ATTRACTION TO MAMMALS OF MALE MOSQUITOES WITH SPECIAL REFERENCE TO *AEDES DIANTAEUS* IN SWEDEN

THOMAS G. T. JAENSON

Department of Entomology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden

ABSTRACT. During investigations in central Sweden on the ecology of mosquito vectors of Ockelbo disease, large numbers of *Aedes diantaeus* males and lesser numbers of *Ae. communis, Ae. excrucians* and *Ae. intrudens* males were captured in animal-baited (rabbit, guinea pig, hen, dove, unbaited control) suction- and net-traps. In the five suction-traps, 57% of the *diantaeus* captured (N = 1,896) were males. Although the guinea pig-baited suction-trap captured the highest mean number of *diantaeus* males, data showed that these males, like the females, were mainly attracted to the largest mammal, i.e., the rabbit. These males assembled in the vicinity of the rabbit presumably to intercept females coming to feed. The net-trap data showed that orientation by the males to the rabbit presumably involved olfactory cues emanating from the mammal.

INTRODUCTION

In most species of mosquitoes mating is initiated in flight, often at a visually determined landmark at which the males usually fly for longer periods than the females, which only remain there long enough to mate (Downes 1969). A few authors consider that the swarming behavior of the male mosquitoes does not play an important sexual role. For many mosquito species, however, it is likely that the swarms play an important epigamic function associated with mating (Downes 1969, Charlwood and Jones 1980).

Certain mosquito species use the vertebrate host itself as a swarm marker. Mating then occurs in the vicinity of, or sometimes on, the host (Downes 1969, Anderson 1974). Other mosquito species, living in marginal or restricted habitats, mate on the ground, without previous dispersal or swarming (Downes 1969).

During entomological investigations in an Ockelbo disease endemic area in central Sweden, animal-baited traps were used to sample mosquito populations. The primary aims were to obtain data on seasonal abundance and potential host preferences of possible mosquito vectors of Ockelbo virus, and to obtain material for virus isolation attempts. An unexpectedly high number of male mosquitoes were taken in some of the traps. Since ethological data for the mosquitoes in northern Europe are sparse the samples were analyzed in detail. This paper reports on the attraction to mammals of male mosquitoes for the eventual purpose of mating.

MATERIALS AND METHODS

Five suction-traps, similar to the ones described by Emord and Morris (1982), were hung in a row 1.3 m between each other and 1 m above the ground in a stand of birch trees in the Sässman area (61° 23′ N, 15° 51′ E), province of Hälsingland, Sweden. Four traps were baited with one domesticated animal each (rabbit, guinea pig, dwarf hen, dove) and one was unbaited. To avoid position bias, each trap with its bait was randomly alternated every morning.

Five net-traps (Jupp and McIntosh 1967) were baited as the suction-traps and placed in a circle 1 m between each trap in open woods about 10 m from the nearest suction-trap. Every morning each animal with its respective cage was randomly allocated to the net-traps.

Traps were usually operating from Monday morning to Thursday morning every week from the end of April to the end of September 1983. The traps were inspected every morning. On June 8, July 13–14 and September 21 one or more of the motors in the suction-traps did not function well. Therefore, data for these days were omitted from the calculations.

The calculations have been limited to those 24-hr periods when at least one individual of the relevant sex and species was captured. The number of each species and sex collected in every 24-hr period in one trap was converted to the log (x + 1). For each trap-type, mosquito species and sex, the data were analyzed as a randomized block design with days as blocks. If a significant ($p < 0.05$) F-value was obtained, the means were compared with the Student-Newman-Keuls test, to determine differences between means. The results in Table 1 were expressed as Williams' mean (M_W), i.e., the antilog (-1) of $\Sigma \log(x + 1)/N$. Data for species taken in a total number of < 32 males in either type of trap are not considered in this paper.

RESULTS

The data in Table 1 show that the males of *Aedes communis* (DeGeer), *Ae. excrucians* (Walker) and *Ae. intrudens* Dyar were not attracted preferentially to any of the baits in the traps. Only

Table 1. Numbers of mosquitoes taken in animal-baited (rabbit, guinea pig, hen, dove) and unbaited (control) suction- and net-traps.

			Mean (M_w) no. mosquitoes taken per 24-hr period						
Species	Sex	Trap-type	Rabbit	Guinea pig	Hen	Dove	Control	Total no.	% ♂♂
Ae. communis	♂	Suction	0.05 B	1.02 A	0.50 AB	0.68 A	0.82 A	58	3.9
Ae. communis	♂	Net	1.21 A	1.00 A	0.70 A	1.28 A	0.87 A	157	14.8
Ae. communis	♀	Suction	9.47 A	3.17 B	3.37 B	2.89 B	0.91 C	1432	—
Ae. communis	♀	Net	5.17 A	2.98 B	2.47 B	2.72 B	1.45 C	906	—
Ae. diantaeus	♂	Suction	4.57 B	15.07 A	6.28 B	7.49 B	6.82 B	1073	56.6
Ae. diantaeus	♂	Net	1.12 A	0.53 AB	0.55 AB	0.10 B	0.05 B	50	19.2
Ae. diantaeus	♀	Suction	7.13 A	4.01 B	3.27 BC	2.39 C	0.78 D	823	—
Ae. diantaeus	♀	Net	2.39 A	1.45 B	1.14 B	0.86 B	0.07 C	210	—
Ae. excrucians	♂	Suction	0.22 B	1.77 A	3.39 A	2.47 A	1.41 A	266*	18.8
Ae. excrucians	♂	Net	1.34 A	1.73 A	1.67 A	1.59 A	1.19 A	200*	20.3
Ae. excrucians	♀	Suction	7.51 A	3.07 B	2.80 B	1.40 C	0.70 D	1149*	—
Ae. excrucians	♀	Net	4.01 A	2.80 AB	2.63 AB	1.88 BC	1.34 C	786*	—
Ae. intrudens	♂	Suction	0.00 A	1.25 A	0.15 A	0.32 A	0.00 A	32	4.4
Ae. intrudens	♂	Net	1.20 A	0.70 A	1.29 A	2.36 A	0.59 A	48	7.1
Ae. intrudens	♀	Suction	8.77 A	1.75 B	0.70 C	0.78 C	0.41 C	694	—
Ae. intrudens	♀	Net	5.61 A	1.45 BC	2.09 B	1.29 BC	0.74 C	625	—

Means with the same letter in the same horizontal row are not significantly different ($p > 0.05$).
* May possibly include a low number of *Ae. beklemishevi* Denisova and/or *Ae. euedes* Howard, Dyar and Knab.

32 *intrudens* males were caught in the suction-traps during the whole season. Between June 21–22, i.e., 3 wk after the appearance of the first *intrudens* male, 28 males were caught in the guinea pig-baited suction-trap.

The total number of *Ae. diantaeus* Howard, Dyar and Knab males exceeded that of the females. The proportion of males of this species in the suction-traps was significantly higher ($p < 0.001$) than that of any of the other *Aedes* species collected (Table 1). The mean catch-levels of *diantaeus* males were high in all of the suction-traps, although significantly highest in the "guinea pig-trap" (Table 1). The mean catch-levels of the females in the two trap-types show the following order of "host attractiveness": rabbit > guinea pig ⩾ birds > control (Table 1). If *diantaeus* males are attracted to the host of the females (Dyar 1920), one would expect the catch of males to be highest in the mammal-baited traps, and because of the larger size of the rabbit compared to the guinea pig, particularly in the "rabbit-trap." However, not in a single of the fifteen 24-hr periods, when at least one *diantaeus* male was caught, did the rabbit-baited suction-trap have the highest catch of *diantaeus* males. On the contrary, during 11 of the periods one of the traps next to the "rabbit-trap" had the highest catch of *diantaeus* males. During the remaining 4 periods the "guinea pig-trap" had the highest catch while one of the traps next to the "rabbit-trap" had the next highest catch. The mean (M_W) catch of *diantaeus* males in traps hanging immediately adjacent to the "rabbit-trap" was 13.5 males compared to 6.7 males in traps not hanging immediately adjacent to the "rabbit-trap." The paired *t*-test shows that the means are significantly different ($t_{14} = 4.13$, $p < 0.002$). The mean for the "rabbit-trap" was 4.6 males and is lower than that of the traps adjacent to the "rabbit-trap" ($t_{14} = -6.85$, $p < 0.001$). There was no significant difference between frequency of peak 24-hr catch of traps hanging at the edges (0.20) and that of traps hanging in the middle (0.27) of the row.

DISCUSSION

The data presented here were derived from an investigation designed primarily to elucidate the possible role of mosquito females as vectors of Ockelbo virus. The high catches of *Ae. diantaeus* males in the suction-traps hanging immediately adjacent to the "rabbit-trap" showed that these males, like the *diantaeus* females, were preferentially attracted to the rabbit. The males were not caught in the rabbit-baited suction-trap to such an extent as could have been expected at first. This was most likely because they were flying at a short distance from the rabbit and because the trap only catches insects flying very close to and above the suction device, which was about 0.2 m from the rabbit. In view of this and because of the relatively short distance between the traps, males attracted to the rabbit should be caught to a great extent by the adjacent trap(s). The guinea pig-baited suction-trap captured the highest mean number of *diantaeus* males. It is considered likely that the males adjust the distance, at which they are "swarming" around a vertebrate, to the size of the vertebrate. They will, therefore, fly closer to the small guinea pig than to the bigger rabbit. In view of this and the trap design the "guinea pig-trap" should, therefore, be more efficient than the "rabbit-trap." This means that a larger proportion of males attracted to the guinea pig should be caught by the "guinea pig-trap" while a lower proportion of males attracted to the rabbit should be caught by the "rabbit-trap." The suction-trap data did not reveal any "edge effect." This means that, if the males were visually attracted to the traps, it was not revealed by the present data. The capture of significantly higher numbers of males and females of *diantaeus* in the rabbit-baited net-trap (Table 1), in which the animal was obscured, than in the unbaited control trap suggests that the males, like the females, orientated to the rabbit by olfactory cues emanating from this animal.

Males of many insects search for mates near resources used by the females. Like males of certain simuliids, phlebotomids and ceratopogonids, males of some mosquitoes (references in: Anderson 1974, Service 1976 p. 232 ff., McIver et al. 1980), assemble in the vicinity of a warm-blooded animal to intercept females coming to bite. For instance, males of *Ae. sierrensis* (Ludlow) form small "swarms" around mammals and mate with females as they come to feed (Dyar 1920). Copulation may take place in flight (Peyton 1956) or while the female is engorging (Peyton 1956, Hearle 1926 referred to in Wood et al. 1979). A similar mating behavior is exhibited by *Ae. diantaeus*. The males do not swarm in the usual manner but are attracted to warm-blooded vertebrates. Here the males fly singly to intercept females coming to feed (Dyar 1920, 1928). Copulation is initiated in the air and may continue after the pair has alighted on the vegetation (Dyar 1920) or on the host, which the female may attempt to bite (Markovich 1957 referred to in Brust 1971). In small cages copulations may readily occur lasting from 20 sec to 1.5 min. They may begin during flight or on the cage walls (Brust 1971).

From the present data and the observations of Dyar and Markovich it is inferred that a significant number of *diantaeus* males were attracted to the mammals, particularly the rabbits, most likely for the purpose of mating. The data suggest that the males "selected" the preferred host of the females, and that the males were flying at a short distance from this host. Selection for such a behavior pattern, i.e., "swarming" at a certain distance from the host, may have evolved from the benefit of being close to the host, where the likelihood to encounter the opposite sex is greatest, and the cost of being too close to a mammal or bird which may show defensive, antimosquito behavior. *Aedes diantaeus* usually occurs in scattered, low-density populations (Natvig 1948, Mohrig 1969, Wood et al. 1979). A mate-locating behavior whereby the males are waiting in a zone likely to be entered by the females is an efficient method for bringing together the sexes from a dispersed population (Downes 1969).

It has not been clear whether the animals (and the traps) are purely acting as visual swarm markers (Clements 1963). Olfactory orientation by the *diantaeus* males to the rabbit, that was obscured in the net-trap, was considered likely. A similar conclusion was drawn by McIver et al. (1980) who demonstrated that in West Africa *Mansonia* males were attracted to goats, probably by olfactory cues. Assembly near the host due to perception of the female's flight tone over distances more than some centimeters is unlikely (McIver et al. 1980). There is no evidence for long range attraction of male mosquitoes through pheromones emitted by the female mosquito. In several species, however, close range recognition of the female through pheromones may be important (Anderson 1974).

Adults of *Ae. diantaeus* are active both day and night in shady forests (Dyar 1928) with maximum activity in the morning and evening (Mohrig 1969). In June and July the daylight and twilight periods are very long in the study area. It is, therefore, likely that visual orientation, in addition to or sometimes even instead of olfactory orientation, to hosts may be important, particularly if they are not concealed (suction-traps). Like males of many other species having plumose antennae, it is likely that *diantaeus* males locate the female at close range by her flight tone (Clements 1963). During copulation contact discriminatory mechanisms may be involved (McIver 1982).

The present results suggest worthwhile areas for future research, including more detailed studies on the behavior of the males near the host, elucidation of which chemical factor(s) may be involved in attraction of the males to the host; and whether or not female sex pheromones are produced, and if so the approximate distance at which they are acting.

Aedes communis, *Ae. excrucians* and *Ae. intrudens* were among the most abundant mosquitoes in the study area. Females of these species were attracted preferentially to the rabbits. On the contrary, the catch-levels for the males of *communis* and *excrucians* indicated that the males were "repelled" by the rabbit-baited suction-trap, while the catch-levels in the other baited traps were similar to those in the unbaited traps. Presumably, in catching males of these species the baited suction- and net-traps were functioning, in principle, as unbaited suction traps and Malaise traps, respectively. It is, however, possible that the males were flying at a longer distance away from the largest of the baits, the rabbit, than from the other baits. If so, this would explain the lower catches in the rabbit-baited suction-trap.

Aedes communis and *Ae. excrucians* form male swarms apparently away from the females' blood hosts (Dyar 1919, Wesenberg-Lund 1920, Frohne and Frohne 1954, Nielsen and Haeger 1960). No specific information on the mating behavior of *Ae. intrudens* seems to have been published (Wood et al. 1979). The present data suggested that, between June 21 and 22, males of this species had formed a swarm close to the guinea pig-baited suction-trap. It is likely that the males had been using the trap as a swarm marker.

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