ON THE FLIGHT BEHAVIOR OF WORKER *VESPULA MACULIFRONS* (BUYSSON), (VESPIDAE, HYMENOPTERA)

W. V. BALDUF
University of Illinois, Urbana, Illinois

ABSTRACT. — Counts of worker *Vespula maculifrons* made as they flew from and to their nest hidden in the attic of a cabin at Eaglenest lakes, Minnesota, was the method employed to observe the effects of normal weather conditions on rates of flight. Flights are (1) faster, hence more numerous on bright windless days when temperatures range from 78 to 90° F; but (2) slow at temperatures of 50 to 60°, and prevented at 40°; (3) retarded but not stopped by light to moderate rains under windless conditions; and (4) gradually brought to a stop as light wanes toward nightfall, when stragglers have some difficulty in finding the entrance to the attic but appear to recognize the area from previous exploratory flights. An attempt is made to identify the factors that cause the often pronounced numerical imbalance observed between nestward and outward flights.

On June 17, 1959, a queen of *Vespula maculifrons* was discovered making flights from and to her nesting site in the attic of a one-story cabin. This building stood in the midst of broad-leaved and evergreen trees that shaded it lightly in midday. Temperatures in the attic were moderated somewhat by small screened openings at the ends.

The area of study lies among the Eaglenest lakes near the town of Ely in northeastern Minnesota at latitude about 49 degrees.

METHOD OF STUDY

Since the nest remained invisible and inaccessible within the attic, my means of obtaining data about the colony, as it developed through the summer of 1959, was to count the workers as they passed in and out through a small hole in the siding on the south wall of the cabin. Each of the "counts" extended through 45 consecutive minutes of time, and was also subdivided into 4-minute intervals, as illustrated in Table 1. Thirty-five such counts were made between July 10 and September 18. Twenty of these were selected for presentation in Table 2.

It should be understood that this method does not yield the precise number of workers that constitute the colony at any one time. However, it does show how the rates of flight are affected by the various kinds of weather conditions that prevailed when the count was taken. In general, each worker probably averaged from two to four flights from nest to field and back within the 45-minute periods.

VARIATION IN FLIGHT NUMBERS

Table 1 illustrates a characteristic that is common to all the 20 sample counts (TABLE 2), namely that scarcely ever do even the short 4-minute intervals show identical numbers of departing and returning flights. Certainly there can be no single cause for this continual variation, but it is presumed to arise from combinations of such considerations

as age and experience of the workers, kinds and weights of loads carried, obstacles encountered en route, distances between nest site and sources of food, wood pulp and water, and kinds of weather encountered during the flights. Indications were observed that workers become tired, hence sometimes "take a break" momentarily.

Seasonal Increase in Flights

On June 27, the colony consisted of the mother queen and the first worker of the year. The first count (No. 1, Table 2), taken on July 29, when conditions were nearly optimum for flight, the arriving and departing flights numbered 98 and 97, respectively. It is estimated that 15 workers were then present. By contrast, the last count made on September 18 (No. 20, Table 2) showed that 364 worker flights were made to, and 392 from the nest. The number of workers then present may be estimated from the 67 that were captured by net at the nest site on and soon after September 20. Thus, the large increase in number of flights between July 29 and September 18 is basically traceable to the normal growth of the colony during this period of 7 weeks.

Incidentally, this increase indicates that the queen lived and performed her reproductive functions through a normal lifetime.

However, the fluctuations in number of flights throughout the 20 counts (Table 2) are due to variations in current weather factors, some of which I attempt to identify and evaluate below.

1. *Near-optimum conditions.* Several of the counts recorded in Table 2 point to the combination of weather conditions that are conducive to maximum number of worker flights. These include count numbers 1 and 2, taken on July 29 and August 5, when the worker population still remained relatively small, and temperatures had neared 90°F. just prior to the counts. Arrivals and departures on July 29 numbered 98 and 97, and a week later, on August 5, 158 and 152, respectively. Much of the increase noticed on the latter date, August 5, as compared with July 29, is credited to the emergence of young workers from their cocoons in the meantime.

Table 1.—Illustrates the form used to record in and out flights of workers through a 45-minute period and also 4-minute intervals. At the same time, the table presents the actual counts taken on September 5, 8.20-9.05 PM. This example is summarized at number 11, in Table 2.

Four-minute intervals	Workers arriving	Workers departing	Four-minute intervals	Workers arriving	Workers departing
8.20—8.24	26	18	8.44—8.48	17	6
8.24—8.28	22	12	8.48—8.52	11	6
8.28—8.32	14	16	8.52—8.56	16	3
8.32—8.36	30	13	8.56—9.00	8	0
8.36—8.40	20	12	9.00—9.04	1	0
8.40—8.44	16	12			
			Totals	164	98

More impressive, due to the larger numbers involved, but not more significant as indications of near-optimum conditions for flight, are counts 6, 10 and 12 made on August 21 and September 5 (midafternoon) and 7, when "in" and "out" flights of workers numbered 275-253, 351-321, and 257-238, respectively, in the three instances. Relatively large numbers of flights occurred on these dates, due principally to the larger worker populations then current. However, these maximum numbers of flights were also favored by the temperatures of about 78 and 79°F. and the absence of wind in midafternoons, which were the warmest parts of these days.

2. *Flights in cool weather.* The effects of low summer temperatures on the number of worker flights is well illustrated by the counts taken on the two successive days, September 9 and 10 (Nos. 15 and 16, TABLE 2). These counts contrast sharply with that made on September 11. All these counts were made in midafternoon hours, and the number of workers present in the colony is assumed to have remained fairly constant through the three days.

An electric storm developed at sunrise of September 9 and brought a cold north wind, so that the temperature at count time (3.52-4.37 PM) was still about 56°F. As a consequence, the number of workers arriving at the nest site was held to 69 and the departures to 50.

At sunrise of September 10 (No. 16, TABLE 2), the thermometer registered 39°F.; a 5-minute watch at that time showed no activity at the nest site. But with the north wind subsiding and under a sunny sky, the temperature behind the cabin attained 62° at count time (3.30-4.15), and the number of arrivals increased to 83, the departures to 80.

By contrast, the record of September 11 (No. 17, TABLE 2) serves to show how effectively the higher temperature of 73°F., with bright sun and warming south breeze stimulated the number of worker flights. Under these conditions, arrivals at the nest site totalled 241 and departures 224, in a count taken at 3.02-3.47 PM.

3. *Flight behavior at nightfall.* Retardation in the rate of flight as affected by diminishing natural light is illustrated by two counts taken on September 5. The first one, made at 3.40-4.25 PM at a temperature of about 79°F., showed that the workers moved at the high rate of 351-321 in nestward and woodward flights, respectively in the period of 45 minutes.

Four hours later, at 8.20-9.05 PM, the thermometer reading 75°, and falling, the second count showed 164 worker flights nestward and 98 outward. This extraordinary spread in numbers of inward and outward flights reflects the influence of waning light on movement. However, these final numbers, taken alone, do not describe the manner in which such changes in intensity of light affect the rates of flight.

Table 1 gives particulars of this sample count taken on September 5, 8.20-9.05 PM. First, the counts in this case show both a reduction of total flights and an increased proportion of nestward over outward movements, as compared with the count made in the midafternoon of the same day. That is, at 8.20 PM, the

workers had already been slowed down by waning light and falling evening temperatures. During the 20 minutes between 8.44 and 9.04 PM, the predominance of nestward over outward flights increased at an ever accelerating rate. A lessening number of workers reached the nest site, but the outward flights dwindled at a still faster rate, and ceased, while nestward flights persisted at a low level. The inclination of workers to return to the field was completely inhibited by the darkness prevailing both in and outside of the nest.

The relation of nightfall to flight is exemplified also by a count taken on September 2 (No. 7, TABLE 2). This example confirms the principles demonstrated in the above case.

A word should be added concerning the behavior of stragglers that return to the nest site in darkness. First, while still 10-15 feet away, they seem to be guided vaguely by the dimly visible white wall in which the entrance is located. It is supposed that the worker remembers the site through "photographic images" acquired in previous exploratory flights. As they come closer to the wall, they commonly fly, with an audible thud, against the vertical surface. Failing to hold to the smooth painted wall, they fall earthward, but regain their wings. This falling and flying may be repeated several times, yet the worker seems in general to move toward the entrance. When only a few inches away it somehow recognizes the sur-

TABLE 2.—*Vespula maculifrons*, flights of workers.

Count No's.	Dates of counts	Hours of counts	Temperatures Fahr.	Nestward flights	Outward flights	Weather conditions
1	7.29	3.35— 4.20 PM	90	98	97	near optimum
2	8.5	5.30— 6.15 PM	88	158	152	cloudy, warm, no wind
3	8.6	10.45—11.30 AM	69	76	93	drizzle, north wind
4	8.7	11.40—12.25 AM	62	76	74	cloudy, cool
5	8.8	11.30—12.15 AM	64	97	95	sunny-cloudy
6	8.21	3.15— 4.00 PM	78	275	253	warm, cloudy, no wind
7	9.2	8.30— 9.15 PM	63	84	50	dark at 9.00 PM
8	9.3	11.03—11.48 PM	58	125	81	cool, gusty, light rain
9	9.4	2.26— 3.10 PM	76	358	325	sunny, no wind
10	9.5	3.40— 4.25 PM	79	351	321	warm, no wind
11	9.5	8.20— 9.05 PM	75	164	98	dark at 9.00 PM
12	9.7	2.30— 3.15 PM	78	257	238	sunny, no wind
13	9.8	10.55—11.40 PM	61	109	124	sunny, cool, east wind
14	9.8	2.50— 3.35 PM	72	156	194	sunny, cool, east wind
15	9.9	3.52— 4.37 PM	56	69	50	cold, northwest wind
16	9.10	3.30— 4.15 PM	62	83	80	sunny, cool, 39° F at sunrise
17	9.11	3.02— 3.47 PM	73	241	224	sunny, warm, south wind
18	9.12	3.14— 3.59 PM	68	342	308	sunny, northeast breeze
19	9.13	4.08— 5.03 PM	74	330	320	warming, no wind
20	9.18	4.36— 5.21 PM	70	364	392	sunny, cool breeze, darkening

face runway made familiar through frequent use by itself and others, then, promptly crawls directly into the entrance.

4. *Reactions to rainy weather.* Table 3. The flight behavior of workers during unsettled rainy cloudy weather is reflected in a 45 minute count taken from 11.03-11.48 AM of September 3 (No. 8, TABLE 2). Temperatures varied from 56°F. in the woodland to 63 at the ventilator of the cabin. Moreover, recognizing that weather factors, obtaining previous to the usual count, have conditioned the responses of the workers, I include under period Number 1 (TABLE 3, above), the flights made in 21 minutes. Likewise, I tabulate the flights made in the 24 minutes that follow the regular count, since they show the contrast in number of flights taken between rainy vs. clearing weather conditions.

Deductions. The number of flights made in the first period fall within the expected range, considering the prevailing atmospheric conditions.

The steady brisk rain from dark clouds in the second period, stimulated workers then in the woods to return quickly to the nest site at the rate of 33 in 3 minutes, while it held outward flights to a minimum of 9.

The imbalance between arrivals and departures in the third period stems from the steady but moderate rain. It permitted some outward flights while stimulating a larger number to return to the nest site.

The proportion of nestward to outward flights in the fourth period, when weather tended to clear, indicates that conditions are becoming favorable to woodward movements, after previous confinement to the nest.

The 103 nestward flights made in period 5, after the usual 45 minute count, seem to indicate that many workers delay in the woods during rain of inhibitive proportions, then promptly return to the nest site when rain ceases.

Rainfall, even though not heavy, is more effective than moderate cloud cover alone, as a deterrent to worker flight. The cool air contributed to the comparatively low rate of flights counted.

Imbalance in worker flights. Reference to the counts recorded on Table 2 will show that the number of nestward flights and outward flights are mostly far from equal. On first consideration, it might be supposed that each worker makes a flight back to the nest site for each flight it makes to the surrounding woodland. If this were true, the number of "in" and "out" flights recorded in each of the 45-minute sample periods should ideally be equal. Granted that some degree of error is involved in the counts, and if allowances were made for these errors, there would still remain an imbalance of considerable size. For the sake of discussion, two variations of the imbalance are recognized. In the majority of instances listed in Table 2, the nestward flights more or less outnumber the woodward flights. On the other hand, the outward flights sometimes outnumber those made to the nest.

Search for the explanation of this phenomenon of differences, points to the changing weather conditions, in which the flights take place. Counts numbered 3, 13 and 14 (TABLE 2)

and Table 3 indicate that the predominance of outgoing flights arises from a combination of pre-existing and current conditions either of fair cool weather, or rainy cloudy weather accompanied by lower temperatures. Such conditions become a drag both on outward and nestward flights, and result in an accumulation of workers in the nest. When conditions change subsequently — within hours, to sunshine and warmer, the workers begin moving out, while few return. Somewhat later, a larger number flies away, and more return from the field. Thus is established the numerical superiority of outgoing over nestward flights. This same reaction to a warming trend appears to take place on most mornings of the Eaglenest summer, where the early morning temperatures frequently stand between 40 and 50°F. Assuming that all or most of the worker force passed the night in the nest, there would at first occur a period of outward flight, with few or no returns to the nest in the first minutes. This reaction is followed by a gradual increase in flights as the atmosphere warms toward noon. Assuming that fair weather continues to prevail through the day, the number of flights nestward would, according to counts made (TABLE 2), gradually equal, then exceed, the outgoing flights.

This predominance of flights to the nest is known to occur (TABLE 2) at least from 11.30 to 4.30 PM, in fair weather. Yet it must be supposed that this pattern of flight cannot be maintained so long a time without alternating periods of major outward flights that replenish the woodland with workers for another period of dominant nestward movement. This speculative situation could possibly have been clarified by taking four or more counts per day between early morning and nightfall, instead of the usual single one.

SUMMARY

Counts of worker *Vespula maculifrons* made as they flew from and to their nest hidden in the attic of a cabin at Eaglenest lakes, Minnesota, was the method employed to observe the effects of normal weather conditions on rates of flight. Flights are (1) faster, hence more numerous on bright windless days when temperatures range from 78 to 90°F.; but (2) slow at temperatures of 50 to 60°, and prevented at 40°; (3) retarded but not stopped by light to

TABLE 3.—Observations on Flights with Varying Weather Conditions.

Period number	Periods of observation	Weather conditions during the periods	Flights to the nest	Flights from the nest
1	21 minutes before the 45 minute count	feeble sun, misty, light rain at times	49	66
2	first 3 minutes of the 45 minute count	steady peppery rain, dark, cloudy	33	9
3	next 18 minutes of 45 minute count	rain continued, dark, cloudy	56	30
4	last 24 minutes of 45 minute count	rain slackened, brief sunshine	36	42
5	24 minutes after 45 minute count	no rain, moderately cloudy, more sunshine	103	24

moderate rains under windless conditions; and (4) gradually brought to a stop as light wanes toward nightfall, when stragglers have some difficulty in finding the entrance to the attic but appear to recognize the area from previous exploratory flights. An attempt is made to identify the factors that cause the often pronounced numerical imbalance observed between nestward and outward flights.

Manuscript received February 7, 1968.