

HOW MOSQUITOES SEE TRAPS: ROLE OF VISUAL RESPONSES

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ABSTRACT. The visual responses of female mosquitoes during appetitive and attraction flights to conspicuous features of their environment were reviewed. These studies showed for both flights long-range orientation (positive) could be followed by a short-range response (negative) to avoid the goal. In conjunction with the optomotor anemotactic response, appetitive flights are controlled by visual orientation toward more or less distant targets, which permits females to make a wider search than upwind flight alone could accomplish. Most attraction flights are controlled primarily by visual and olfactory cues. The influence of visual targets upon mosquito flight behavior and the effect of this behavior upon trap catches is discussed.

INTRODUCTION

The orientation of biting insects to their hosts has recently been reviewed by Sutcliffe (1987) and their visual ecology reviewed by Allan et al. (1987). The object of this paper is not to provide another review but to propose that vision plays a larger role in guiding mosquito flight paths before and during goal-oriented flights than has been appreciated.

The mosquito eye performs a variety of functions (Bowen 1991). In addition to monitoring the level of light intensity, it can discern movement, colors, shapes, and patterns, with edges being particularly noticeable (Brown 1951, Sippel and Brown 1953, Smart and Brown 1956, Wood and Wright 1968, Browne and Bennett 1981). The minimal optical angle for visual perception has been variously determined to be between 4° and 8° (Kennedy 1940, Rao 1947, Bidlingmayer and Hem 1980). Thus, by human standards, mosquitoes can perceive only coarse features of their environment. Although the compound eye has less resolving power than found in man, the wide aperture provides it with better vision on dark nights than most vertebrates possess (Muirhead-Thomson 1940, Hocking 1964).

The wind is a major environmental factor and the visual responses of mosquitoes must accommodate the effects of wind. Mosquito flight speeds are quite low, approximately 1 m/sec (Hocking 1953; Nayar and Sauerman 1973; Snow 1976, 1980; Gillies and Wilkes 1981; LaSalle and Dakin 1982) and therefore most controlled flight occurs when wind velocities are low. In 1940, Kennedy demonstrated in the laboratory that flight orientation in mosquitoes was based upon an optomotor response to floor patterns. Forward flight required a contrasting pattern to pass beneath the mosquito from front to rear within

acceptable rates. Floor patterns that approached from the side or rear always elicited an immediate turn to balance the pattern in both eyes and face the approaching pattern. The mosquitoes only perceived an approaching pattern through a forward arc of 180°. Kennedy concluded that, provided wind velocities did not exceed flight speeds, the need for flying mosquitoes to balance approaching ground patterns in both eyes would result in upwind flight.

An upwind flight would not be direct. Because mosquitoes may respond to illumination levels as low as ¼ that of starlight (Muirhead-Thomson 1940), ground pattern boundaries may be perceived when differences between patterns are slight. In most habitats, ground pattern boundaries would be quite irregular. Encountering the pattern's edge at an angle, a turning motion to balance the pattern in both eyes would result in flight, both to the right and left, at an angle into the wind.

Wind consists of eddies of all sizes within which both direction and velocity differs from that of the air mass as a whole (Murlis 1986). Because of the turbulence, an insect flying upwind by employing the optomotor anemotactic response to ground patterns would fly both to the right and left of the true wind direction. The flight path would zigzag upwind.

In some circumstances, such as dark habitats or because of heavy cloud cover, nocturnal illumination levels could be too low for the perception of ground patterns. Gillett (1979), noted that wind velocities close to the ground decrease with increasing rapidity with decreasing height. If a flying mosquito abruptly changed its flight elevation it would be subjected, depending upon the wind direction, to a sense of acceleration, deceleration, or lateral displacement. He proposed that by an appropriate response to the wind shear upwind flight could occur even in the ab-

sense of visual cues. Wind turbulence, however, would produce a zigzag flight. Even if confirmed, wind-shear guidance is outside the subject of this paper.

Below the odor source the plume becomes entrained within the eddies as each eddy passes by (Murlis 1986). Consequently, an odor plume consists of odor pulses, varying in concentration and frequency, separated by clean air. A technique for upwind orientation that utilizes only olfactory responses has been described (Kennedy 1986). In many Lepidoptera the optomotor anemotactic response is supplemented by self-steering. Following the initial upwind orientation, an internally driven nervous generator produces alternating left and right turns, the turning rate being controlled by the reception rate of the odor pulses. The turning rate increases as the pulse rate increases, thereby narrowing the upwind flight path as the odor plume narrows. If the plume is lost, the turning rate decreases and the zigzags become wider, until the plume is again encountered. Self-steering in mosquitoes needs investigation.

During its life the female mosquito must satisfy its successive physiological requirements. These are energy and protein sources and suitable resting and oviposition sites. As do all traps, mosquito traps capture their victims either by taking them while unsuspecting or by luring them with a suitable attractant. Ideally, the first method is completely nonattractive; the collection is made before the mosquitoes can avoid capture and it provides a sample of the gonotrophic structure of the population. A common feature of these techniques, examples being the truck trap and the collection of resting mosquitoes, is that they are mobile methods that invade the mosquito's habitat. Collections made by such methods are not applicable to a discussion of how mosquitoes see and respond to traps.

Most adult mosquito sampling methods employ, sometimes unknowingly, one or more attractants that increase the numbers of one segment of the population near the trap. Taken at fixed locations, the numbers will be affected by adjacent features of the trap site. Such features commonly include shrubs, hedge rows, meadows, buildings, trees, and skylines. Less frequent features would be holes, flowers, hosts, or other objects that may be visible.

The searching flights of mosquitoes have been classified by Sutcliffe (1987) as first, an appetitive flight that is internally driven by an unmet physiological need (e.g., hunger), 2nd, the reception of external olfactory or visual stimuli from the environment (*viz.*, a host), and last a goal-oriented attraction flight to the objective. Although there are etymological objections to these terms,

their use here does not imply that insects can anticipate their goals.

The flight behavior of mosquitoes is variable with the greatest differences probably occurring between diurnal species and those species most active during crepuscular and nocturnal periods. This paper examines the visual responses of crepuscular/nocturnal species only.

LONG-RANGE VISUAL RESPONSES

Appetitive flights

Appetitive flights have been little studied because the use of attractants is precluded. A foraging insect responds to 3 environmental levels: the habitat, the patch, and the resource item (Prokopy 1986). Objects, such as clearings, individual shrubs, or trees, form the patch to be examined for the resource item. For species whose daytime resting habitat differs from their nocturnal habitat, the first orientation of these females may be toward the mass or skyline of the alternate habitat (Klassen 1968, Gillies and Wilkes 1974). Thereafter the primary means of controlled appetitive flight available would appear to be dependence upon ground patterns. However, if during the flight a host-seeking female simply flew upwind, patches would be encountered only by chance. Odor plumes would also be intercepted much less frequently than if crosswind or flights angled into the wind were possible. Kennedy (1940), had reported crosswind flights and Haskell (1966) noted that after losing an odor trail females made traversing flights across the wind. Mosquitoes overshooting an objective can return (Kalmus and Hocking 1960). An insect's upwind flight path, whether determined by irregular ground patterns, wind turbulence, wind shear, or self-steering, will necessarily zigzag with a limited amplitude. If mosquitoes are to conduct wider searches for odor plumes some other mechanism is needed.

Attraction flights

Upon reception of an appropriate olfactory or visual stimulus, the female embarks upon a goal-oriented flight toward the source of the stimulus. If the stimulus is a host odor plume, the optomotor response orients the host-seeking female in a generally upwind direction. Little is known of female flight behavior if the scent is lost (Sutcliffe 1987). A response to movement (Sippel and Brown 1953, Haddow 1954, Kalmus and Hocking 1960) and the attractiveness of dark shapes

and colors to mosquitoes (Brett 1938, Sippel and Brown 1953, Smart and Brown 1956, Browne and Bennett 1981) necessarily overrides the role of ground patterns in determining flight paths. An example of the change from olfactory to visual responses occurred in an unpublished experiment by the late Richard P. Dow during a study on the epidemiology of western equine encephalitis. He placed 3 transparent lard can traps (Bellamy and Reeves 1952) on a lawn side by side, spaced about 1 m apart and parallel with the wind direction. A flexible tube, hidden in the grass, released CO₂ from a distant cylinder into the center trap. The traps on either side were unbaited but one was partly concealed by a few leafy twigs and the other marked by a crisscross pattern of black tape. The largest numbers of mosquitoes (*Culex tarsalis*?) were captured in the 2 outside traps. Many mosquitoes had followed the CO₂ plume upwind, not to the transparent source but to the 2 visually conspicuous adjacent traps. Kalmus and Hocking (1960) reported the inability of some Canadian *Aedes* to find a human host after he lay down.

Visual cues are more important than olfactory cues in some attraction flights. Early malariologists noted the daily use of tree holes, cavities, and other dark shelters by anophelines. That vision was the means whereby the shelters were located was widely accepted. During their studies of *Culiseta melanura* (Coq.) Edman et al. (1968) constructed resting boxes painted black inside. Boxes placed on the ground in clearings attracted more mosquitoes than boxes in vegetated areas. A few fern fronds across the box entrance reduced collections whereas placing a black frame about the box entrance—to increase its apparent size—increased collections. Shelter-seeking mosquitoes were most attracted to the most visually conspicuous boxes.

Visual responses to other stimuli, such as nectar sources and oviposition sites, have also been reported (Magnarelli 1979, Bentley and Day 1989), with the role of odor reduced to short range and probably used more to evaluate the suitability rather than the location of a stimulus. In these searches odor detection apparently follows, not precedes, visual orientation. Mosquitoes that forage in open areas at night but return to woodland resting sites at dawn may use the tree horizon as a guide (Bidlingmayer and Hem 1981). The visual behavior of mosquitoes clearly includes responses to vertical targets as well as to ground patterns.

Although effective for alerting mosquitoes and stimulating flight, odor plumes are less precise for locating goals than vision (Prokopy 1986). Their boundaries are irregular and they provide little information to the mosquito about distance

to and the exact location of the source. Controlled by the ground pattern, as the plume narrows upwind the risk to the female of flying out of the plume increases as the distance to the source decreases. At some time during the flight most females will lose the plume. Having followed a zigzag flight path while in the plume, many females would exit at an angle into the wind. Scanning 180° forward, even visual targets a little downwind of their present position could be visible. Lacking further clues as to the distance to or location of the source, it may be supposed that these females would now respond to nearby visual targets. Only for females near the head of the plume could the visual target prove to be the source. Attractancy to visual targets would be of greater advantage to host-seeking mosquitoes than to many insects (e.g., male Lepidoptera following a sex pheromone), as the goal of a host-seeking mosquito is many times larger than itself.

The visual attractiveness of dark colors and shapes to host-seeking females has been regarded as an extension of the odor-stimulated attraction flight. Unless the behavior pattern released by an olfactory stimulus persists after the stimulus has been removed, the flight to visual targets should be described as a return to that prior to entering the plume, that is, an appetitive flight. The significance of this interpretation of the process of host location lies in the conclusion that during most appetitive flights visual attractancy to conspicuous objects would be a major factor in determining mosquito flight paths. Because odor drifts downwind in pulses, whenever odor levels in the air between pulses are too low for detection, even females directly downwind of an odor source could be alternating between appetitive and attraction flights. Habitats either so densely vegetated that individual targets are too small to be visually resolved or featureless habitats, such as grasslands, would be exceptions for the role of visual orientation.

If appetitive flight paths are flown by females that, while basically oriented upwind, also flew—within an arc of 180°—from one conspicuous visual target to the next, a means would be provided for not only making a wide search for odor plumes but even for making direct host contacts. Several studies can support this hypothesis.

Appetitive flight studies

Suction traps have been extensively used to sample aerial populations of insects such as aphids, thrips, and moths as well as mosquitoes. In most instances, these traps are the least biased technique available (Service 1977). Suction traps

mounted on a tower for the purpose of sampling mosquito populations at various elevations were biased by a "tower effect" (Snow 1980, 1982). Because of the high wind velocities at the higher elevations, he found downwind flying mosquitoes were visually attracted to the tower. Once in the wind shadow of the tower and its traps, they then flew upwind into the traps. Thus, the field station became a factor in the mosquitoes' environment and affected the mosquitoes' flight paths by acting as both a visual target and a windbreak.

The suction traps I used were large unpainted plywood boxes measuring 2.4 m long and 1.5 m high at the trap intake (Bidlingmayer 1974). Initially they were thought to be nonattractive and thus unbiased. Later it was observed that the proportions of bloodfed and gravid females in the catches were approximately intermediate between the large proportions of these stages taken by the truck trap and the much smaller proportions found in bait and light trap collections. The suction trap contained larger proportions of host-seeking females than the truck trap, indicating that the trap was an attractant for these females. The corollary would be females with other physiological needs were less strongly attracted to the trap. An exception was the behavior of *Anopheles crucians* Wiedemann. Presumably because they were attempting to use the suction trap as a shelter, the catches contained equal or even larger proportions of bloodfed and gravid females of this species than did truck trap catches (Bidlingmayer 1974).

The following studies were conducted in the open, either in a large field or on a dike crossing a salt marsh (Bidlingmayer and Hem 1979, 1980). Each experiment and the results are presented.

1a: Two suction traps were spaced 30 m apart in a field and another pair spaced 40 m apart on the dike. One set of plywood panels, painted black, was made for one trap of each pair. The panels, which enclosed the traps, were alternated nightly between traps.

Results: Traps covered with black panels made larger catches than uncovered traps for 12 of the 13 species captured.

1b: Two suction traps were constructed of transparent acrylic plastic and spaced 30 m apart in the field. Although transparent, acrylic plastic is not invisible as it can be reflective. One set of unpainted plywood panels was made to cover one trap and was alternated nightly between traps.

Results: The trap covered with the unpainted panels made larger catches than the transparent trap for 8 of the 9 species captured.

Conclusion: The rank order of visual attractiveness was black plywood > unpainted plywood > acrylic plastic.

2: Four suction traps were placed in a row in the field and spaced 15 m apart. Later they were spaced 30 m apart.

Results: When spaced 15 m apart, traps at the ends of the row captured about twice as many mosquitoes as traps in the center, that is, catch ratios were approximately 2:1:1:2. When spaced 30 m apart, all traps captured approximately equal numbers of mosquitoes.

Conclusion: When spaced 15 m apart, mosquitoes would fly from trap to trap but accumulated near the end traps for lack of another visual target. At 30 m apart mosquitoes could not see a neighboring trap and thus each trap, being visually isolated, functioned as a single trap.

3a: Sixteen suction traps were placed in the field spaced 15 m apart in a 4 × 4 grid, that is, there were 4 traps at the corners of the grid, 8 traps along the sides between the corners, and 4 traps inside the grid. Consequently each corner, edge, and inside trap had, within a distance of 15 m, 2, 3, and 4 neighboring traps, respectively. Catches are expressed as ratios with the numbers captured in an inside trap = 1.0.

Results: Catch ratios for corner, edge, and inside traps ranged from 1:1:1 for *Culex quinquefasciatus* Say and *Uranotaenia sapphirina* (Osten Sacken) to 2.7:1.8:1.0 for *Aedes vexans* (Meigen), respectively. For all species combined the mean ratio was 2.1:1.5:1.0. Catches were inversely related to the number of neighboring traps. From these ratios the distance a visual response to a trap of this size occurred was estimated to be between 15.5 and 19.0 m.

3b: The suction traps were arranged as in *3a* but with 4 additional traps placed 15 m beyond the corner traps and in line with the center of the grid. The new traps had but one neighboring trap.

Results: The mean catch ratio for all species combined for the beyond corner, corner, edge, and inside traps was now 3.3:1.8:1.3:1.0.

Conclusion: Mosquitoes fly from one visual target to the next. Departure from the vicinity of a trap inside the grid is facilitated by the presence of visual targets in all directions. As the number of adjacent visual targets declined, mosquito densities about the trap increased due to: 1) an inhibitory effect of flight in a direction that lacks visual targets, and/or 2) any chance turn during an outward flight that brought a visual target behind a mosquito into view could result in flight back to the departure area. Some mosquito species have been found to spend more time in the vicinity of an isolated trap than others (Bidlingmayer et al. 1985).

Although the suction traps used here were visually attractive to mosquitoes, this is not a serious objection to their use for studying appeti-

tive flight behavior. As large boxes, they formed a visual image not too dissimilar from other common features of the mosquito environment. A grid of 16 shrubs of comparable size to the traps would be expected to produce a similar distribution of mosquito densities. The most severe mosquito problems noted in coastal Georgia were suffered by residents of small peninsulas that projected into the wide and grassy salt marshes. Lacking visual targets in 3 directions, mosquito numbers were several times greater than for residents along the marsh embayments (Bidlingmayer, unpublished data). The use of ground patterns is often subordinated to targeting when targets are present.

SHORT-RANGE VISUAL RESPONSES

Appetitive flight

Another aspect of mosquito behavior during a flight toward a visual target is how closely do mosquitoes approach? The question is important because suction traps effect their captures only when insects are close to the air intake. A comparison of air intake velocities and mosquito flight speeds indicated capture would be quite certain within 20 cm of the intake with diminishing effectiveness to 40 cm (Bidlingmayer and Hem 1979). During an approach the visual target will occupy an increasing proportion of the insect's field of view. At some distance the target will be perceived as an obstacle, lose its attractivity, and be avoided. The flight of mosquitoes in the presence of barriers, varying from impenetrable to open mesh has been reported (Kellog and Wright 1962, Service 1974, Bidlingmayer 1975, Gillies and Wilkes 1978). Mosquito sensitivity to visual barriers is evidenced by their reluctance to penetrate them even when the apertures are much greater than the mosquito's dimensions. Short-range visual responses were again revealed when 2 suction traps were buried 40 m apart in a dike with the air intake at ground level (Bidlingmayer and Hem 1979).

4a: Both traps were equipped with transparent acrylic risers that elevated the air intakes to 1.2 m above ground. On alternate nights one riser was wrapped in black cloth.

4b: Both traps were equipped with a 1.2-m-high transparent acrylic baffle and on alternate nights one baffle was wrapped in black cloth. The baffles provided the same silhouette as the risers but the air intake was at ground level.

Results: A comparison of catch ratios between the traps with black and transparent risers and between black and transparent baffles showed

specific differences. (Florida mosquitoes were later classified into 3 groups depending upon their habits [Bidlingmayer and Hem 1981]. Woodland species [*Culex nigripalpus* Theobald, *Cs. melanura*], both rest and forage primarily in woodland. Woodland commuter species [*Ae. vexans*, *An. crucians*] rest in woodland during the day but at night many forage in adjacent pastures. Field species, [e.g., *Psorophora columbiae* (Dyar and Knab)], both rest and forage in grasslands.) The woodland *Cx. nigripalpus* was taken in larger numbers in traps with black risers and baffles than transparent ones. *Culex nigripalpus* evidently approached dark targets closely and was easily captured. *Aedes taeniorhynchus* (Wied.), a commuter species, was taken in approximately equal numbers whether the trap risers and baffles were black or transparent, whereas *Anopheles atropos* Dyar and Knab was taken in smaller numbers by the traps with black risers and baffles than when these were transparent. Although *An. atropos* had been more attracted to black plywood than to weathered plywood (compare with experiment 1a), despite the presumably larger numbers attracted to the black risers and baffles, this species apparently maintained so great a distance from the targets that few of the attracted females were captured.

Conclusion: If equal numbers of woodland and field species of mosquitoes are attracted to visible suction traps, smaller numbers of the field species will be captured because their closest approach to a trap is more distant than for woodland species.

Attraction flights

Gillies and Wilkes (1982) studied the visual responses of host-seeking mosquitoes about the entrance into a transparent animal-baited trap. The top and sides around the entrance were: 1) alternately darkened or left clear, and 2) alternately darkened or left clear in combination with black or clear baffles that reduced the size of the trap entrance. They found: 1) larger catches were made when the entrance area was darkened, and 2) when the darkened entrance area was furnished on alternate nights with black or clear baffles, no differences were found between catches. However, when the entrance area was clear, the trap captured fewer mosquitoes with a black baffle than with a clear baffle. They interpreted these results to indicate that, although the black baffle was attractive to mosquitoes at a distance, at very close range contact was more easily avoided than if the baffle was transparent. Similar results were obtained by Schreck et al. (1972) who reported that a transparent CO₂-baited oc-

tagonal trap was superior to similar visible traps. They concluded that most mosquitoes had turned away shortly before reaching the visible traps. Odor plumes excite females but not to the extent of inducing lemming-like behavior near trap entrances.

These results seem to conflict with those of Dow (unpublished data), whose visible lard can traps captured larger numbers of mosquitoes than the transparent trap. As Dow's females lost the narrowing plume, they could target either of the 2 adjacent visible traps. Arriving on the downwind side and resuming upwind flight, they were confronted by a single large cone leading into the trap's interior. Large catches would result if a close approach to visual barriers was characteristic of that species. In the experiment by Schreck et al. (1972), the nearest competing visual targets were a ring of outward facing ramp traps. These were about 5 m distant from the centrally located CO₂ source, which was either a transparent or visible octagonal trap with 12 small entry funnels. Mosquitoes that had lost the narrowing plume within a few meters of the source could easily target a ramp trap but were not captured because all trap entrances faced outward. For females still within the plume, smaller catches in the visible trap would result if their closest approach to targets was too great for them to enter small funnels. Although confirmation of this explanation for the differing results obtained from the 2 experiments will depend upon further behavioral studies of the species involved, it is compatible with known differences among woodland, commuter, and field mosquito behavior.

CONCLUSIONS

Long-range responses are defined as positive responses that shorten the distance between the mosquito and its goal. Short-range responses are negative responses that, following the reception of nonconfirming cues which may be visual, olfactory, or other, result in avoidance or rejection of the goal. Short-range responses are distinct from appetitive and attraction flights.

Stimulated by an internal physiological need, it is proposed that, in conjunction with the optomotor anemotactic response, the female's long-range appetitive flights are directed toward selected visual targets. This flight continues until terminated by either the start of a long-range attractant flight or by a short-range response to avoid the target. A long-range attraction flight is initiated and guided by various goal-associated external cues, which may be visual, olfactory, or other, that indicate the existence and direction

of the goal. The attraction flight is terminated either by making contact with the goal or by a short-range response rejecting the goal and a return to appetitive flight.

Orientation to successive visual targets during appetitive flight enables host-seeking females to make a broader search for a scarce resource than would be possible using upwind flight only. Visual orientation to targets is probably employed less stringently during the appetitive flights of females with physiological needs other than blood.

Except for the attractivity of movement, visual orientation to targets by host-seeking females during attraction flights must include olfactory or other cues, as visual orientation alone to targets is appetitive flight. During attraction flights the utilization of visual targets by females with physiological needs other than blood would probably be greatest among those species that rest in dark shelters or oviposit in containers and least for those that rest and oviposit in grasslands.

The visual responses of mosquitoes to suction traps should be similar to their visual responses to the common features of their habitat. Because long- and short-range visual responses differ among species, collections from traps that employ olfactory attractants can be strongly affected by trap design. Further studies of flight behavior would improve trap design and the evaluation of catches.

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