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Temporal dynamics of mating and predation in mosquito swarms

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Abstract. We determined the numbers of copulations and predatory attacks in swarms of *Anopheles freeborni* (Diptera: Culicidae), and the distribution of these events throughout the duration of the swarming period each day. On 19 evenings of observation, we recorded 2724 copulating pairs leaving swarms and 1351 dragonfly (*Pantala hymenaea* and *Erythemis collocata*) attacks. Mating activity partially coincided with predator activity. Most copulations occurred between 10 and 20 min after the swarms formed, while predation events were most frequent during the initial 15 min of the swarm. We calculated the ratio of copulations to predatory attacks during the swarming period. This ratio was significantly higher in an area sheltered by trees than it was in the open. We suggest that physiological and ecological constraints other than predation operate on the mating system of this anopheline to affect the timing of swarm initiation and swarm site selection.

Key words: Mating success – Swarm – Predation – *Anopheles* – Odonata

Mating systems based on aerial male aggregations that function as encounter sites for mate searching females have evolved repeatedly in various groups of insects (Sullivan 1981; Cooter 1989). In most swarming species the swarms are composed of males; females typically approach a swarm, acquire a mate, and leave *in copula*. There may be advantages for both sexes in this arrangement. Females have a large selection of males to choose from, and can exercise mate choice or mate with the winners of competition between males. The advantage for a male who joins a swarm is that conspecific, sexually receptive females will be attracted to the same area (e.g. Parker 1978; Thornhill and Alcock 1983). Although alternative mating tactics have been reported in some swarming insect species, for many species males may only encounter receptive females within swarms (Downes 1969; Mclachlan and Neems 1989).

Several studies have examined the determinants of mating success in swarms (Thornhill 1980; Flecker et al. 1988; Petersson 1989, 1990; Neems et al. 1990; Yuval et al. 1993). The costs of swarming are less well understood. Males that swarm invest energy in flight and are potentially exposed to predators. The entomological literature contains many references to predation on swarms (Corbet 1963; Downes 1969; Sullivan 1981); however, there is no consensus on the impact that this factor has in regulating the swarming habit. To date only one study has attempted to analyze the relation between predation and mating in swarms. Neems and co-workers (1992) found that in swarms of a chironomid midge (*Chironomus plumosus*) the probabilities of both predation and mating were relatively greater in smaller swarms. No information exists on the distribution of these events within a swarm's duration, or if these probabilities affect when individuals join a swarm and how long they remain in it.

In the central valley of California, swarms of male *Anopheles freeborni* mosquitoes assemble on most evenings from July to late September, and libellulid dragonflies prey on them intensely (Yuval et al. 1993). Swarms form 5–10 min after sunset, last 30–35 min and disperse when twilight ends, or earlier when conditions are windy. The caloric cost of swarming is severely limiting for these mosquitoes, and the time a male can sustain swarming flight depends on his past success at foraging for plant-derived carbohydrates (Yuval et al. submitted). Furthermore, body size of anopheline males appears to determine when individuals join a swarm and is correlated with their mating success in these aggregations (Yuval et al. 1993).

In the present study our objective was to determine the relative probabilities of copulations and predatory attacks in swarms, and whether patterns of male and female behavior reflect these probabilities. In particular, we established the frequency of mating and predation

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events throughout the duration of swarms, in two distinct areas and throughout one season of activity.

Methods

Field observations

We observed swarms on 19 evenings, from July 15 to September 23, 1992, on a farm adjacent to rice fields, near Pleasant Grove, Sutter Co., California. We concentrated on two distinct areas where swarms formed. The first was sheltered by a row of oak trees (approximately 10 meters tall), bordering a service road adjacent to a 16 hectare rice field. Here mosquitoes formed typical space swarms (Nielsen and Haeger 1960) by limbs of the trees, and marker swarms over objects on the service road. The second was an open area, by the edges of the rice field, where marker swarms formed over ruderal vegetation encroaching into the rice field.

Numbers of individuals in anopheline swarms change constantly throughout a swarms duration. We have determined, (by photographing anopheline swarms every five minutes and counting individuals off the prints), that numbers of mosquitoes in these swarms build up during the first 15 min, and then gradually decline (Yuval et al. 1993). At their peak density, swarms contain from 500 to 3000 individuals. In the present study we estimated (from visual reckoning), that at the time of peak activity the numbers of individuals observed under the trees ranged from 1000–2000, while over the rice field 500–1000 mosquitoes were active at the corresponding time. Inferences on absolute probabilities of mating and predation should be based on precise estimates of swarm size. Because numbers of individuals in anopheline swarms change constantly, we decided to analyse the temporal distribution of mating and predation events, and to determine the relative probabilities of these events throughout the duration of the swarming period.

To determine the number of mating and predation events in swarms we used a portable computer as an event recorder and recorded events in real time. Later we transformed the records to be relative to the initiation of the swarm. A copulation was recorded when a pair of mosquitoes was seen leaving a swarm in tandem; a predation event was recorded when a predator swooped into a swarm, slowed down and dipped into the mass of mosquitoes, and flew out. We assumed each attack by a predator and each observed copulation to be successful. The predators were identified as belonging to two species of libellulid dragonflies-*Pantala hymenaea* and *Erythemis collocata*; voucher specimens have been deposited in the Bohart Museum of Entomology, U.C. Davis. Illumination levels and wind speed were measured every five minutes (with a Gossen Luna-pro light meter and a hand-held anemometer), from the time swarms formed until they dispersed.

Statistical analysis. The raw data were parcelled into 6 units of 5 min each, from the initiation to decline of each swarm. This created a discrete record of mating and predation events in each unit of five minutes. Because some swarms lasted up to 35 min, the last time unit also included all events recorded past the 30 min point. This does not cause a serious bias because less than 1% of the events occurred in this period. The numbers of events were analyzed in a multivariate repeated measure analysis of variance (O'Brien and Kaiser 1985; von Ende 1993) with individual swarms as the experimental units. Time from initiation of the swarm and type of event were included as the repeated factors (within-group), and the area where the swarm was observed as a between-group factor (von Ende 1993).

As a measure of relative risk and reward, we divided the numbers of matings by the number of predator attacks in each time unit. This measure is normalized in respect to swarm size. The mating/predation ratio was also analyzed with a multivariate repeated measure analysis of variance.

Table 1. Copulation and predation in swarms of *Anopheles freeborni*

Date	Area Observed[a]	Number of Copulations	Number of Predator Attacks
15. VII	Sheltered	114	22
23. VII	Sheltered	67	11
27. VII	Exposed	238	71
29. VII	Sheltered	64	63
3. VIII	Sheltered	323	30
10. VIII	Exposed	45	248
17. VIII	Exposed	119	393
19. VIII	Sheltered	98	19
24. VIII	Sheltered	71	3
26. VIII	Exposed	261	10
31. VIII	Sheltered	438	34
2. IX	Exposed	74	41
9. IX	Sheltered	248	17
10. IX	Exposed	60	166
16. IX	Exposed	21	22
17. IX	Sheltered	81	4
23. IX	Sheltered	234	24
24. IX	Exposed	27	29

[a] We observed swarms which formed under trees (sheltered), and in an open space over a rice field (exposed). Numbers of individuals in swarms were estimated (15 min after they begun) to peak at 1,000–2,000 individuals in the sheltered area and 500–1,000 in the exposed area

Results

On 19 evenings of observation, we recorded 2724 copulating pairs leaving swarms and 1351 dragonfly attacks. The variability of these events from day to day was considerable. Predator attacks ranged from 3 to 393, while copulations ranged from 21 to 428 (Table 1). Swarms began on average 7.9 min after sunset under the trees (range 4–10), and 9.7 minutes (range 6–14) after sunset in the open area ($t = -1.6$, $P = 0.055$). Light intensities at the time when swarms initiated were 350 lux (SD = 20) and 0.5 lux when they dispersed (Fig. 1).

The temporal distribution of copulations differed from the distribution of predatory attacks ($F = 12.3$, d.f. = 5, $P = 0.0001$). Most copulations occurred between 10–20 min after swarms formed, while predation events were more frequent during the initial 15 min of the swarm and dwindled thereafter (Fig. 1). To compare the relative variability of these events we plotted the coefficient of variation against time (Fig. 2). There was greater variability in predatory attacks during the initial 15 min of the swarm, while during the same time period variability in mating was relatively low. Conversely, during the latter 15 min of the swarm, there was a high variability in mating events, whereas the variability of predatory attacks was low.

Copulation and predation events were not distributed evenly between the 2 areas. We observed 63.8% of all copulations in the area under the trees, while 83.1% of the predatory attacks were seen over the rice field ($F = 6.11$, d.f. = 1, $P = 0.024$). The average patterns of copulation were quite similar in both areas, but preda-

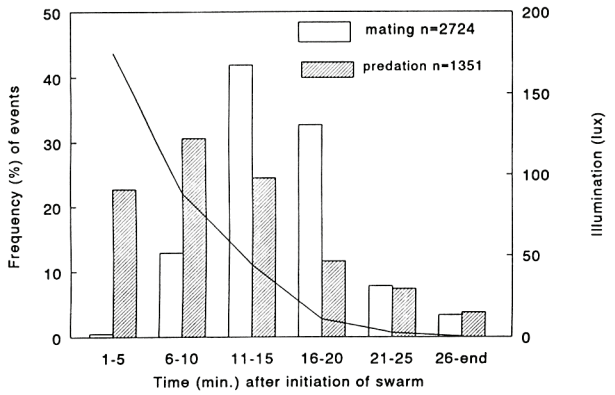


Fig. 1. Frequency of mating and predation in swarms of *Anopheles freeborni*

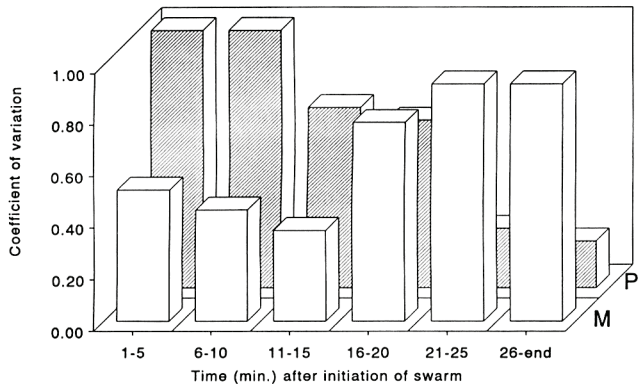
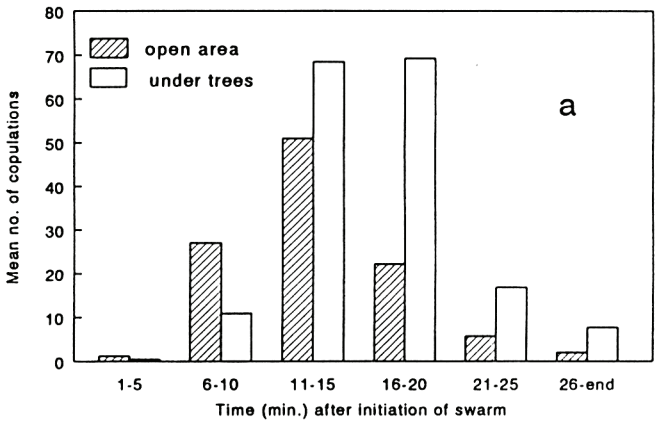


Fig. 2. Relative variability of mating (*M*) and predation (*P*) events in swarms of *Anopheles freeborni* throughout their duration



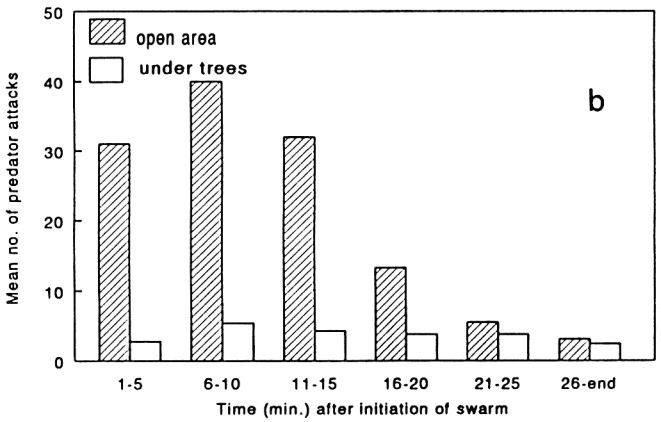


Fig. 3a, b. Mating (**a**) and predation (**b**) in swarms forming under trees or in an open area

tion was markedly more intense over the rice field, particularly during the first 15 min of swarming (Fig. 3, d.f. = 5, F = 2.17, $P = 0.064$).

Overall, the ratio between mating and predation events was highest 10–20 min after the swarms formed (d.f. = 5, F = 7.5, $P = 0.0001$). The mating/predation ratio for males swarming over the rice field was significantly lower than in the area sheltered by the trees (Fig. 4; F = 4.08, d.f. = 5, $P = 0.002$).

Discussion

In our study system, predation on swarms was clearly common and intense. Intensity of predation was highest during the first 15 min of the swarms duration, which corresponds to the time when the numbers of individuals in swarms gradually increase (Yuval et al. 1993). Mating began while predation was still intense, peaking from 10 to 20 min after initiation of swarming. Furthermore, the mating/predation ratio was significantly lower in the swarms which formed in the open area. These findings suggest that the risk of predation is not the only factor governing initiation of swarming, mating in swarms and swarm site selection. We shall discuss these points in light of what we know of the ecological and physiological constraints which operate on this mating system.

The patterns of predation reflect the foraging biology of the predators. Dragonflies locate their prey visually, and cannot do so effectively as darkness gathers. We observed that 20–25 min after sunset, although swarms still contained numerous individuals, most dragonflies ceased feeding and flew into nearby treetops to roost. The greater incidence of predation in the open area (Fig. 3b) is probably due to the foraging preferences of anisopteran dragonflies, who tend to range over open spaces (Corbet 1963; Samways and Caldwell 1989).

Numerous males appear in swarms at times when few matings take place and the risk of predation is relatively high. Furthermore, many females approach swarms and mate at times when the risk of predation is still considerable. Experimental studies and field observations on a variety of species have established that the physiological trigger for initiation of swarming is, within a rather broad range of temperatures, a visual perception of changes in light intensity (Nielsen and Greve 1950; Nielsen and Nielsen 1962; Harwood 1964; Riesen et al. 1977; Allan and Flecker 1989). The actual illumination threshold which initiates swarming is highly species-specific, and this specificity in effect temporally partitions the same swarm sites among sympatric species (Nielsen and Greve 1950; Wharton 1953; Downes 1969; Riesen et al. 1977). In our study site we consistently observed a succession of species using the same swarm sites. Neverthe-

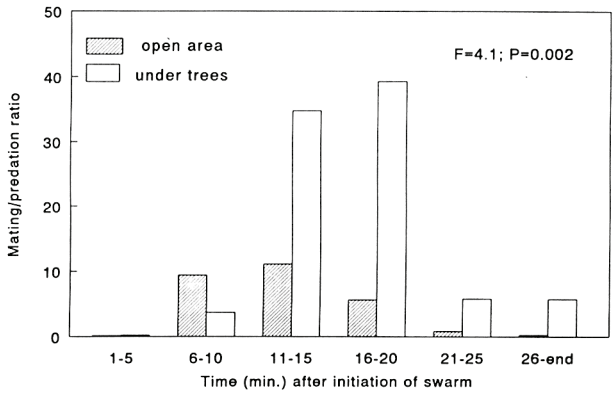


Fig. 4. Ratio of mating to predation in swarms forming under trees or in an open area

less, within the window of activity available for *An. freeborni,* why not initiate swarming 15 min later, and minimize the risk of predation by dragonflies? Specific physiological and ecological constraints may compel individuals to behave in apparently maladaptive or suboptimal ways (Krebs and Davies 1987; Bouskila and Blumstein 1992; Sih 1992). We suggest that at lower light intensities there are visual constraints on mating in swarms, which have edged mating activities to partially coincide with predatory activity.

Within the species-specific window for swarming, individual phenotypic or genotypic variations may exist. The threshold of response to stimuli which elicit the expression of complex behavior patterns may vary among conspecific individuals, depending on their physiological status (e.g. Blaney et al. 1986; Rowland 1989). In *An. freeborni* the initiation of swarming by males is correlated to individual size: smaller males commence swarming earlier than large males (Yuval et al. 1993). Because larger males appear to obtain a greater share of matings, we hypothesized (Yuval et al. 1993) that this behavior is a result of male-male competition, whereby the smaller males are relegated to start swarming earlier, exposing themselves longer to predators, but increasing their own probability of mating. Our findings here support this view. The mating/predation ratio during the initial 10 min of swarms, though lower than the ratio in the next ten minutes, is nevertheless greater than zero. Males who begin to swarm early could tradeoff increased exposure to the highly unpredictable predators with decreased competition for the few females who occasionally but consistently show up early (Fig. 2). Predation invariably decreases as light fades during the final minutes of the swarm (Fig. 2), so all males risk little by maintaining station in the swarm for as long as their energy reserves allow.

Most females approach the swarm when it contains the greatest number of individuals, a behavior that would decrease their probability of encountering a predator due to the dilution effect (Foster and Treherne 1981; Wrona and Dixon 1991), as well as provide them with the largest choice of potential mates.

There was a significant difference in the mating/predation ratio between the sheltered and exposed areas we observed (Fig. 4). This difference begs the question: Why swarm anywhere but the best spot? Swarm markers are perceived visually (e.g. Downes 1969; Charlwood and Jones 1980; Marchand 1984), have an arrestant effect on individuals who perceive them, and some are more attractive than others (Downes 1969; Sullivan 1981; Gibson 1985; Cooter 1989; Svensson and Petersson 1992). Genetic variability, individual size, energy reserves, competitive exclusion, per capita predation risk and mating success could all determine, to varying extents, whether an individual will join a particular swarm. In future studies we hope to establish the relative weight of each of these factors in determining swarm site selection by anopheline males.

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