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SWARMING AND MATING IN *AEDES PROVOCANS*
(DIPTERA: CULICIDAE)Stephen M. Smith¹ and Randy M. Gadawski^{1,2}

ABSTRACT

Male *Aedes provocans* formed canopy-level linear swarms in association with prominent trees along hedgerows or convex prominences along woodlot margins. Males oriented along the east-west or north-south axis of the swarm site and flew continuously in alternating directions along the longitudinal axis of the swarm. Swarming began shortly before (mean = -0.78 crep) and ended after sunset (mean = 0.81 crep). The time of onset of swarming was more variable than the time of cessation; on 3 of 5 occasions, swarming stopped abruptly at 0.94 crep, about 2 minutes before the end of civil twilight. Swarming began 4 d after the onset of emergence of the adults and persisted for 3 weeks, but copulations were observed for only the first 6 d. In-flight mating always took place after sunset, many minutes after the onset of swarming. On average, copulation lasted 9.9 s.

In most species of Diptera, males aggregate at species-specific times in species-specific arenas, and there fly, hover, or perch, and respond to females that enter the arena by pursuing and capturing them (Downes 1969); mating is initiated and often completed in flight. Among the *Aedes* mosquitoes the aggregation is usually a lek-like swarm (inter alia: Frohne and Frohne 1952; Nikolaeva 1976; Reisen et al. 1977), but the swarming sites and behaviors of most species remain undescribed or poorly known. Swarming is the critical species-isolating mechanism (Downes 1969) and may provide a mechanism for sexual selection via scramble-competition polygyny or even female choice (Thornhill and Alcock 1983). An understanding of the multi-species communities of mosquitoes that are common in many parts of the world could be enhanced by knowledge of the swarming habits of the constituent species.

Aedes provocans (Walker) is among the first of the snow-melt *Aedes* to emerge in eastern Ontario (Wood et al. 1979, Gadawski and Smith 1992). The species provides a convenient model for the field study of mosquito behaviors: emergence is highly synchronous and occurs over a narrow time window; the species is abundant (Gadawski and Smith 1992); and, as compared to most snowmelt *Aedes*, the adults are unusually easy to identify (Owen 1937). Here we present observations of swarming and mating of *Ae. provocans* through an entire season.

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MATERIALS AND METHODS

Field studies were conducted near Read, Ontario (44°18'N, 77°10'W; UTM: 18TUE271072; ca. 20 km NE of Belleville) in May-June 1978. The study area (Fig. 1) provided a diversity of habitats, including hayfields, pasture, fields abandoned since 1975, hedgerows and mature deciduous forest (predominantly *Acer rubrum* and *A. saccharinum*) with abundant, temporary, snowmelt pools. Both nectar and blood sources were abundant and nearby (Gadawski and Smith 1992; Smith and Gadawski 1994).

Emergence traps (Hayton 1979) were used to ascertain dates of adult emergence. Three traps were placed on woodland pools in late April before adults had emerged; sites with different degrees of canopy closure were selected to ensure that the range of emergence dates in the study area would be well represented.

Host-seeking females were captured at human bait throughout the adult flight season. For capture and dissection methods, see Gadawski and Smith (1992).

Swarming behavior was studied with the naked eye and with the aid of 8× binoculars. Copulation times were measured with a digital stopwatch. Air temperatures at the conclusion of swarming were measured with a shaded thermistor at 1 m. Males were captured from swarms with a standard insect net and identified using Wood et al. (1979). The height of swarming males was measured with an optical range finder aimed at trees immediately adjacent to and at the elevation of the swarms. Times of sunset and the duration of civil twilight were computed by The Floppy Almanac (Carroll 1991); corrections for local altitude, refraction and parallax were deemed unimportant biologically and were not made. Because the time of sunset advances rapidly from day to day in the spring, times of swarming and mating are given in crep units (Nielsen 1963) as well as real time (EDT); 1 crep unit is equal to the duration of civil twilight, with negative values indicating times prior to sunset. As a point of reference—on 18 May, the day that mating was first observed, sunset is at 2032 h; civil twilight lasts 34 min, ending at 2106 h.

Means for copulation times were examined by a 2-tailed t test and variances by a 2-tailed F test. The maximal probability of a type-1 error was set at 0.05. Error terms are standard errors.

RESULTS

Male *Ae. provocans* emerged over the 7-d period from 14 to 21 May, peaking on 16 May; females emerged over the 5-d period from 16 to 21 May, peaking on 19 May (Fig. 2). Swarming males were first seen on 18 May, 4 d after male emergence had begun (Fig. 2) and males continued to swarm, in diminishing numbers, until 7 June (Fig. 2), for a total swarming duration of 21 d. However, copulations were observed for only the first 6 d (18–23 May) of the swarming period (Fig. 2). Uninseminated females were encountered in the population until 27 May, 6 d after the last detected female emergence and 4 d after the last observed copulation in swarms (Fig. 2). Host-seeking females were encountered over a 38-d period, from 16 May, 2 d before the first swarming, until 23 June (Fig. 2). Thus, male swarms were present for a little more than half the period of time that females were on the wing but copulations were observed for only a small proportion of that time (Fig. 2).

In the evening of 18 May, the first pleasant evening since the beginning of emergence, males of *Ae. provocans* were found in a single, large swarm at site 1 (Fig. 1) along the southern boundary of a woodlot, about 50 m south of the nearest larval habitats. The swarm was situated at about 15.5 m, about 1 m



Figure 1. Aerial photograph, taken in late summer in the year of the study, showing swarm sites (arrows) used by male *Aedes provocans*. Numbered sites are discussed in the text. Larval habitats were in both the north and south woodlots.

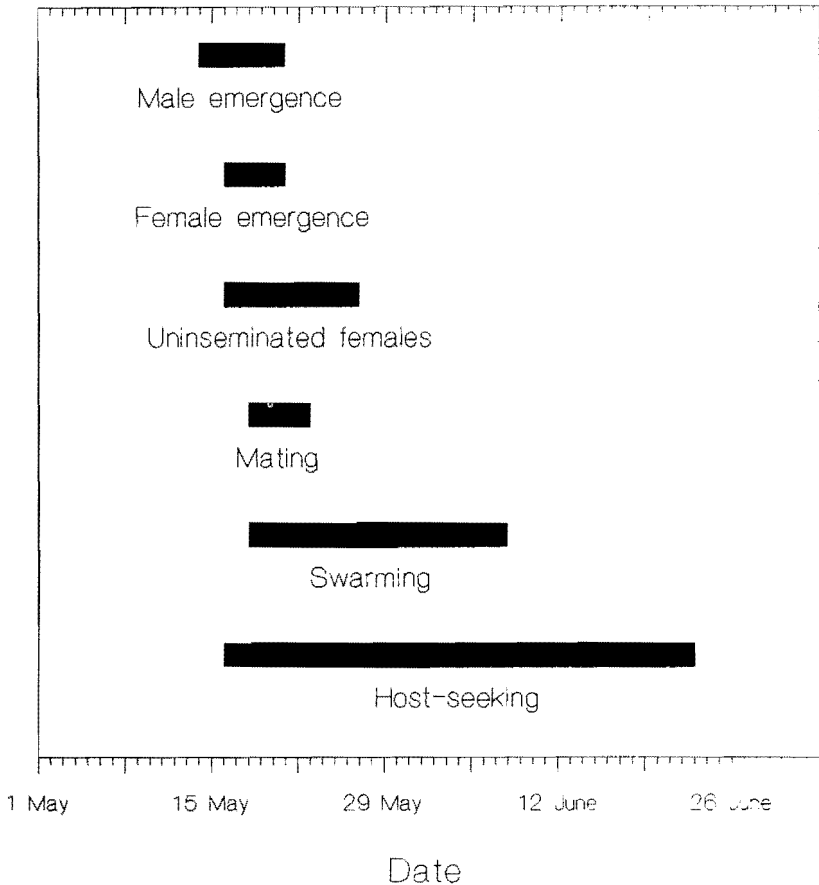


Figure 2. The duration of major events in the life history of adult *Aedes provocans*. The period shown for uninseminated females includes females taken during the emergence period, swept from resting sites and while host seeking at man.

below the forest canopy and 1-2 m out (south) from the forest margin. The long axis of the swarm was parallel to the ground and extended from east to west, bending slightly along the convex margin of the woodlot. The swarm measured 20 m long by 1 m wide by about 1 m deep and we estimated a density of several hundred males per cubic meter, so that the swarm comprised at least several thousand individuals. The noise of the swarm was audible from a considerable distance. Swarming began at 2020 h (-0.35 crep) (Table 1) under a cloudless sky with almost no wind. As light intensity declined, the elevation of the swarm decreased slightly; at 2038 h (0.18 crep) the swarm was at about 12 m.

Two additional swarms appeared about 2040 h (0.24 crep) at sites 2 and 3 (Fig. 1), each also associated with convex prominences of the woodlot bound-

Table 1. Time of initiation, termination and duration of swarming and mating in *Aedes provocans*.

Date	Swarming ^a			Temp. (°C) ^b
	Beginning	Ending	Duration (h)	
18 May	-0.35	0.94	0.73	13.3
19 May	-0.66	0.77	0.83	19.8
20 May	-0.83	0.46 ^c	0.75	15.3
21 May	-1.29	0.94	1.30	14.3
23 May	-	0.94	-	18.0

Date	Mating ^a			Temp. (°C) ^b
	Beginning	Ending	Duration (h)	
18 May	-	-	-	13.3
19 May	-	-	-	19.8
20 May	-	-	-	15.3
21 May	0.43	0.69	0.15	14.3
23 May	0.23	0.83	0.35	18.0

^aTimes of beginning and ending of swarming and mating are given in crep units.

^bAir temperature at 1 m at the end of the swarming period.

^cHeavy rain falling at this time.

ary. The height, orientation and behavior of the males in these swarms was identical to those of the males swarming at site 1. Males did not swarm along the concave sections of the forest edge (Fig. 1). Cessation of swarming was abrupt. A slight reduction in the density of swarming males at site 1 was evident at 2058 h (0.76 crep) and the remaining males had moved closer to the trees. One minute later (2059; 0.79 crep) the reduction in density was marked; only scattered individuals remained at 2104 (0.94 crep). In total, then, males swarmed for slightly less than 45 minutes at a temperature of about 13°C (Table 1).

Flights of males within the swarm were along the east-west axis. Males flew toward the western sky in a leisurely, dance-like fashion, with up-and-down bobbing, then turned abruptly and flew east at a faster pace, turned and resumed a westward flight. Individual males pursued flight paths that were shorter (8–10 m) than the length of the swarm.

On 19 May, swarming began at 2010 h (-0.66 crep) at sites 1 and 2; no males swarmed at site 3. In addition, swarms were found at two sites (site 4 and 5, Fig. 2) along a fence row about 100 m to the east of the original swarm sites. At these sites male *Ae. provocans* swarmed contemporaneously with the males at sites 1 and 2 but their orientation was quite different. Males at sites 4 and 5 swarmed along a north-south axis on the western margin of the hedge-row, again near the summit of the adjacent trees: males at site 4 swarmed at 9.5 m in a swarm about 5×1×1 m in size and those at site 5 at 16 m in a swarm 20×1×1 m in size. In these sites, the slow dance was performed toward the south and the fast return flight toward the north. On this second evening of swarming, males began swarming earlier and ended earlier so that the total duration of swarming (0.83 h) was only slightly longer than that of the previous evening (Table 1).

On 20 May observations were restricted to sites 1–3. Swarming had not yet begun at 2000 h (-0.97 crep); light rain was falling and there was a gusty, light, west wind. Swarming began abruptly at 2005 (-0.83 crep) at both sites 1 and 2 but, again, males did not swarm at site 3. The density of males in the swarm increased rapidly, reaching a maximum about 2010 (-0.69 crep). At

2013 h the swarm was dispersed by a strong gust of wind, driving some males to within 2 m of the ground where a net sample was taken; all 30 males haphazardly selected from the sample were *Ae. provocans*. The males regrouped following this wind disturbance and resumed swarming near the canopy, to be disrupted by wind several more times. Swarming ended abruptly at 2050 h (0.46 crep) in heavy rain.

On 21 May, additional swarm sites were discovered along the hedgerows (Fig. 1); elevation of these swarms was often lower owing to the reduced height of the trees but males were always oriented along the long axis of the site (east-west at site 6 and north-south at the 4 other sites) and were associated with prominent trees or copses along the hedgerows. Observations at site 1 at 2030 h (-0.14 crep) and at site 6 at 2041 h (0.17 crep) revealed small groups of males moving across the open meadows from the south at an elevation of 2-4 m and then entering the high swarms. Swarming ceased at 2108 h (0.94 crep), yielding a swarming period of 1.3 h (Table 1).

On 23 May, observations of the relatively low swarm at site 6 permitted more detailed inspection of male behavior. The males flew 4-5 m above the ground in a swarm subdivided into 2 portions, each about half the length of the swarm (about 8 m). A male would fly back and forth about 10 times within about half the swarm length, would then traverse the entire length of the swarm, and then repeat the entire pattern. Movement during the shorter flights was characterized by periodic bursts of speed so that a male might fly 2-3 m at a slower speed and then 1-2 m at a faster speed. The longer flight through the entire swarm was at the lower speed. Males turned and accelerated independently of one another. Swarming again ended abruptly at 0.94 crep (Table 1). 60 vouchers collected on 2 occasions from this swarm were all *Ae. provocans* (59 males, 1 female).

Over the first few days of swarming, the time of onset of swarming was more variable than the time at which swarming ended (Table 1). On 3 of 5 occasions, swarming ceased abruptly at 0.94 crep; illumination at this time (Nielsen 1963) would be about 5 lux. Inclement weather, as on 20 May, caused swarming to end much earlier (Table 1).

Observations on 27, 28 and 31 May showed that swarming continued to occur at all sites except 3, 4 and 5 but the abundance of swarming males was markedly reduced. By 2 June, the swarm at site 6 was reduced to a few scattered males and there were no swarms at sites 8-11. By 4 June, only small numbers of males could be found swarming at sites 1, 2 and 6 and after 7 June, no swarming males could be found at any site.

Copulations were seen frequently during the first 6 d of swarming (Fig. 1), and detailed observations were made on two occasions at site 6. On 21 May, copulation began at 2050 h (0.43 crep), 15 min after sunset and well after the beginning of swarming. Pairing was usually initiated within the swarm but occasionally first contact was made 1-2 m outside the swarm. After initial contact, the pair moved out of the swarm, flying horizontally or downward. Mating was completed in flight; the mean copulation time was 12.3 ± 2.37 s (range 5-29; $n=12$). After separation, the male rejoined the swarm but the female left the swarm site, either flying across the meadow or into adjacent vegetation. A copulation was observed every several seconds until 2059 h (0.69 crep) when all mating activity stopped abruptly. A reduction in swarm density was evident at 2104 (0.83 crep) and swarming ceased at 2108 (0.94 crep). On 23 May, mating began at 2045 (0.23 crep), 8 min after sunset, and continued until 2106 (0.83 crep). Swarming ceased at 2110 (0.94 crep). The mean copulation time was 7.7 ± 1.14 s (range 2-16; $n=13$). The variance of copulation times was large and on 21 May was possibly greater than that on 23 May ($F_{11,12}=3.99$, $p=0.025$) but the mean copulation times were not different ($t_{23}=1.79$, $p=0.087$). The pooled mean copulation time was 9.9 s ($n=25$).

DISCUSSION

The spring of 1978 was cool and the emergence dates of *Ae. provocans* observed in this study were somewhat later than indicated by the historical data in James et al. (1969) and by observations in the years since 1978 (Smith and Gadawski 1994); however, the durations of the emergence periods were similar over that period. Thus, the relative durations of demographic events observed in this study are probably typical but the calendar references are later than is usual for *Ae. provocans* in eastern Ontario.

There are only a few reports of the swarming of *Ae. provocans* in the literature, one questionable and the others very brief. Dyar (1923) described small "swarms" of *Ae. provocans*, about 50 males in each, drifting from a woods over a meadow in Warroad, MN on 21 May 1922. It is not clear from the description that these were really swarming males; the observation is similar to the behavior we observed, coincidentally on the same day in 1978, when males moving across the meadow subsequently joined active swarms. Perhaps what both Dyar and we witnessed was pre-swarming dispersal of males from day-time resting sites; certainly, males were commonly encountered during the day resting in vegetation both in the woods and in vegetation along the hedgerows. Maw (1961) described the swarm site of *Ae. provocans* as being defined by the electrostatic potential of the air space and hypothesized that steep electrical gradients are necessary to direct individuals into well-defined flyways. That hypothesis has not been tested and is not supported by our observations of male *Ae. provocans* swarming in a variety of directions always with reference to prominent visual markers. James et al. (1969) reported "diffuse swarms at margins of woods, with a definite circulating form similar to that described by Downes (1958) for *Aedes hexodontus*", an observation that, in part, is similar to our findings. And Wood et al. (1979) stated that they had observed males swarming after sunset in clearings in the forest, at about 5 m above the ground. Although we commonly encountered males of *Ae. provocans* swarming at that height, the swarms we observed were associated with edges (forest margins or hedgerows) and not with forest clearings, and invariably began before sunset. None of these papers provided detailed information about location and duration of the swarms on either a diel or phenological basis, and only Maw (1961) related the swarming activity to mating (2 copulations were seen over 2 years).

Swarming in *Ae. provocans* began on 18 May, 4 d after emergence had begun. Swarming may have been delayed by weather until that time but it is perhaps noteworthy that, at the temperatures near the emergence sites, males of *Ae. provocans* require about 4 d to complete hypopygial rotation (Smith and Gadawski 1994). As well, time will be needed between emergence and first swarming to obtain a nectar meal (Smith and Gadawski 1994). It is unlikely, therefore, that swarming would have begun much before 18 May even if weather conditions had been permissive. Fedorova (1988) found that swarming in *Ae. communis* (De Geer) began on the 5th day after emergence.

Our observations of crepuscular swarming in *Ae. provocans* are in agreement with the periodicities noted for most swarming mosquitoes (Nielsen and Greve 1950; Haddow and Corbet 1961; Corbet 1964). It seems clear that light intensity around the time of sunset is an important regulating or releasing stimulus for swarming (Nielsen and Nielsen 1962). The important role of light intensity is supported by our observations of *Ae. provocans* ceasing hovering at exactly the same time (0.94 crep) on 3 of the evenings on which matings were seen (Table 1). The light intensity at this time (about 5 lux) is similar to the low light intensities at which *Ae. cantans* (Meigen) (Nielsen and Greve 1950) and *Anopheles freeborni* Aitken (Yuval and Bouskila 1993) ceased swarming (7 and 0.5 lux, respectively). Dawn swarming of *Ae. provocans* was

not observed; perhaps early-morning temperatures in May are usually too low to permit sustained flight.

Commonly, mosquito swarms keep station and are situated in relation to a visually distinct marker—a treetop, roadway, patch of lichen or moss, margin of a pool, tip of a branch, and so forth (Downes 1958). *Aedes provocans* always swarmed at near tree-top level, adjacent to trees at the margins of woods or in hedgerows. The specific nature of the marker is not known but is likely to be the light-dark edge provided by trees against sky. The height above ground varied from swarm to swarm, depending on the site, but the height below the top margin of the adjacent trees was much less variable. Clearly, males of *Ae. provocans* “measure” swarming height from the top down and not from the bottom up; this is additional evidence that the marker is not ground-based. Maw (1961) observed swarms of *Ae. provocans* at an elevation of only 0.5 m flying continuously in a clockwise direction; however, details of the vegetation in the site in which the swarms formed are not given other than that it was a “small glade” in a plantation of red, white and jack pine; the ages and heights of the trees and the dimensions of the glade are not given.

Many workers (e.g. Nielsen and Greve 1950; Haddow and Corbet 1961; Downes 1969) have reported that swarming mosquitoes maintain an upwind orientation. Downes (1969) further reported that the morphology of the swarms of *Ae. hexodontus* Dyar changed as wind velocities changed; in low-wind conditions, the swarms were vertical columns, becoming progressively elongated as wind speeds increased. In striking contrast to these observations, we observed males of *Ae. provocans* orienting not with respect to wind but to the linear axis of the assembly site, and we observed males under both low- and moderate-wind situations. Males did orient to the brighter portion of the sky (west in east-west swarms and south in north-south swarms) but they flew actively in both directions within the swarm, slowly toward the brighter sky and more rapidly toward the darker sky, in striking contrast to the pattern described by Downes (1969) for *Ae. hexodontus*, in which the males flew upwind and then drifted backwards. Reisen et al. (1977) also reported that the swarms of *Anopheles*, *Culex* and *Aedes* mosquitoes in Pakistan adopted a wide variety of swarming directions. It may be that the dynamics of orientation in mosquito swarms are a function of size and position (i.e. elevation) of the marker. The purpose of the within-swarm flights and the significance of species differences in such flights are unknown.

The swarms of *Ae. provocans* are clearly mating stations. We frequently observed mating in swarms but in several years of study of *Ae. provocans* we have seen no copulations in any other situation. Most mating in *Ae. provocans* took place in the first few days of swarming. However, we encountered unseminated females in the host-seeking population for several days after we last saw mating in swarms, so some low level of mating activity may have continued for the duration of the swarming period. Fedorova (1988) found a similar pattern in *Ae. communis*, in which 80% of the females were inseminated on the third to fourth day of adult life. The emergence period in *Ae. provocans* is brief and matings were restricted to a subset of the swarming period, a pattern also reported by Yuval and Bouskila (1993), who observed mating in *Anopheles freeborni* to be most common 10–20 min after swarming had begun; in *An. freeborni*, the time of mating coincides with the maximal swarm size and a reduced risk from predation. We did not observe predation events in the swarms of *Ae. provocans* but there was a progressive increase in the size of swarms over time so females may be delaying an approach to the swarm until the swarm contains large numbers of males. The in-copula time of *Ae. provocans* (9.9 s) was brief in comparison to the copulation times reported for *Anopheles culicifacies* Giles (15.6–33.6 s) and *Culex pipiens fatigans* Wiedemann (19.7–33.0 s) by Reisen et al. (1977) but much longer than the

copulation times reported for *Mansonia fuscopennata* (Theobald) (1-3 s) (Corbet 1964).

Relative to both the temporal and seasonal durations of swarming, copulation in *Ae. provocans* is a rare event. This is probably a not-uncommon situation in many species and it is perhaps not surprising therefore that some early workers, on observing swarms without seeing copulations, questioned the functional role of swarming (Nielsen and Greve 1950). However, the high energetic costs of swarming, its almost universal occurrence, and the now-frequent correlation of swarming with mating, make it clear that mating in most *Aedes* species takes place in swarms (Downes 1969). In general, the frequency of observed mating is low in landmark-based mating systems such as those used by *Aedes* mosquitoes (Thornhill and Alcock 1983). For species such as *Ae. provocans* in which emergence is highly synchronized and occurs over a brief time period, it would be very easy to conclude that swarming was not associated with mating if the first few days of swarming activity were not sampled intensively.

Differential mating success among swarming male mosquitoes has rarely been examined. Yuval et al. (1993) found that swarming males of *Anopheles freeborni* were larger than the resting population, suggesting that some males never swarm at all. As well, early-swarming males were smaller than later-swarming males and most matings took place 10-20 minutes after swarming had begun. It is conceivable that the delay of mating seen in *Ae. provocans*, in which mating also took place late in the swarming period, may be related to differential male mating success. Such possibilities are currently under investigation.

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