae. cantator* include both mammals and passeriform birds, and that multiple feedings were common. He also found that longevity was sufficient for virus incubation and transmission (Magnarelli 1978). These findings suggest that *Ae. cantator* could be involved in transmission of EEE from avian to mammalian populations during epizootic conditions. Therefore, age distribution, density and dispersal data were also gathered as a part of our study, to delineate the locations of

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greatest vector potential with respect to the breeding site.

#### MATERIALS AND METHODS

During 1978, *Ae. cantator* was monitored from 10 May–10 July in the vicinity of Parker Creek Marsh in Calvert Co., Maryland, USA. This salt marsh, predominantly of *S. patens* vegetation, is located more than 8 km from the nearest similar breeding habitat. Approximately 200 ha of suitable salt-meadow habitat are available for salt-marsh *Aedes* breeding, and broods large enough for distribution studies are often produced. The marsh is surrounded by a relatively uniform deciduous woodland.

Four sites were selected for adult population sampling, each at the edge of an open field where both grasses and shrubs provided mosquito resting places. The 4 sites were as follows: (A) at the marsh-upland ecotone, (B) 0.5 km inland, (C) 1 km inland and (D) 2 km inland. Landing rates were estimated semiweekly at each site. *Aedes cantator* is reportedly a crepuscular biter (Carpenter & LaCasse 1955, Magnarelli 1979), although Taylor et al. (1979) collected most females between 0800 and 1700 h in a New Brunswick study. Since annoyance from this species appears to be maximal around dusk in southern Maryland, landing rate counts were begun 5 min after sunset. Counts were not taken during rainfall or when winds exceeded 13 km/h. The sampling order of the 4 sites was determined randomly on each of the sampling evenings.

Upon arrival at a site, the collector stood motionless for 1 min and counted mosquitoes landing below the waist. He then moved about the area for 5 min aspirating host-seeking mosquitoes. A 2nd 1-min count was taken before proceeding to the next site. All counts were conducted by the same individual, and temperature and relative humidity were determined on each evening.

Mosquitoes collected at each site were frozen in petri dishes lined with moistened filter paper. Each sample was later separated according to species and the percentages of each recorded. Landing rates were calculated as the mean of the two 1-min counts multiplied by the percentage of *Ae. cantator*.

Since *Ae. cantator* is predominantly an anautogenous species (Magnarelli 1978), parity is one factor related to the potential for biological transmission of pathogens. Ovaries were removed from 15 *Ae. cantator* specimens in each sample, and parity was determined by the Detinova (1962) method

of ovarian tracheolation. Although small numbers of females were biting at all collection sites during late July and August, ovarian dissections were terminated on 5 July because too few specimens were available for dissection of 15 from each site.

Beginning in June, a standard New Jersey light trap was operated at the marsh-upland ecotone (site A) to monitor the emergence of salt-marsh mosquitoes. Light trap data were plotted using a 3-point moving mean to reduce excessive fluctuation caused by changing weather conditions. In addition, the marsh was inspected at least twice weekly for mosquito breeding. One hundred dips were taken in predetermined transects using a standard .47-litre (1-pt) dipper. Mean larval density was determined when the majority of larvae in a brood had reached the 4th instar. Since freshwater breeding has been reported for this species (Saugstad et al. 1972, Smith 1904), potential inland breeding sites within the study area were also examined for the presence of immature *Ae. cantator* throughout the study period.

#### RESULTS AND DISCUSSION

Landing rate, parous rate and larval sampling data all indicate that 3 distinct broods of *Ae. cantator* occurred during May and June (Fig. 1). Egg hatch of all but the 1st brood was preceded by rainfall of 3 cm or more. Additional breeding took place during July and August but, in each case, the marsh dried and few adults emerged.

Third- and 4th-instar *Ae. cantator* larvae were present in the marsh at the 1st inspection on 10 May. Cool temperatures are known to slow larval development in mosquitoes (Bar-zeev 1958, Nielson & Evans 1960) and are probably responsible for the extended period of emergence from 15–25 May. Development of early season larvae also may have been delayed by a very high larval density, which limited food availability. Another possibility would involve delayed egg hatching. The 18 May landing rate of 24 per min reveals that newly emerged females were biting at the marsh edge (site A). Concurrently, 2 mosquitoes were coming to bite each minute at site C (1 km inland), and no mosquitoes were biting at site D (2 km inland). The 22 May landing rate of 7 per min at site D indicates that some females had dispersed at least 2 km inland within 4 days of peak emergence.

Parous rates began at or near 0% at all sites on 18 May, reflecting the newly emerged nulliparous *Ae. cantator* population. Rates then rose at all sites as females took blood meals and completed a gono-

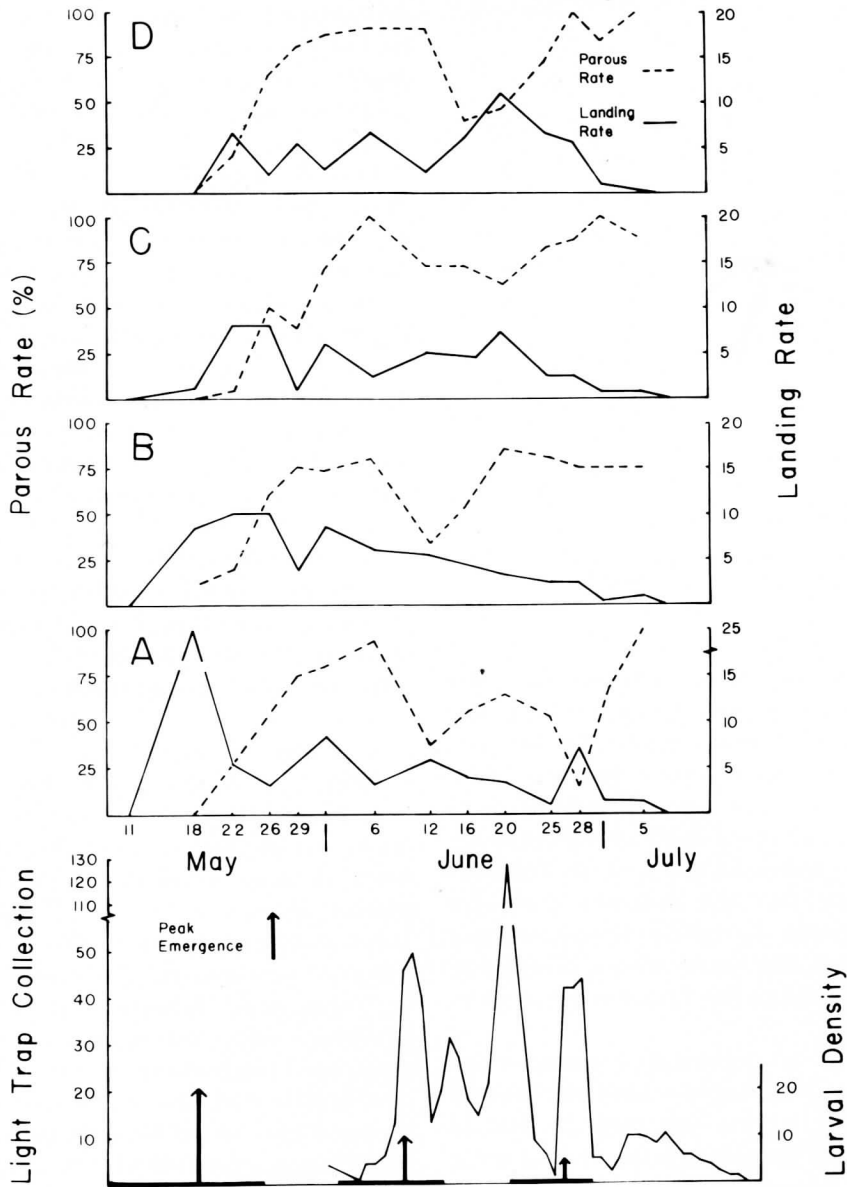


FIG. 1. Light trap collections of *Aedes cantator* (♀/night) at site A, with concurrent landing rates and parous rates at the 4 sampling sites superimposed. Bold lines on bottom axis indicate occurrence of immatures and arrows show peak emergence dates, with arrow height corresponding to larval density at the 4th instar (larvae/dip).

trophic cycle. The increase in parity continued until emergence of the 9 June brood.

Landing-rate data are somewhat variable owing, in part, to variation in environmental conditions affecting host-seeking behavior. Site A shows a very high landing rate at the time of adult emergence, followed by a sharp decline. This suggests inland dispersal of most females for blood and nectar feeding as suggested by Magnarelli (1978) and

Main et al. (1968). Landing rates increased at sites B, C and D until 22 May and decreased at the marsh ecotone as more mosquitoes reached inland locations. Decreasing landing rates after 26 May might simply reflect attrition of the aging population.

A sharp rise in the light-trap collection on 9 June and a concurrent decline in the parous rate indicate a 2nd adult emergence. Part of the reduction

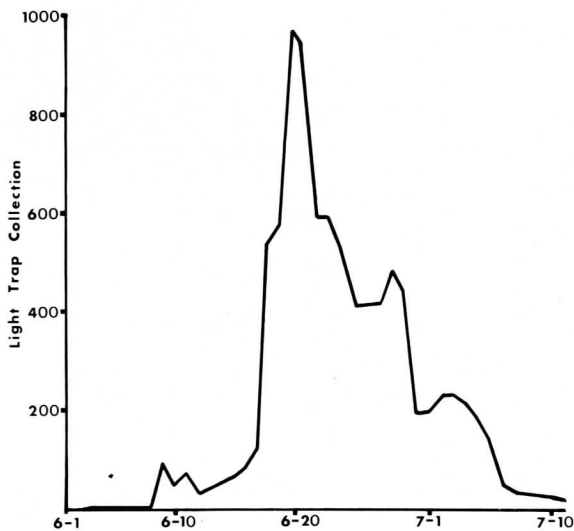


FIG. 2. Light trap collections of *Culex salinarius* (♀/night) at site A.

in larval density in comparison with the 1st brood is attributed to an aerial larvicide application.<sup>3</sup> The parous rate at site D decreased only 6% between 6–12 June, and the landing rate remained low. Apparently, most of the newly emerged mosquitoes moving inland reached the 2 km site after 12 June, over 3 days past peak emergence. This corresponds well with the 2-km dispersal time of 4 days observed for the 1st brood. It appears that the inland dispersal did not involve a prolonged, unidirectional migration, but rather a more gradual dispersal.

A sharp increase in light-trap collections appeared on 19 June, and they exceeded 100 females on 20 and 21 June. Larval data indicate that no breeding took place immediately preceding those dates and parous rates remained above 60%. Since these are the 2 most reliable measures of adult emergence used in the study, mosquitoes appearing in the light trap are assumed to be from previous broods. Since *Ae. cantator* increases host seeking with rising humidity to 85% and rising temperature to 32 °C (Rudolfs 1923), very hot and humid weather during this period may, in part,

explain the large collections. Unusually large numbers of *Culex salinarius* (Coquillett) as well as other species were also trapped during this period at the study site (Fig. 2) as well as at other traps in the county.

The 3rd major *Ae. cantator* brood is indicated by the 27 June peak in light-trap collections and a decrease in the parous rate at site A. The larval density of 5 per dip may overestimate the actual adult population produced, since the marsh was rapidly drying during the period immediately preceding emergence. Data suggest that few females dispersed inland, since parous rates did not drop significantly nor did landing rates increase at the 3 inland sites. Small numbers of biting *Ae. cantator* females were collected at sites B–D during late July and August (<1/min).

Crans et al. (1976) report that *Ae. sollicitans* undergoes a reduction in migratory tendency with increased physiological age. In order to compare this behavior with that of *Ae. cantator*, parity data were compared among the 4 sampling sites. If *Ae. cantator* undergoes a similar behavior modification, parous rates at inland sites should differ from those at the marsh edge. Lower parous rates inland would indicate a decrease in inland dispersal of parous mosquitoes, while higher rates inland would indicate an increased dispersal tendency in parous flies.

Parous rates, transformed to arcsine, were tested using a 2-way analysis of variance (ANOVA) without replication. Distance from the marsh had no significant effect on parous rates ( $P > 0.5$ ), but days past brood emergence was highly significant ( $P < 0.001$ ). Transformed parous rates were also grouped into ½-wk intervals past emergence and tested using a 2-way ANOVA with replication. Results were similar and interaction was not significant ( $P > 0.5$ ). A regression analysis was conducted on transformed parous rates (percentage to arcsine) vs. days past emergence ( $Y = 4.11 + 3.37X$ ). Regression was highly significant ( $P < 0.001$ ), while deviations from regression were insignificant ( $P > 0.05$ ). This indicates that parous rates increased sinusoidally with time at all sites after brood emergence.

These findings for *Ae. cantator* would appear to contrast with the Crans et al. (1976) report that parous *Ae. sollicitans* are inhibited from moving inland for subsequent blood feeding. Ebsary & Crans (1977) also reported that significantly fewer parous and multiparous *Ae. sollicitans* were found 2.9 km inland than at the marsh edge. However, re-ex-

<sup>3</sup> The Maryland Department of Agriculture Mosquito Control Program conducted aerial applications of Abate 4E® prior to emergence of all but the 18 May brood as part of aerial larviciding experiments. Bioassays involving pre- and postspray sampling indicated that these applications reduced larval density by 40–60% in the broods studied. Larval density determinations were made at least 24 h after larvicide applications.

amination of the Crans et al. (1976) data reveals that, following adult emergence, this species undergoes a subgeometric increase in parous rates both at the marsh and 3.2 km (2 mi.) inland. Inland parous rates probably would have approached 100% had dissections continued several weeks after brood emergence. Parous rates appear to lag behind those at the marsh edge by approximately  $\frac{1}{2}$  week, suggesting an average dispersal time of 3–4 days to reach 3.2 km inland. This corresponds well with our finding for *Ae. cantator* and suggests that dispersal in both of these species is gradual, rather than a prolonged, unidirectional flight such as that characterized by *Ae. taeniorhynchus* (Provost 1952).

Although older *Ae. sollicitans* may be inhibited from inland dispersal (Crans et al. 1976), this reduction in dispersal is apparently not caused by physiological age, since parous rates 3.2 km inland approximate those at the marsh edge if one allows for a  $\frac{1}{2}$ -wk dispersal time. If only parous flies were inhibited from inland dispersal, the inland parous rate would remain near 0% and only flies that had not yet completed the 1st gonotrophic cycle would be found inland. The paucity of females inland soon after brood emergence must be related to another time-dependent factor, possibly overall age or density of the *Ae. sollicitans* population.

Biological vector potential of a mosquito population is usually correlated with the number of parous flies coming to bite (Detinova 1962). Although parity is but 1 factor determining vector potential of a mosquito population, parous rates are very useful in the spatial and temporal delineation of pathogen transmission. Vector potential has been defined and calculated as the landing rate multiplied by the parous rate (Crans et al. 1976). Fig. 3 illustrates this vector-potential index for *Ae. cantator* plotted for each sampling site. It is apparent that some degree of vector potential existed at all sites during 22 May–5 July and was actually highest at the inland-most locations during the latter part of June. This suggests that *Ae. cantator* could act as a biological vector at any location up to 2 km or more from a breeding marsh.

Testing of vector potential data using a 2-way ANOVA without replication revealed that distance from the marsh was not significant ( $P > 0.5$ ), while days past adult emergence significantly affected the vector potential index ( $P < 0.05$ ). This represents a marked contrast to *Ae. sollicitans* vector potential. Crans et al. (1976) reported that parous

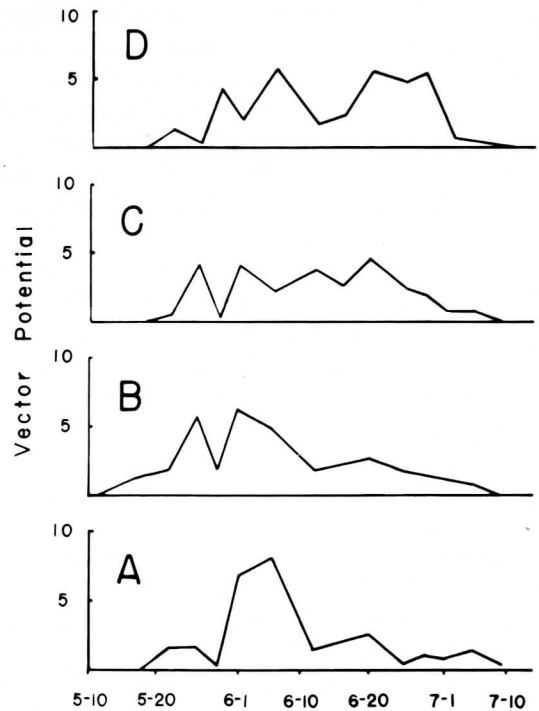


FIG. 3. Vector potential (parous flies landing per min) of *Aedes cantator* at the 4 sampling sites.

mosquitoes of that species were nearly always absent 3.2 km inland, and vector potential was substantially greater in areas close to a breeding marsh. While *Ae. sollicitans* appears most likely to transmit a pathogen only at locations very close to a breeding marsh, *Ae. cantator* could act as a vector over a broader geographical range. While vector control measures can be concentrated on *Ae. sollicitans* populations in the vicinity of coastal marshes, control measures should be directed toward the entire *Ae. cantator* population.

A comparison of dispersal patterns of *Ae. cantator*, *Ae. sollicitans* and *Ae. taeniorhynchus* reveals both similarities and distinct differences. Clearly, efficient dispersal is essential in salt-marsh mosquitoes in order to escape extremely high densities at the expansive breeding sites. However, 2 distinct forms of dispersal are evident. One involves the prolonged, unidirectional, nonappetential flight characteristic of *Ae. taeniorhynchus* (Provost 1952). This dispersal pattern closely fits current interpretations of insect migration in that it is nonvegetative, prereproductive, unidirectional and persistent in nature (Johnson 1969, Dingle 1972). In contrast, initial dispersal of *Ae. cantator* and *Ae. sollicitans* appears to involve more limited move-



ment from the marsh. In *Ae. cantator* this flight is apparently appetential, since host seeking begins as soon as females leave the marsh. Crans et al. (1976) also report that *Ae. sollicitans* moves inland in quest of a blood meal, although they refer to this appetitive flight as migration. Dispersal in *Ae. cantator* and *Ae. sollicitans* appears to be both pre- and postreproductive. However, *Ae. cantator* females can be found at inland locations several weeks past emergence, whereas *Ae. sollicitans* dispersal is apparently limited to a shorter period immediately following emergence. Also, inland movement of both species seems to require several days, implying less prolonged flight than seen in *Ae. taeniorhynchus*.

Although inland dispersal characteristic of *Ae. cantator* and *Ae. sollicitans* can fit some definitions of migration (see Atkins 1978), such usage is not in keeping with current interpretations. The inland movement of these species is best referred to as a specialized form of dispersal. It seems likely that true migration sometimes occurs in *Ae. cantator* and *Ae. sollicitans*, since long distance flights have been reported for both species (Smith 1904, Carpenter & LaCasse 1955). *Ae. taeniorhynchus*, a true migrator, also exhibits dispersal variability among broods produced at different localities (Elmore & Schoof 1963).

Magnarelli (1978) suggests that *Ae. cantator* might oviposit in fresh water at inland locations following dispersal and remain there until death. This appears highly unlikely in southern Maryland, since sampling records of mosquito-abatement programs indicate that *Ae. cantator* larvae are restricted to the salt-marsh habitat in this region. It appears that *Ae. cantator* females disperse inland for blood feeding and return to the marsh to oviposit. They then return inland in the parous condition for additional feeding.

#### CONCLUSIONS

Newly emerged *Ae. cantator* females often disperse inland 2 km or more for blood feeding and later return to the salt marsh for oviposition. Parous females exhibit no inhibition of dispersal tendency and return inland for subsequent feeding. The Crans et al. (1976) vector-potential index does not differ significantly within 2 km of the breeding marsh. This suggests that *Ae. cantator* could act as a biological vector at inland locations as well as in the vicinity of salt marshes.

*Acknowledgments.* We wish to thank Mrs Tamea W. Bowen of the Calvert Co. mosquito control program for providing light-

trap data for this study. We are also grateful to Drs E. W. Cupp, Gisela Fashing and Louis A. Magnarelli, and Mr C. Marvin Keenan for their suggestions concerning the manuscript.

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