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FLIGHTS OF THE ANT FORMICA DAKOTENSIS EMERY*

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Formica dakotensis is a small ant of the *rufa* group whose red and black workers are easily recognized by the petiolar scale, which is thick and flat on top and has sides that are parallel along the upper half and taper inward only in the lower half.

This is the first report of F. dakotensis in Michigan. However, its presence here is not surprising since it has been taken in Indiana and Wisconsin. Other records have been west of this range. Although ant collecting has gone on at the Edwin S. George Reserve in southern Michigan (Livingston County) since 1951, it was not until August 20, 1969 that a colony of this ant was found. Subsequently, two other nests have been located on the Reserve and W. F. Buren discovered a colony in Branch County, near the Ohio border.

The Edwin S. George Reserve is a two square mile inclosure of rolling country with woods, fields, swamps and marshes. The three colonies (in grids G22, N26, and C10 of the Reserve map) each lay near the border of a field, close to a good growth of shrubs, such as *Spirea alba* Du Roi or *Cornis stolonifera* Michx., which grew near a swamp edge.

This paper is primarily concerned with one colony, which was studied during the summers of 1970 and 1971 to determine its flight activities, nest structure, development of brood and foraging habits.

The colony was discovered because the grass border of a road had been cut, revealing the series of small grass mounds in the high grass just behind. This strip (6 to 9 feet wide) of uncut grass, scattered shrubs and forbs formed a field-wood border. In front of it, across the road, an open field stretched to the northeast and allowed continuous sun from shortly after sunrise until mid afternoon, when the nest was shaded by trees. Behind lay a small poplar (*Populus tremuloides* Michx.) wood, which extended back to a swamp 18 yards away. Plants in the nest strip were mostly grasses (*Poa pratensis* L., *Panicum oligosanthes Scribnerianum* (Nash) Fern., *Aristida purpurascens* Poir.), together with shrubby meadowsweet

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(Spirea alba Du Roi) and some not very flourishing berries: red raspberry (Rubus idaeus L.), creeping blackberry (Rubus flagellaris Willd.) and common blackberry (Rubus sp.). Just back of the nest more vigorous Spirea alba made an almost complete wood-field fringe and extended back into the wood for 6 to 14 feet, forming a shrub layer until the more moist ground near the swamp was taken over by a thick growth of sensitive fern (Onoclea sensibilis L.).

The visible parts of the nest consisted of a series of inconspicuous low grass-thatch mounds strung along parallel to the woods edge behind and to the road in front. In 1969 there had been seven major mounds along 30 feet, but in 1970 those of the northeast half of the line had been abandoned and the ants occupied 10 mounds along the south-west 15 feet. A main cluster, lying near the center of the line, was composed of five, which rose into peaks of three to six inches and intercommunicated by low thatch structures barely above ground level. This made a conglomerate which stretched out into a very irregular shape, which was four feet at its longest extension. The five other mounds had no above-ground thatch connections. Three of these extended to the north-east of the main group and were 16, 33 and 38 inches from it. A fourth was 9 feet to the south-west and the last was five feet back from the main group and lay at the base of a poplar tree at woods edge. The mounds varied in diameter from 8 \times 10 inches to 18 \times 21 inches and in height from two to six inches.

Structure of the mounds. The mounds were built of grass thatch with bits of poplar and spirea leaves intermingled. Live grasses growing through them gave some reinforcement but major support was furnished by spirea and berry stems. Superficially they looked much like enlarged igloo mounds of Dolichoderus mariae but inside there was no large central chamber. Instead, the grasses formed floor and ceiling for two or three stories of chambers and galleries. These provided a surprisingly dry place for pupae to mature. Concealed runways at the bottom of the mounds extended out just under the compressed leaf layer and were cut into the ground for about one-fourth of an inch. They ran to other mounds and to foraging areas. In addition there were galleries and chambers cut beneath the ground surface down among the plant roots for three or more inches. Thus part of the nest was underground and the mounds served primarily for hastening the maturing of brood.

The mound set back at the base of the poplar tree at woods edge had a special significance. It was large, 20×21 inches across, and was built up partly of soil. On September 24, 1971, considerable

dug-out soil was noticed just in front of it and workers were beginning to carry other workers from various mounds to this one. When leaves were cleared away a labyrinth of pathways was found cut into the soil and going into the mound's base. Each day hereafter, until observations ceased on October I, ants were seen carrying other ants into the lower part of the mound. Evidently this was the hibernating place for the whole colony. On June 3, 1971 workers were carrying other workers out from this mound.

Trails and foraging grounds. Among the grasses of the nest area there was a superficial trashy layer of loose tree leaves, stems, etc., and under this the usual matted layer of compressed leaves decaying into the soil. It was this soil-leaf stratum which the ants used for tunneling to their foraging grounds. Their food seemed to be aphid honey dew but very little attending of above-ground aphids was seen. In 1970 the only workers seen foraging above-ground went by tunnel for about 10 feet and then up into a small poplar tree. Here 5 to 15 ants at a time attended aphids on leaf petioles.

Most of the hidden aphids were on bases of spirea stems. Only the young, green stems were used and all such stems investigated had the lowest inch or two covered with aphids. If the lower stem had leaves piled about it, no structure was built but if the aphids extended above the leaf layer, a very tight thatch shelter encircled them. These thatch collars were rather easy to see and were very abundant but no ants were seen upon them because runway tunnels took the ants directly into their bases. Perhaps the ants also attended root aphids. There were some tunnels extending into the soil beneath the plants but no aphids were found on roots. In the grassy area in front of the nest ants were seen going into several holes at sides of clumps of grasses. One such clump was dug and aphids were found at the base of leaves, where stem and roots joined.

The other two colonies were more typically field ants, being further away from shrubs and trees and more directly dependent on field plants to harbor their aphids. The larger colony, near Southwest swamp, had 8 major mounds spread over 19 feet. It lay in a field of *Poa compressa* grass, goldenrod (*Solidago nemoralis* Ait.), ironweed (*Verononia altissima* Nutt), Queen Anne's Lace (*Daucus carota* L.) and small scattered dogwood (*Cornus stolonifera* Michx.). Runways radiated from the mounds to many of these plants which had small thatch shelters surrounding their bases. All of the aphids found were just below ground level where roots and stems met.

The smaller colony, on a grassy slope above a cattail marsh, had only three main mounds spread over 27 feet. It had a number of

)		;
Time* Temp.* Light*	Time	Time Temp. Lig	Light	Time	ne Temp. I	Light	Time	Temp.	Light	flight
	11:10	92°	8600	11:50	°06	7600	12:15	93°	7600	66 min.
5400	11:42	84°	4600	11:59	87°	4200	12:50	91°	6800	69 min.
2600	11:37	91°	7400	12:23	87°	7400	1:03	93°	7500	86 min.
7000	12:32	88°	7200	12:53	88°	7000	1:01	89°	7200	30 min.
6100	11:09	86°	6600	12:29	84°	7200	1:25	83°	7400	137 min.
2400	11:40	76°	2200	12:17	78°	2500	12:43	75°	1000	64 min.
3600	9:34	85°	3600	10:03	89°	4500	10:50	92°	5000	77 min.
3871	11:20	86°	5744	11:59	86°	5771	12:37	89°	6071	76 min.
	5400 2600 7000 6100 2400 3871	11:10 5400 11:42 2600 11:37 7000 11:37 6100 11:03 2400 11:03 3600 9:34 3871 11:20		11:10 11:42 11:37 11:37 11:32 11:09 9:34 9:34 11:20	11:10 92° 11:42 84° 11:37 91° 12:32 88° 11:09 86° 9:34 85° 9:34 85° 11:20 86°	11:10 92° 8600 11:42 84° 4600 11:37 91° 7400 11:37 88° 7200 11:09 86° 6600 11:40 76° 2200 9:34 85° 3600 11:20 86° 5744	11:10 92° 8600 11:50 11:42 84° 4600 11:59 11:37 91° 7400 12:23 11:37 91° 7400 12:53 11:37 88° 7200 12:53 11:09 86° 6600 12:29 11:40 76° 2200 12:17 9:34 85° 3600 10:03 11:20 86° 5744 11:59	11:10 92° 8600 11:50 90° 11:42 84° 4600 11:59 87° 11:37 91° 7400 12:23 87° 11:37 91° 7400 12:23 87° 11:37 91° 7200 12:23 88° 11:09 86° 6600 12:29 84° 11:40 76° 2200 12:17 78° 9:34 85° 3600 10:03 89° 111:20 86° 5744 11:59 86°	11:10 92° 8600 11:50 90° 7600 1 11:42 84° 4600 11:59 87° 4200 1 11:37 91° 7400 12:23 87° 7400 1 11:37 91° 7400 12:23 88° 7000 1 12:32 88° 7200 12:29 84° 7000 11:09 86° 6600 12:29 84° 7200 11:40 76° 2200 12:17 78° 2500 1 9:34 85° 3600 10:03 89° 4500 1 111:20 86° 5744 11:59 86° 5771 1	11:1092° 8600 $11:50$ 90° 7600 $12:15$ $11:42$ 84° 4600 $11:59$ 87° 4200 $12:50$ $11:37$ 91° 7400 $12:23$ 87° 7400 $12:63$ $12:32$ 88° 7200 $12:23$ 88° 7000 1.01 $11:09$ 86° 6600 $12:29$ 84° 7200 1.25 $11:40$ 76° 2200 $12:17$ 78° 2500 $12:43$ $9:34$ 85° 5744 $11:59$ 86° 5771 $12:37$

Michigan 4 . é . . . 5

[September

small grass shelters around such plants as strawberry (*Fragaria* virginiana Duchesne), yarrow (*Achillea millefolium* L.) and golden Alexanders (*Zizia aurea* L.), all of which had aphids at the union of stem and root.

Worker activity. Workers seemed more stereotyped in their behavior than did many Formica. They moved in files in their tunnels or when going up a tree trunk. At the nest some carried grass to replace thatch, some carried out empty pupa cases and occasionally one carried a pupa into the open. Ants could come out of the nest just before sunrise at temperatures as low as 50° to 53° F. and they avoided temperatures in the high 80's.

If the nest was disturbed they ran up onto hands quickly and bit hard, hanging on so tenaciously that they had to be picked off one at a time. They gave off a strong odor when thus disturbed.

Development of brood. Numerous small clusters of eggs were present on June 3 and more were in the nest on June 7 and 11. The first larvae were seen on June 12 and the first newly formed worker pupae on June 16. Pupae soon became very numerous and were scattered in piles through all of the central mounds. By August 2 the first alate pupae were present. At this time pupae were very abundant and larvae were declining in number until after September 5 no more larvae were found.

Callow workers began appearing by July 6 but worker pupae remained abundant through August and much of September and a few were still in the nest on October 1. Adult alates were found on August 24, 1969 and on August 27, 1970. By September 1 most alates were adult but as late as September 15 a few were still in the pupal stage. In 1970 flights began on September 5 and, after 7 flights, there were still both males and females in the colony on October 1, when observations ceased. It is presumed that October provided a few days warm enough for the rest to fly.

Care of brood. The moving of pupae went on constantly and was easy to watch by making tears in the thatch. At the height of the season they could be found in most mounds but by mid-September, as their numbers dwindled, they were gradually consolidated into the central mounds, leaving the outlying ones empty. There was a daily task of bringing pupae up into the mounds when the air temperature rose above that of the ground and of taking them back underground in the late afternoon as the air temperature fell. Thatch in the mounds remained dry even when the outer surface and the soil beneath were drenched, and it was here that the pupae were concentrated during wet weather. To give ventilation and greater warmth, workers often made small openings in the thatch and sometimes pupae were placed out in the light at these openings. Although mounds were connected by covered runways workers sometimes found it convenient to carry pupae across the surface to other chambers and sometimes they carried them outside to place them under curled up leaves. They were removed from the exposed places if temperatures became too high or too low. One afternoon there was a 10 degree drop (from 86° to 76° F.) in 5 minutes and workers were very busy taking pupae into underground chambers and repairing openings in the thatch which they had made that morning. In early September, when many alates and workers were emerging, there was a conspicuous bringing out of empty pupa cases which were discarded in the grass 6 to 36 inches away.

Flights. In 1970 the first adult males were seen on August 27 and the first female on August 29. Each day after that the colony was watched for flights. The next six days were either rainy, cold or windy and the first flight took place on September 5, 1970. It is not known if alates would have flown earlier in good weather or if they needed this time to mature.

By 9 a.m. on September 5 there was more activity of workers outside the nest than had occurred all summer. Some workers were making an opening at the base of the center mound and others seemed to be guarding it. No males were in sight at this time, but one was seen when a superficial oak leaf was moved. The morning continued to be bright and clear and the temperature rose to 94° F. (10 inches above the ground, in sun) by 10:50 a.m. At this time the first two males emerged. A worker came up after one and it dropped out of sight. Suddenly at 11:05 three males climbed from the shade of grasses into the sun (92° F.) and flew immediately. Twenty minutes later a fourth flew and then a fifth. The males were escaping from an opening down in the shade which was being guarded by 8 to 10 workers. Temperatures in the sun seemed to be too high for the workers and when males reached a sunny spot they flew quickly or ran down into the shade. At ground level, in the shade, the temperature was a moderate 82° F. During the next 40 minutes 10 more males flew, with periods as long as 13 minutes between flying. At one time there were six males in sight but usually there were only one or two or even none. After 12:15 p.m. no more males flew but from time to time one would climb a bit of vegetation and then drop. Conditions had become unfavorable for flying. Temperature at the 10 inch level (about grass top) was not higher than before but the ground was becoming equally

warm. At 12:30 p.m. it was 95° F. down in the grasses as well as up in the sun.

The one female sighted acted quite differently. She was seen down among the grasses at 11:45 a.m. and at 12:32 p.m. she appeared again walking on a bramble stem. A male lit near her, wings spread. He found her and they mated on the under side of a leaf.

During the 70 minute flight only 15 males were observed to fly and only one female appeared. The sparseness of the flight may have been due to high temperature or there may have been only a few males and females mature enough.

The next three flights (September 6, 9 and 12) were equally sparse with only 10, 19 and 8 males flying and only 3, 5 and 3 females seen. Temperatures were again high and at flights end males again tended to drop as they fluttered and tried to take off. In each case weather conditions were not ideal. On September 6 the ants disappeared entirely when a cloud dropped light from 3400 to 2800 foot candles, and no males were in sight for 12 minutes, until the light began to brighten. On September 9 flight was troubled both by little gusts of wind and by passing clouds, which not only caused fluctuating light but also slight rise and fall of temperature. On September 12 the sky was bright and clear but a little wind $(\frac{1}{2}$ to 2 m.p.h.) blew almost constantly so that males could climb and fly only during brief quiet intervals. In all four flights very few alates came out trying to fly and at no time were there more than six males and two females in sight.

The following three flights were quite different in that alates were abundant and eager to fly and many flew under conditions no better than those of the first flights.

The largest flight occurred on September 19 after a week of bad weather had kept the ants inside. The cool and foggy morning $(51^{\circ}$ F. at 7:25 a.m.) warmed quickly and by 10:15 the sun was bright (6000 ft. c., 71° in sun and 68° in shade at nest). A few workers were performing the usual chores of adjusting bits of grass on the mounds but none was guarding an entrance. At 10:30 (82° in sun) workers were guarding exits out in front, but not behind the nest where it was still cool (68°). Two males had just escaped and were at the bases of grasses. By 11 a.m. (82°, 6600 ft. c.), two males had started to climb and a female was out on the ground. Just then a 5 m.p.h. gust of wind turned them all back. Immediately after the gust stopped several males climbed and at 11:09 the first flew (86°, 6600 ft. c.). When the wind again moved plants and took the temperature down 4 degrees, the males stood still or retreated. In between gusts they climbed again but no more flew until 11:25. During this time workers were gathered at all five central mounds, trying to keep males down. In spite of delays caused by the wind, flying accelerated until between 12:18 and 12:41 p.m. 299 males flew (average of 12.5 a minute). During this time temperature ranged from 81° to 88° and light from 7200 to 7400 ft. c. Several females had appeared at intervals, either on the ground or climbing up and down brambles. At about 12:40 another activity, not seen in the earlier, sparse flights, became evident. Although some males continued to fly off, more and more began flying from plant to plant over the nest area. Females continued to climb up and down plants and whenever a male lit near one he moved toward her and they mated. Thus, there was a shifting from flight to swarm activity.

Gradually males ceased flying away and spread so that they were flying over the entire grassy strip and females also spread by walking on the ground or by flying from plant to plant. The activity became a typical, but small ground swarm. Transition between flight and swarm was blurred but by 1:23 all the males were flying among the grasses and matings were taking place. The colony produced very few females and only five were seen to mate and 10 to fly away (evidently mated). Females which were ready to mate appeared to attract males from a distance of two or three inches. When a female stretched forward and extended her antennae any males near by converged on her. If two or three reached her the extra males tried to hang on to the mating male. Once a female mated twice in a short time. A mated female, ready to fly, did not seem to attract males. The last mating was seen at 1:50 and by 2:00 p.m. only four males were flying over the grasses. By this time the nest area had come into light shade from the woods behind it.

The next day (6th flight) males came out and flew readily in spite of low temperature $(82^{\circ} \text{ to } 74^{\circ})$ and overcast sky (3400 to 1400 ft. c.). At 12:43, when 141 males had been seen to fly, the sky darkened to 1000 ft. c. stopping the flight. Rain began five minutes later. During the last ten minutes of flight one female was seen and males began swarming activity, but all was cut short by the rain.

The urge to fly was extremely strong the next day (7th flight). Flying started very early because the morning warmed quickly, but the whole flight was hindered by frequent little gusts of wind of 2 to 3 m.p.h. At 9:25 a.m. $(84^{\circ}, 3600 \text{ ft. c.})$ no alates were in sight but workers were guarding exits. Two minutes later a male which had reached the outside was pulled back by an antenna and in another two minutes a male succeeded in climbing a berry stem. Immediately others climbed and at 9:34 (85° , 3600 ft. c.), one flew and a female was seen back in the spirea. Rate of flying of males increased rapidly, with about 4 a minute flying during the first 14 minutes, then 8 a minute for the next 9 and, during the heighth of flight (9:58 to 10:08) 169 males flew at the rate of 17 a minute. During the most favorable period the temperature was 86° and light 3700 ft. c. One male took off in a gust of 3 m.p.h., but wind continued to bother most and flying off declined rapidly until it ended about 10:50. Males had begun the swarming flying over plants by 10:10 and their number gradually increased. When wind blew they settled on plants and resumed flying during lulls.

During the early part of the flight a female could be seen occasionally on the ground or a plant stem and by 10:05 one had flown away. Seven were seen to fly between then and 11:00 and 10 females were seen to mate. As before, as many as four males might converge on a female and one or two males would hang on the mating male.

In all seven flights 1055 males were counted flying away and 20 or more females were seen. This was a definite undercount because, during abundant flights, the alates spread out so far that not all could be seen. Since there were still winged ants in the nest on October 1, no approximation could be made of the number of alates produced by the colony.

The watch continued each day until October I but bad weather prevailed and no further flights occurred during this period. In all there were 20 days between September 5 and October I when no flights took place. Records kept on these days told much about unfavorable conditions. On 9 days temperature never reached above 69° and no alates came out. On 8 days temperature reached into the 70's or low 80's but these higher temperatures were brief and other conditions were unfavorable. Clouds or wind might give rapid alternating of temperature, the ground in shade might stay very cool or there was rain during flight time. Three days were very warm, with highs up to 98°. On the first a few males came out but kept dropping. There was also a wind up to 8 m.p.h. On the second day there was no wind but clouds gave a very rapid alternating of light intensities. The third day seemed favorable except that the shade remained cool. At 12:55 p.m. when it was 92° in the sun it was only 73° in the shade. Perhaps the nest never warmed enough to stimulate alates to emerge.

Summary of flights of F. dakotensis. Alates developed very late. No winged individuals have been seen before August 24 and a few were still in the pupal stage on September 15. Flights began on September 5 in 1970. On October 1, when 7 flights had occurred, there were still alates in the nest.

On flight days males and females came from openings at the bases of mounds and from under leaves nearby. Workers had made the exits and a few guarded them in an attempt at keeping the alates from leaving. Occasionally a worker came up a plant after a male and pulled sim back or nudged him until he walked down or dropped.

Time of day of flight depended primarily on rising temperature and flights took place in the morning when the sun had warmed the air and nest area sufficiently. Flights tended to be late in the

	Formica obscuripes¹	Formica obscuriventris²	Formica dakotensis
Dates of			
flights	6-3 - 7-1	7-27 - 8-24	9-5 - 9-21 ⁸
Beginning of flights			
Time	6:08 - 11:35	7:00 - 8:43	9:34 - 12:32
Temp.	69° - 72°	63° - 69°	76° - 92°
Height of flight			
Time	7:05 - 9:40	7:07 - 9:24	10:30 - 12:53
Temp.	71° - 77°	66° - 70°	78° - 88°
End of flight			
Time	8:00 - 11:40	8:48 - 10:04	10:50 - 1:2
Temp.	74° - 81°	68° - 72°	75° - 93°

Table II. Comparison of flights of three species of *Formica* of the *rufa* group at the E. S. George Reserve, Livingston Co., Michigan.

Temperature — Fahrenheit, 10 inches above the ground Time — Eastern Standard, morning to early afternoon

¹Talbot 1959 and unpublished data ²Talbot 1964 ³alates still in nest on Oct. 1 morning because temperatures at which they occurred were rather high. No alates were seen below 74° and flying started at about 75° . The most favorable flying temperatures were between 78° and 88° F. (in sun, 10 inches above the ground.)

When wind swayed the vegetation alates held still or turned and went down. Flying ceased during a gust and was resumed when the wind subsided.

Ants flew under a wide range of light conditions, from rather dim to quite bright light (2400 to 8600 ft.c.), but fluctuating light, due to moving clouds, tended to disrupt flight. Lessening light and the accompanying lowering of temperature (even in a favorable range) could stop flying.

Swarms. Ground swarms formed towards the ends of flights, with males flying over the whole nest area and females standing on grasses or berries. Females seemed to attract males at a short distance and sometimes two or three males converged on a female at once. These swarms were quite similar to those of F. obscuripes except that they involved only one colony and took place at the nest, while those of F. obscuripes were made up of alates from many colonies that met at a swarming ground unassociated with any.

Comparison with two other rufa ants. The late development of alates and late flights of F. dakotensis are in marked contrast to the habits of two other members of the rufa group on the George Reserve. F. obscuripes Forel has not only worker and alate pupae but also adult males and females when observations begin in the first week of June. Flights can begin as early as June 3 or before and are over by the last of June. F. obscuriventris Mayr has alate pupae by the middle of June and adult alates by the middle of July. Flights take place between the third week of July and the middle of August. The late flights of F. dakotensis may be linked with the fact that their females are thought to be temporary social parasites of such ants as F. fusca and by September there may be numerous new colonies which can be invaded.

Table II gives a summary of flights of the three species.

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