Wind-Guided Landing and Search Behavior in Fleshflies and Blowflies Exploiting a Resource Patch (Diptera: Sarcophagidae, Calliphoridae)

MARLA SPIVAK,[1] DONNA CONLON, AND WILLIAM J. BELL

Department of Entomology, University of Kansas, Lawrence, Kansas 66045

ABSTRACT   The methods used by sarcophagid and calliphorid flies to locate and utilize an ephemeral resource were studied in the field. Their arrival sequences and orientation to an odorous food source on a vertical arena were examined. The first flies arrived at a feeding site soon after a resource became available, and subsequent flies followed rapidly. Sarcophagids tended to arrive before calliphorids. Smaller muscids and chloropids were the last to leave the patch, which indicates a size-based sequence of resource use among flies. The time required by flies to walk to the resource after they had landed nearby decreased significantly as the number of flies increased. This suggests that visual orientation to a group of other flies, in addition to olfactory orientation, improved resource localization. Trials were made with and without wind blowing across the resource. In the wind, flies approached using anemotaxis, landed downwind of the food source, and then walked upwind toward the resource. While walking, anemotactic orientation was more direct and more rapid than was nonanemotactic orientation.

KEY WORDS   Insecta, Sarcophagidae, Calliphoridae, orientation

CALLIPHORID AND SARCOPHAGID flies arrive at feeding and oviposition sites soon after a resource such as fresh carrion becomes available (e.g., Johnson 1975). The arrival ecology and changes in the resource-utilizing population of some species of flies at carrion and dung have been reported in some detail (e.g., calliphorids, Norris 1965; calliphorids and sarcophagids, Denno & Cothran 1975; scatophagids, Parker 1978). Stoffolano et al. (1990) showed that reproductive status differed among female *Phormia regina* attracted to food resources and oviposition sites.

As in other cases where animals must use a localized resource quickly, orientation to wind currents would seem to play a major role in improving efficiency (review in Bell 1990). Our field experiments examine the behavior of sarcophagid and calliphorid flies, to elucidate the effects of wind on the exploitation of a resource patch, the sequence of arrival of different families of flies, and the influence of other individuals on orientation to the patch. The objective is to understand behavioral adaptations for exploiting an ephemeral resource under competitive conditions.

Materials and Methods

Data were recorded on videotape in a residential area of Lawrence, Kansas, during June 1987. A 25 by 25 cm grid (1-cm² squares) was placed in the center of a plastic-covered vertical arena (1 by 1 m) to which a wind direction indicator was attached. The arena was positioned in a 10-m² open field within a city plot. The field was surrounded by elm and maple trees, and was partially shaded in the early morning and late afternoon, and so data were collected between 1000 and 1500 hours CDT when the arena was consistently in direct sunlight. All trials were carried out with the arena in the same place within the field. Ambient temperature was ≈30°C.

Decaying squid 7–12 d-old, corresponding with the "putrification stage" of carrion decomposition (Bornemissza 1957), was used as an olfactory cue in the experiments. In each trial, a 0.05-ml drop of liquid from decaying squid was applied to the center of the arena (covering a 1-cm² area).

In the first series of trials (conducted over two days, 10 trials per day), the arena was oriented parallel to the wind current ('wind' condition), so that the wind moved across the arena from zones 6–7 toward zones 2–3. In the second series (also conducted over two days, 10 trials per day), the arena was rotated 90°, so that the wind flowed perpendicular to the arena (from behind it), and essentially eliminated wind currents from the grid ('no-wind' condition).

The time of arrival, anemotactic orientation, and local search patterns of the flies toward the food source were recorded on videotape by a camera placed 2 m from the arena. Each of 20 trials typically lasted for at least 5 min. Between trials, the (plastic) grid was washed with water. At least 5

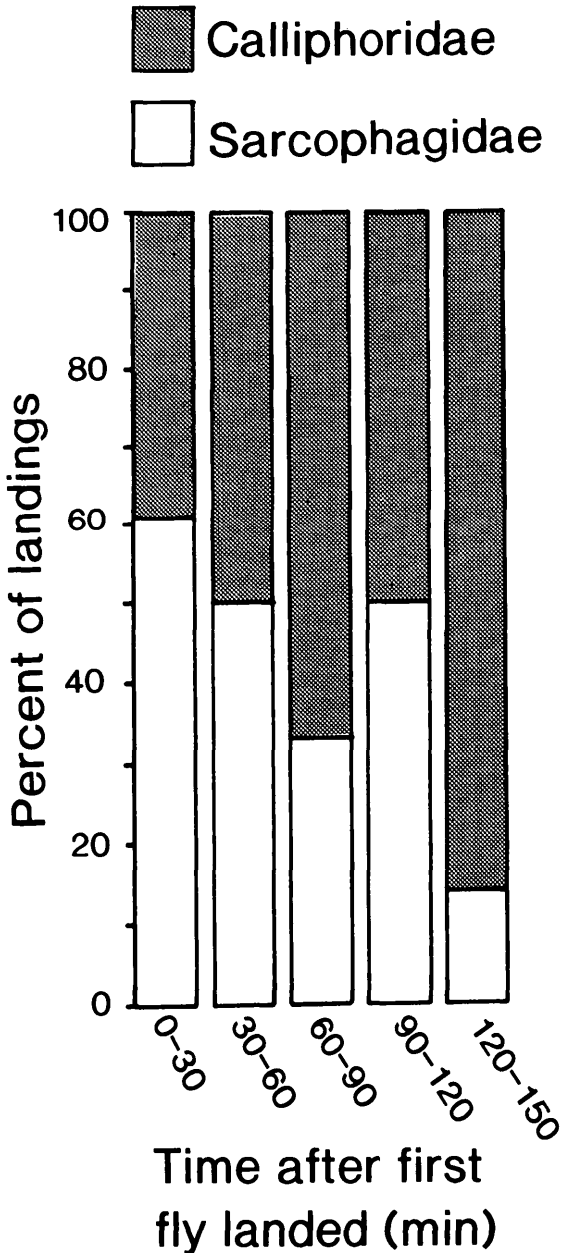[1] Address: Center for Insect Science, University of Arizona, Tucson, Ariz. 85721.

Fig. 1. Percentage of calliphorid and sarcophagid flies landing (*n* = 146) on the resource grid in relation to the time after the first fly landed.

Boettcheria were most common. These four genera comprised >90% of the flies attracted to the arena. In addition, a few muscid species, especially *Trichops*, and several chloropid species were present.

Walking pathways of flies were digitized with a sonic digitizer interfaced with a microcomputer. A cursor pen was used to follow a videotaped fly image and input the path in real time into the computer at 11 data points per second. Fly paths were digitized from the point of landing on the arena to the resource. Twenty paths were analyzed: 10 where the fly oriented upwind toward the resource and 10 where there was no wind blowing across the arena (flies did not walk downwind toward the resource often enough to provide a sufficient sample size for analysis). Pathways of early arrivals were digitized to minimize the level of social interaction.

Computer programs were used to obtain the following five path parameters: (1) linearity index, a measure of path straightness, obtained by dividing the pathlength into the beeline distance between the first and last *x,y*-coordinate; (2) locomotory rate in millimeters per second; (3) turning rate in degrees per second; (4) turn bias, the sum of signed turn magnitudes, indicating a tendency to turn more in one direction (left or right) than another; and (5) percent time spent moving.

Mann-Whitney *U* tests were performed on the above measures to test for differences between anemotactic and nonanemotactic orientation toward the squid resource. The Rayleigh test (Batschelet 1981) was used to test for randomness of orientation among the 10 anemotactic pathways as well as among the 10 nonanemotactic paths. A *V* test (Batschelet 1981) was performed on the anemotactic orientation vectors to test for a significant difference of the mean compass heading from the upwind direction.

Results

Dynamics of Immigration and Emigration. The following observations refer to data collected in 20 trials with wind movement parallel to the vertical arena. A median period of 64 s (range, 13–210 s) was required for the squid odor to disperse sufficiently to begin attracting flies. The first fly to arrive was a sarcophagid in 70% of trials. The ratio switched over the next 120 s; after 120–150 s 86% of arrivals were calliphorids (Fig. 1). The last flies to leave were always the smallest calliphorids, sarcophagids, and chloropids, which fed on the last remaining food droplets.

After the first fly arrived, others quickly followed (Fig. 2). In 89% of the cases the second fly landed relatively soon after the first (median 17 s, range, 1–33 s), as compared to the longer time (noted above) between establishment of the food patch and the landing of the first fly. Once flies began to arrive, they arrived in pulses. In the two examples shown in Fig. 3, as long as 60 s elapsed between
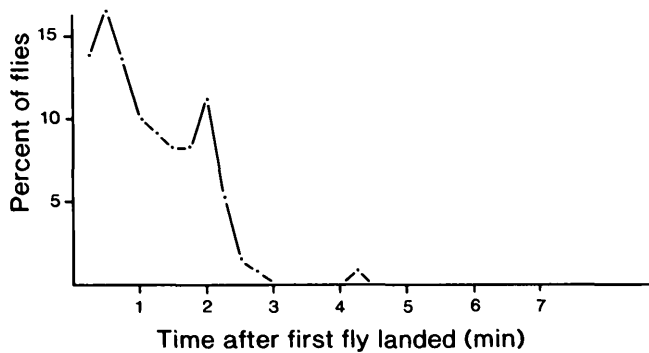
min were allowed to elapse between trials. No flies landed on the arena between trials, verifying that all confounding odors had been eliminated.

As flies landed, they were identified by sight to family, and to genus within the Calliphoridae. No flies were removed during the trials, but at the end of the trials each day, a sample of flies was captured for laboratory identification. Among the Calliphoridae attracted to the food patch, the genera most commonly represented were *Calliphora* and *Phaenicia*. Among Sarcophagidae, *Sarcophaga* and

Fig. 2.   Percentage of all flies landing (n = 146) as a function of time since the first fly landed.

periods of intense arrival activity. The number of flies arriving peaked at ≈1.5 min (Fig. 4). The abrupt decrease in arrivals after 3 min correlates closely with the mean time when the food was depleted (indicated by the horizontal bar in Fig. 4). These observations may suggest a size-based transition sequence, in which immigration may be related to olfactory abilities and flight speed, and emigration is probably related to the profitability of a decreasing resource.

Figure 5 shows changes in the spatial distributions of flies on the grid. Initially, most flies (groups of 5–6 individuals) were feeding on the food patch. As the food became exhausted, represented by the horizontal bar in Fig. 5, flies left the patch and either searched elsewhere on the grid (2–5 and >5 cm in the figure) or flew away. Although searching (which included periodic revisits to the patch) continued for several minutes, most flies responded to food depletion immediately by leaving the arena. Although no flies remained on the patch after the resource was depleted, it is not known if the flies left the area. Cragg & Hobart (1955) estimated that, over a 4-wk period, 64% of marked *Lucilia*

caesar remained within 0.5 miles of the liberation site.

The Role of Wind Currents. In tests with a wind current moving across the plane of the arena from zones 6–7 toward zones 2–3, flies tended to land downwind of the food patch (zones 2 and 3) (Table 1; Fig. 6B). In the 'no-wind' condition, there was no significant bias in landing positions (Fig. 6A). Observations of the flight paths of approaching flies indicated that they tend to fly across lower zones (3, 4, 5, and 6) of the grid rather than upper zones (1, 2, 7, and 8) before landing (P < 0.005, Chi square). This effect was independent of wind direction.

Most sarcophagids landed 2–8 cm from the food patch (median 7 cm; range, 2–22 cm), whereas the smaller calliphorids tended to land 5–8 cm from the food patch (median, 8.5 cm; range, 3–18 cm). In only a few approaches (18 of 157) did any flies land directly on the food patch.

Table 2 shows that the landing distance relative to the food patch location was not influenced by the number of flies already on the grid (P > 0.05). However, the time to locate the food source after landing decreased significantly as the number of flies on the grid increased (P < 0.05). These data
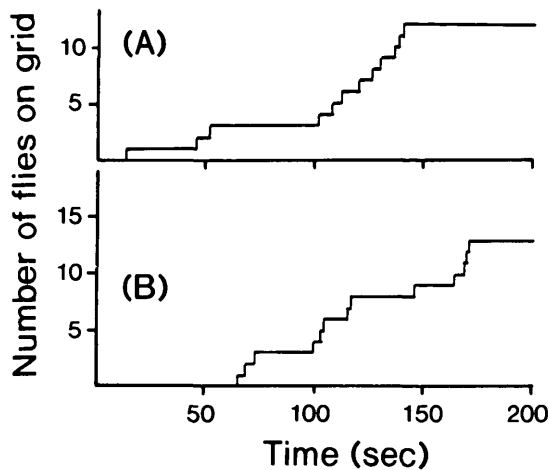

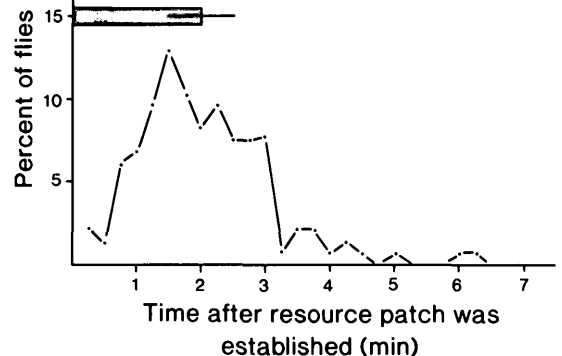Fig. 3.   Two examples of tests showing cumulative numbers of flies on the resource grid.

Fig. 4.   Arrival times of flies attracted to a squid odor food patch. Percentage of flies landing (n = 146) as a function of time since setting out the food patch. Horizontal bar indicates period before food depletion; line represents 1 SD.
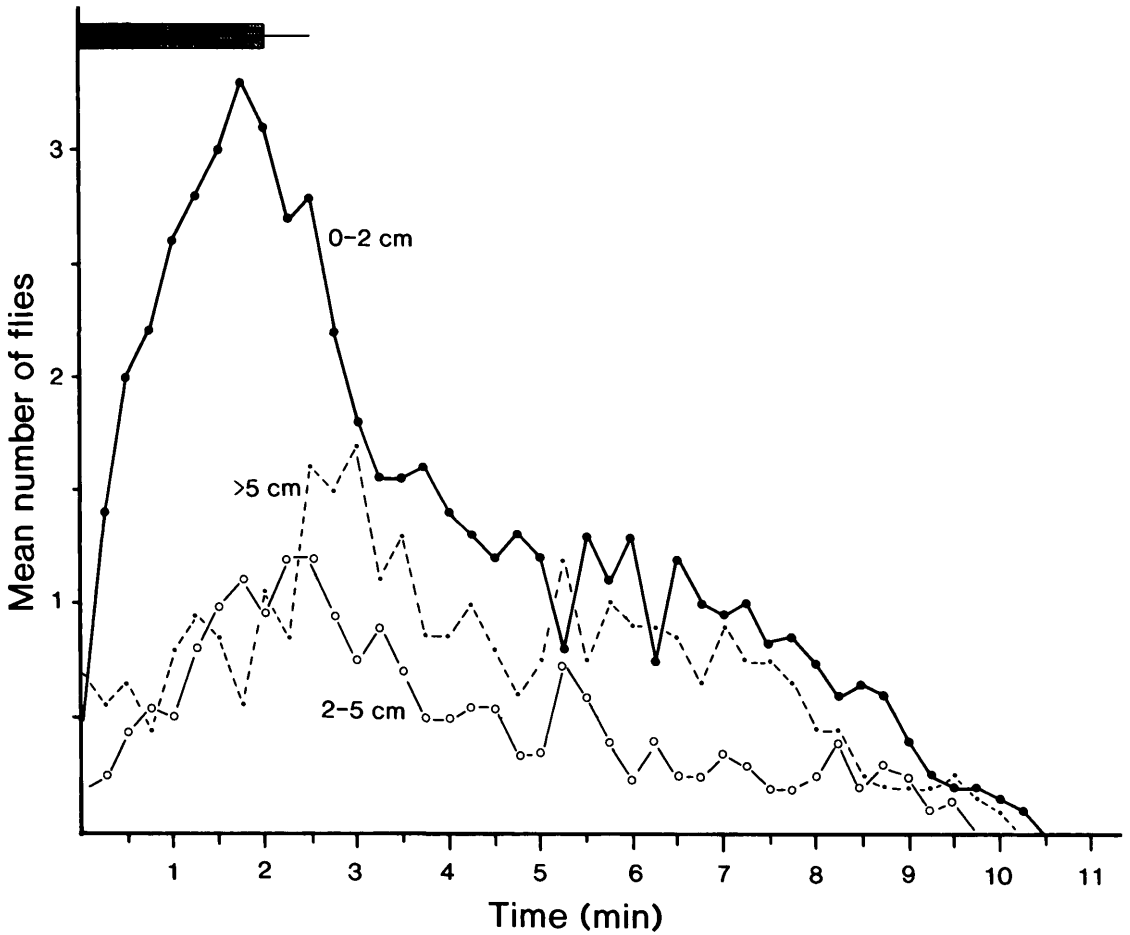
Fig. 5. Mean number of flies ($n = 20$ trials) at various distances (0–2, 2–5, >5 cm) from the food patch during the course of experiments. Horizontal bar indicates period before food depletion; line represents 1 SD.

suggest that flies orient visually or olfactorily (or both) toward a group of feeding individuals, and thus take less time to arrive at a resource if other flies are there first.

Walking Search Patterns. After landing, flies walked rather directly to the resource patch in both the wind and no-wind conditions, but in wind they moved straighter (refer to linearity index and turning rate in Table 3) and faster (locomotory rate in Table 3) than in the no-wind condition. Compass headings of flies in the no-wind condition are ran-

Table 1. Percentage of sarcophagid and calliphorid flies landing on grid from up- or down-wind of the food odor source in a directional wind or in a wind perpendicular to the grid

Condition	n	Arriving from left (zones 2 + 3)	Arriving from right (zones 6 + 7)
Wind from right	250	78.4	6.1
No-wind	81	34.4	30.4

A G test showed a significant dependence of arrival direction on wind condition ($P < 0.001$).
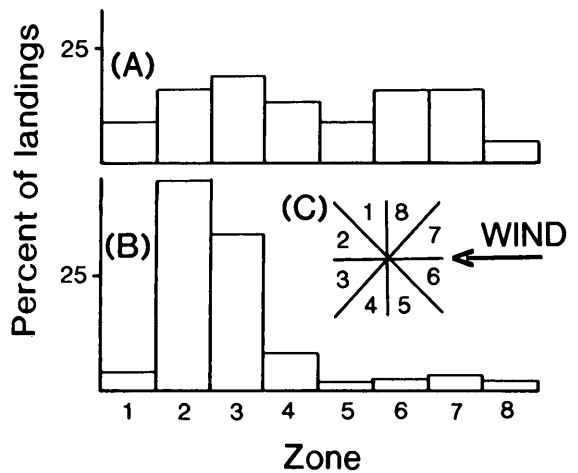

Fig. 6. Landing positions of flies approaching the resource grid. Percentage of landings in direction zones when wind was absent (A) or present (B). Diagram (C) shows the positions of direction zones, and the food patch represented by a dot in the center.

Number of flies on patch	n	Distance, cm	Time, sec
0	16	8.5 ± 5.7a	6.6 ± 4.4a
1–2	24	8.7 ± 5.0a	6.2 ± 3.6a
3–4	20	9.0 ± 5.7a	5.2 ± 4.3ab
>5	25	8.1 ± 3.4a	3.3 ± 2.0b

Means compared using Student's t test, values in columns followed by different letters are significantly different at the $P < 0.05$ level.

domly distributed ($P > 0.05$, Rayleigh test, $z = 2.368$, $r = 0.487$), whereas headings in wind are significantly concentrated ($P < 0.05$, Rayleigh test, $z = 9.552$, $r = 0.977$), and they are not significantly different from the expected upwind direction (expected 0°, observed -12.3°; $P < 0.05$, V test). When wind was blowing across the arena, flies tended to approach the patch from downwind and walk straight into the wind toward the resource, whereas they walked to the patch from any direction if wind was not involved. A general paucity of flies walking in a downwind direction indicates a lack of tendency to do so.

Discussion

The sequence of arrival of flies at the food resource, beginning with sarcophagids and followed by calliphorids, was similar to that described for arrival sequences at carrion. Denno & Cothran (1975) termed the early arrival of sarcophagids at rabbit carcasses as "a strong pioneering strategy," with regard to the oviposition of females before those of other species. In the present study we also found that the last flies to leave were always the smallest calliphorids, sarcophagids, and chloropids. Once flies began to arrive, they arrived in pulses, and then arrivals abruptly decreased when the food resource was depleted. These observations frame a dynamic series of events depicting arrival, localization of a food resource, resource assessment, utilization, and departure.

Wind currents provide an important source of orientation information for flies searching for an odorous food source, both in flying and walking

orientation. The efficient walking orientation mechanism documented here, which leads the flies directly upwind to a food source, indicates why they tend to land downwind, even though they still might be some distance from the food patch.

Flies tended to land farther from a food source if they landed downwind than if there was no wind. Also, fewer flies landed directly on the food source with wind than without wind. It would seem to be a good tactic for flies that follow airborne smells to land and head directly upwind to correct for error caused by air movement. This is because wind might shift olfactory information, making it difficult to land directly on the patch, but relatively simple to orient to the patch anemotactically after landing downwind.

Flies that arrive at a resource after others are already present seem to be influenced by the presence of earlier arrivals, as shown previously by Cragg & Ramage (1945) and Eisikowitch (1980). Therefore, the orientation of early arrivals probably relies largely on olfactory stimuli emanating from a resource, whereas orientation of later arrivals may depend on olfaction initially and then on visual information (a clump of feeding flies) to locate a resource more precisely. Experiments by Eisikowitch (1980) seemed to support the use of vision. Employment of another modality may enable flies to locate ephemeral resources more rapidly under competitive conditions.

References Cited

Batschelet, E. 1981. Circular statistics in biology. Academic, N.Y.

Bell, W. J. 1990. Searching behavior patterns of insects. Annu. Rev. Entomol. 35: 447–467.

Bornemissza, G. F. 1957. An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. Aust. J. Zool. 5: 1–12.

Cragg, J. B. & J. Hobart. 1955. A study of a field population of the blowflies Lucilia caeser (L.) and Lucilia sericata (Mg.). Ann. Appl. Biol. 43: 645–663.

Table 3. Median values (and range) of path parameters in the wind and no-wind condition

Parameter	Pathways in wind condition[a]	Pathways in no-wind condition[a]	Level of significance[b]
Linearity index	0.96 (0.77–0.99)	0.75 (0.45–0.97)	$P < 0.005$
Locomotory rate, mm/s	51.6 (32.9–78.5)	23.7 (10.7–82.7)	$P < 0.05$
Turning rate, degrees/s	7.5 (4.8–20.5)	15.8 (11.6–32.4)	$P < 0.001$
Turn bias, degrees/s	1.7 (0.0–7.8)	2.3 (0.1–10.2)	NS
Percent time spent moving	98 (90–100)	95 (90–100)	NS

[a] $n = 10$.
[b] Mann-Whitney U tests.

Cragg, J. B. & G. R. Ramage. 1945. Chemotropic studies on the blowflies *Lucilia sericata* (Mg.) and *Lucilia caeser* (L.). Parasitology 36: 168–175.

Denno, R. F. & W. R. Cothran. 1975. Niche relationships of a guild of necrophagous flies. Ann. Entomol. Soc. Am. 68: 741–754.

Eisikowitch, D. 1980. The role of dark flowers in the pollination of certain umbelliferae. J. Nat. Hist. 14: 737–742.

Johnson, M. D. 1975. Season and microseral variations in the insect population on carrion. Am. Midl. Nat. 93: 79–90.

Norris, K. R. 1965. The bionomics of blow flies. Annu. Rev. Entomol. 10: 47–68.

Parker, G. A. 1978. Searching for mates, pp. 214–244. *In* J. R. Krebs & N. B. Davies [eds.], Behavioral ecology: an evolutionary approach. (First edition) Blackwell, Oxford.

Stoffolano, J. G., Jr., M. M. Bartley & C.-M. Yin. 1990. Male and female *Phormia regina* (Diptera: Calliphoridae) trapped at two different baits in the field. Ann. Entomol. Soc. Am. 83: 603–606.