cence, segments three to about seven carinate, spine of third segment short, segments four and five with decreasingly smaller spines, sixth segment spiculate, third segment much longer than first, fourth shorter than third, fifth slightly shorter than third. Pronotum longer than broad, sides rounded; disk coarsely almost reticulately punctate, impressed each side of middle; pubescence sparse, short, recurved, long erect hairs numerously interspersed; prosternum impressed, rugulose, sparsely pubescent, coxal cavities narrowly open behind; meso- and metasternum faintly scabrous, finely pubescent, metasternum subglabrous medially. Elytra over 3 ½ times as long as broad, slightly tapering posteriorly; basal punctures rather fine, well separated, becoming finer toward apex; pubescence sparse, short, depressed, with a few long erect hairs interspersed; each elytron vaguely bicostate; apices truncate to vaguely emarginate. Legs slender, densely, shallowly punctate; all tibiae bicarinate. Abdomen finely, densely punctate at sides, pubescence fine, dense, sternites medially subglabrous; last sternite truncate at apex. Length, 10–14 mm.

Female: Form similar. Antennae about as long as body. Abdomen with last sternite broadly rounded at apex. Length, 12–14 mm.

Holotype male, allotype (Canadian National Collection) and 12 paratypes (10 males, 2 females) from 25 MILES W DURANGO, DURANGO, MEXICO, 10 June 1964, 20 June 1964, 23 June 1964, 29 June 1964, at lights (H. F. Howden, J. Martin, J. A. Chemsak, J. A. Powell). Additional paratypes include: 1 male, 23 miles W Durango, 29 June 1964 (L. A. Kelton); 1 female, 20 miles E El Salto, Navajos, Durango, 23 July 1964 (Kelton); 1 male, 25 miles E El Salto, 17 July 1964, on *Quercus* (Howden); 1 male, 28 miles E El Salto, 22 July 1964, on *Quercus* (Howden); 1 male, Tepalcates, 30 miles W Durango, 4 to 8 August 1972 (Powell, Veirs, MacNeill); 1 female, 8 miles W El Palmito, Sinaloa, 9 August 1972 (Powell).

The slender form, distinctive coloration, and very coarse punctation of the pronotum will separate this species from other *Aneflomorpha*. There is very little variation in color in the type series.

Natural History of *Veromessor pergandei*
I. The Nest[1]
(Hymenoptera: Formicidae)

JEANETTE WHEELER[2] AND STEVEN W. RISSING[3]
Laboratory of Desert Biology, Desert Research Institute, University of Nevada System, Reno, Nevada 89507

An interesting feature of the Hot Desert landscape is the craters made by the black desert harvesters *Veromessor pergandei* (Mayr) (see Fig. 1). We studied these ants intensively in the north end of Death Valley National Monument, California, near Grapevine Ranger Station where this species is near the northern limit of its range. The area is in a side canyon off the main valley at an elevation of 800 meters. The living-trailer belonging to the Laboratory of Desert Biology of the Desert Research Institute was stationed here. All nests in the intensive study were in the compacted sand, gravel and boulders deposited in the bottom of the canyon by flood waters and were in an area 75 by 250 m (18,750 m^2). The duration of the study was 19 May to 22 June, with a re-check 7–9 July, 1973. Less intensive studies were carried on during 1968–1970 in the Philip L. Boyd Deep Canyon Desert Research Area of the University of California, Riverside (near Palm Desert, California) and in Death Valley National Monument from 1968–1974.

The dominant vegetation of our study area is *Larrea divaricata* Cav. Smaller shrubs are abundant, including *Atriplex hymenelytra* (Torr.) Wats., *Franseria dumosa* Gray, *Hymenoclea salsola* T. & G., and *Lygodesmia spinosa* Nutt. Prior to the study period, the winter annuals (mainly *Chaenactis carphoclinea* Gray, *Chorizanthe brevicornu* Torr., *C. rigida* (Torr.) T. & G., *Cryptantha angustifolia* (Torr.) Greene, *Mohavea breviflora* Cov., *Oenothera clavaeformis* Torr. & Frém., *Phacelia calthifolia* Brand. and *P. crenulata* (Torr.) had bloomed in profusion. In the winter of 1972–1973 rains fell at the proper times and in the correct amounts to produce an impressive display of winter ephemerals in Death Valley National Monument.

The daily air temperature and amount of cloud cover during the study period are shown in Fig. 2. Precipitation usually occurs during late autumn, winter and early spring, with rare summer rains. On 31 May

[1] The second portion of this study will contain our report on: "Behavior" and "Literature."
[2] The authors gratefully acknowledge the financial support by the National Science Foundation, Grants GB 17731X and GB 37241, Dr. Frits W. Went, Principal Investigator.
[3] Present address: Department of Zoology, University of Washington, Seattle, Washington 98105.

THE PAN-PACIFIC ENTOMOLOGIST 51: 205–216. JULY 1975

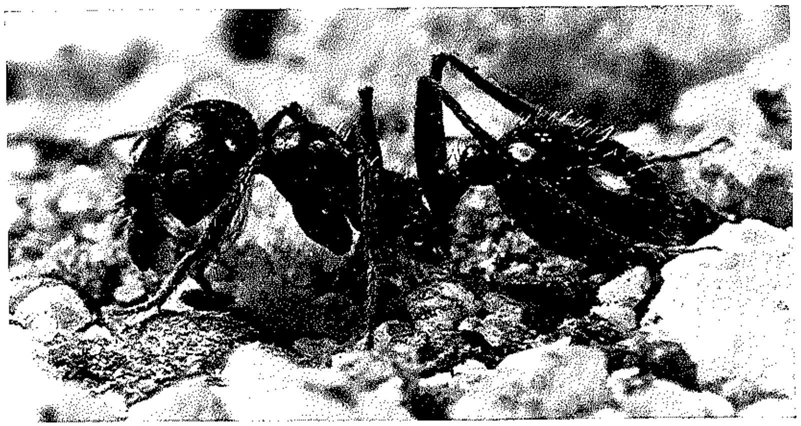

FIG. 1. Worker of *Veromessor pergandei*, × 15. Photograph of living worker by Kenneth Middleham (Wheeler and Wheeler 1973).

there was 0.25 mm of rain and on 1 June 3.0 mm; on 14 June there was a trace both morning and afternoon. The average annual precipitation at the nearest weather station (Furnace Creek, 80 km south and 48.8 m below sea level) is 42 mm, but the extremes are 0.00–115.7 mm.

THE NEST

Incipient Colonies.—On 7 June 1973 in the study area, we saw a small crater about 65 mm in outside diameter at the smoothed edge of a gravel road. Very small black ants were harvesting at 0800 Pacific Standard Time; each worked alone and moved very quickly. We excavated the nest, and at a depth of 15 cm we found 9 queens, 40 nanitics (dwarfed first workers produced by founding queens), and a packet of

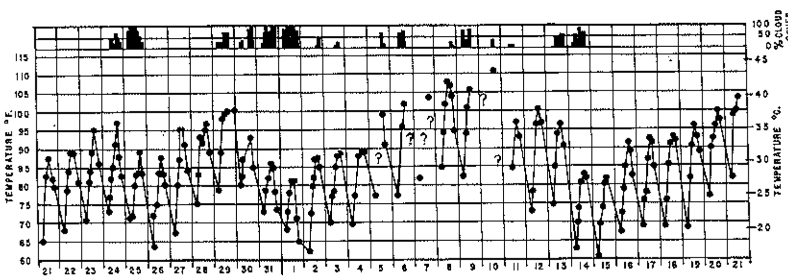

FIG. 2. Daily air temperatures and approximate percentage of cloud cover at the study area, 21 May to 21 June 1973.

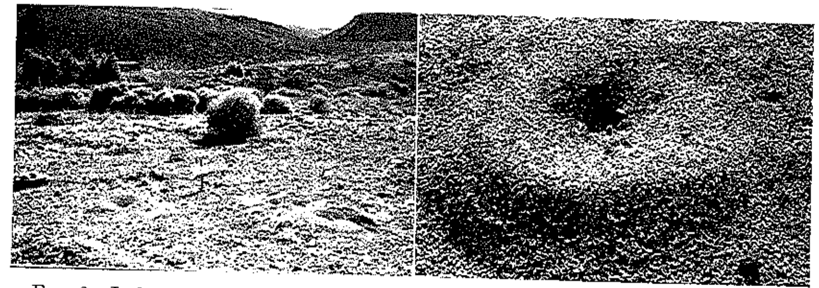

FIG. 3. Left, nest of *Veromessor pergandei* in Death Valley National Monument. There are 3 craters in front of the stake bearing the 3 by 5 card. Right, close-up of one of the craters. Refuse is piled in the foreground and to the left of the crater.

brood. We transported the colony to Reno and placed it in an artificial nest. The nest had wet paper toweling in the bottom chamber, ants and brood in the middle chamber, and numerous seeds collected by mature colonies of *V. pergandei* in the top chamber. The queens behaved as workers, moving soil in the chamber, opening their jaws as if they would attack a disturbing hand or forceps, and tending the brood packet.

The nanitic workers collected seeds of *Chenopodium pumilio* R. Br. and *Calycoseris parryi* Gray and placed them in the brood packet. The packet consisted of eggs, larvae, and pupae and seeds. We did not see the queens or workers eating the seeds or paying much attention to them at any time. One larva had its mouth parts on a seed of *Calycoseris*; another had a seed of *Chenopodium* on its belly. On 7 July nanitics harvested seeds of *Cryptantha* sp. and *Phacelia calthifolia* from the top chamber.

Although we continued to observe and water the colony, the queens and workers began dying. Since no new workers were produced, we preserved the remnants of the colony on 28 July. Later, about 100 more nanitics were found at the excavation. Therefore, we judged that our captive colony failed because there were too few workers.

On 21 June in the study area, we examined numerous craters of about the same size as the first nest, excavating several. One nest had no queen that we could find and only a few nanitics. We found 1 or 2 queens in each of the others, and the workers were more numerous. None of these nests seemed as prosperous as the colony with 9 queens which we had excavated on 10 June. On 5 September 1968, in Death Valley, we found nanitics using an entrance 3 mm by 6 mm beside a rock. In 1970 we found two incipient nests in Clark County, Nevada. At Mesquite, 2 March (490 m), we excavated 2 queens beneath a small pile of gravel

Table 1. Data on nests studied in Death Valley National Monument.

Nest number	Abandoned craters	Active craters	Length & width (cm)	Chaff pile location	Chaff pile size (cm)	Entrances	Entrance size (mm)	Location in crater
1	3	1	45 × 60	E	13 × 30	A	19 × 25	W
						B	13 × 63	E
		2	30 × 45	E	10 × 15	C	13 × 13	SE
						D	15 × 18	NW
		3	23 × 33	N	8 × 20	E	30 × 31	NW
				S	13 × 20			
		4	35 × 48	N	18 × 33	G	15 × 31	center
						H	15 × 18	center
						I	8 × 8	NW
2		1	40 × 48	SW	33 × 33	A	13 × 13	E
			Became inactive during study			B	30 × 50	NW
		none				C	13 × 13	
		2	15 × 18	S	6 × 15	D	25 × 25	N
		3	23 × 28	S	8 × 15	E	15 × 63	N
3	3	1	40 × 45	NE	30 × 45	A	40 × 50	center
		2	55 × 70	N	8 × 75	B	19 × 195	N
				S	5 × 45	C	25 × 25	center
						D	18 × 18	S
		3	40 × 43	N	5 × 75	F	25 × 30	S
		4	29 × 35	N	16 × 21	G	35 × 38	center
				E	25 × 5	H	18 × 25	N
				SW	12 × 17			
5	none	1	85 × 65	E	5 × 90	A	31 × 81	E
						B	31 × 31	center
						C	13 × 19	N
						D	13 × 38	N
						E	38 × 75	N
						F	5 × 5	N
8	none	1	45 × 45	SW	1 × 40	A	19 × 241	N
		2	31 × 43	SW	6 × 9	B	20 × 35	N
10	5	1	58 × 48	NW to SE	10 × 90	A	19 × 25	W

on a road shoulder; the entrance was closed. Nearby at Cactus Springs, 4 March (100 m), in *Larrea*, *Franseria*, *Atriplex* and scattered *Prosopis*, we found a 25 mm crater which we excavated, finding a few nanitics only.

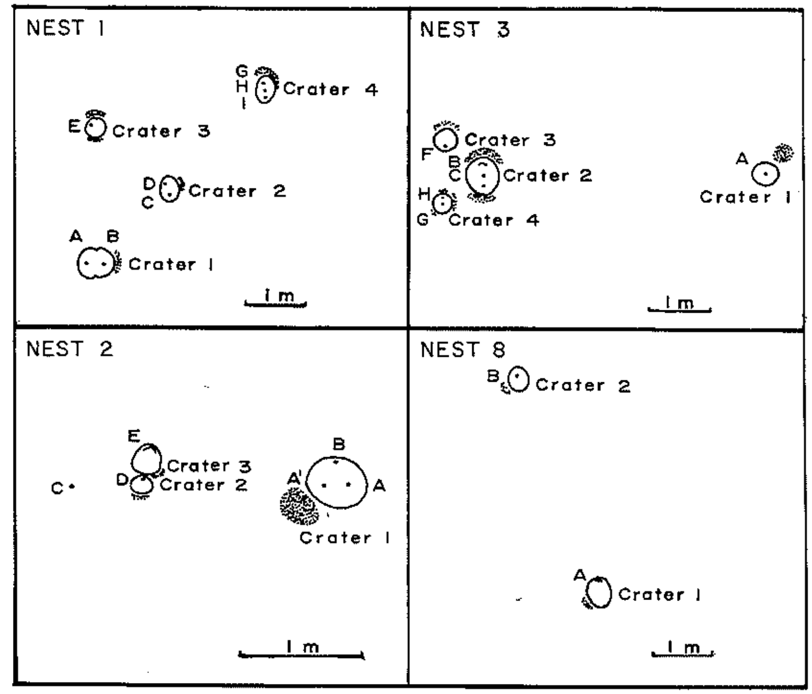

FIG. 4. Maps of active craters (outline), refuse piles (stippled), and entrances (solid spots or lines within crater) which are lettered. Nest 2, entrance C lacked a crater.

Winged males and females were found at the entrances of Nest 2 (Table 1), 20 March 1974, by Dr. F. W. Went. Females were more numerous than males and scurried back into the nests when approached. In Deep Canyon on 9 March 1970 at 914 m elevation, we found 72 winged females and 18 males with over 2000 workers in a nest with 2 craters about a meter apart. We could not find any brood (Wheeler and Wheeler 1973: 171). Therefore we judge that mating flights take place in April and that our captive colony was about 2 months old when excavated.

Craters.—The portion of the mature nest (Fig. 3) above ground consists of one or more craters within an area of several square meters. Active craters, entrances and refuse piles of 4 of the intensively studied nests are shown in Fig. 4. Table 1 gives the dimensions of the craters; locations and dimensions of the refuse piles; numbers, dimensions and locations of the entrances within each crater for all intensively studied nests. The crater of Nest 5 has remained about the same size since about 1968. Its entrance is through the asphalt in a service road.

A typical nest has 2 or 3 active craters, each 35 by 43 cm in outside diameter, with a refuse pile on the northern periphery, 11 cm wide and in a 37-cm arc adjacent to the crater. The craters are made of sand and fine gravel removed from the underground excavation. The typical crater has 2 entrances 20 by 40 mm. The sand nearest the entrance—on both the upper and lower surfaces—is held together by a yellowish cement. This same material is apparently used as a coating on the walls of the galleries and chambers, for we found a stain here also. This cement seems to be fecal material of workers. It dissoves readily in water and has a distinctly foul odor, similar to that of urine. Drops of what appeared to be the same material were found in the refuse pile in the shape of miniature (about ½ mm) discs. Ants were picked up in a teaspoon to induce them to drop their seeds. When annoyed thus, they smeared the spoon with a drop of greenish-yellow material from the anal region; it hardened to a varnish-like finish. This substance might also play a role in defense, in navigation or in marking territory.

On 23 May, Nest 9 was partially excavated, leaving a trench 45 cm wide and 45 cm deep. New entrances were opened by the workers in both walls and excavated material and organic refuse dropped into the trench. The trench was then lined with cellophane. From 29 May to 10 June, about 570 g of sand and organic refuse were dropped into the trench by the workers; 10–17 June, 790 g; 17–21 June, 275 g. Hence, at this one entrance an average of 80 g per day of refuse and excavated material were removed from the nest. Two factors decreased accuracy in these measurements: (1) wind blew some of the material away; (2) it was impossible to distinguish between what the ants had carried out of the nest and what had been blown into the trench.

Underground Nest Structure.—Our earlier attempts to excavate nests of *V. pergandei* were unsuccessful. Even with the enthusiastic help of a class of students we have never been able to dig quickly enough to find a large concentration of ants. We have also tried to make molds of the underground nest structure with roofing cement, aerosol foam, liquid plastic, and other substances. On 4 June 1973, about 4½ liters of maximally thinned casting resin (Fiberglas Evercoat) was poured into one large entrance of Nest 12. The plastic was allowed to set for 2 days before excavation. A trench was dug beside the entrance and the cast carefully excavated. Pictures were taken with a Polaroid-Land camera at various stages to facilitate reconstruction.

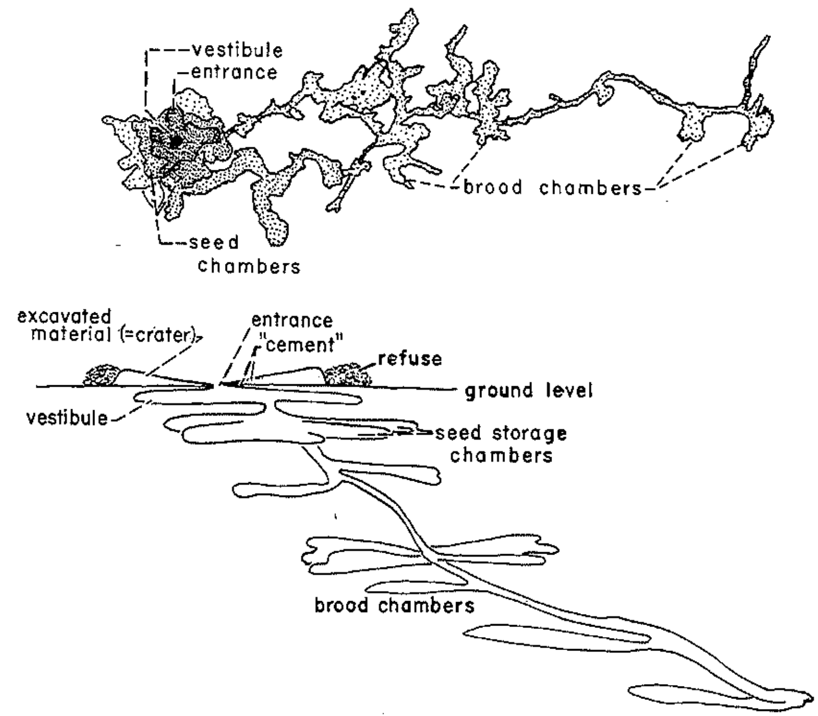

FIG. 5. Structure of excavated nest. Tracing of reconstruction, with labels on most important structures is shown above. Darkest stipples indicate structures nearest surface. Highly diagrammatic side view of nest structure under one entrance is shown below.

In one place the plastic had followed the lower of 2 intersecting galleries, and it also left a chamber 75 by 125 by 19 mm completely empty. Other chambers in the excavated nest showed bevelled edges where the plastic had failed to fill the complete depth of the chamber. The plastic flowed to a depth of 104 cm and to a distance of 250 cm horizontally from the entrance. (See Fig. 5.)

The cast was taken in pieces to the Laboratory of Desert Biology in Reno. There, each piece was cleaned of as much of the adhering debris as possible. When larvae, fruits or seeds were in the chamber the pieces were cleaned under a stereomicroscope. After each piece had been cleaned and examined and the interesting structures photographed the cast was reassembled.

Just below the entrance was a large chamber (hereafter called the vestibule) in which there was chaff but only a few seeds. This seemed to be the seed-cleaning chamber. The entrances to each lower series of chambers were offset horizontally from the entrance above. The vestibule opened into a series of anastomosing chambers which covered an area about 38 cm in diameter. Seeds were on the floor of these chambers, 4 cm below the soil surface. All seeds had been husked, but all seed coats were entire. We could germinate these seeds in the laboratory. Seeds were not sorted but were mixed.

At a depth of about 53 cm was another series of chambers which were low-ceilinged (up to 10 mm) and covered an area 40 by 48 cm. Each chamber ranged from 5 cm by 5 cm to 15 cm by 19 cm; the largest had what looked like two supporting columns near the middle. These columns were of gravel and were easily cleaned out after the piece had been soaked. Brood was present from this level to the lowest chamber (104 cm). Larvae and pupae were mixed. We did not find the queen nor any young larvae. This did not surprise us, because we had excavated only about a fifth or sixth of the nest. The other entrances for this colony were all to the north and west, while our excavation extended to the south and east.

There was no concentration of workers with the brood, therefore we concluded that the workers had not attempted to remove the brood in front of the advancing plastic. In the upper chambers the ants were imbedded near the edges of the plastic, as if pushed aside, but in the lower chambers the larvae were found across the entire floor. They were piled as we have seen them in the nests of many other species when we uncovered brood-chambers by turning over a stone or lifting a piece of wood lying on the soil surface. Since we had not previously found brood, we concluded that the workers of *V. pergandei* behave as do other species and that the plastic had trapped the brood and workers *in situ*. Some of the seeds which the larvae had next to their mouths had had the seed coats removed. We did not find any workers near seeds.

Colony-duration.—Figure 6 gives the summaries of the nest counts on the grids in Deep Canyon and in Death Valley. [Each grid is marked with stakes every 15¼ m and there are 14 stakes on a side (= 3.9 hectares)]. Well established colonies lasted longer than our 3 (Deep Canyon) or 5 (Death Valley) years of surveys. A quarter of the Deep Canyon nests that were present on our first survey (1968) were still present on our latest (1970), while half of the Death Valley colonies that were counted in 1968 were still present in 1973.

The fact that a colony was the same from one survey to the next did not mean that the same entrances were used. We recognized a colony

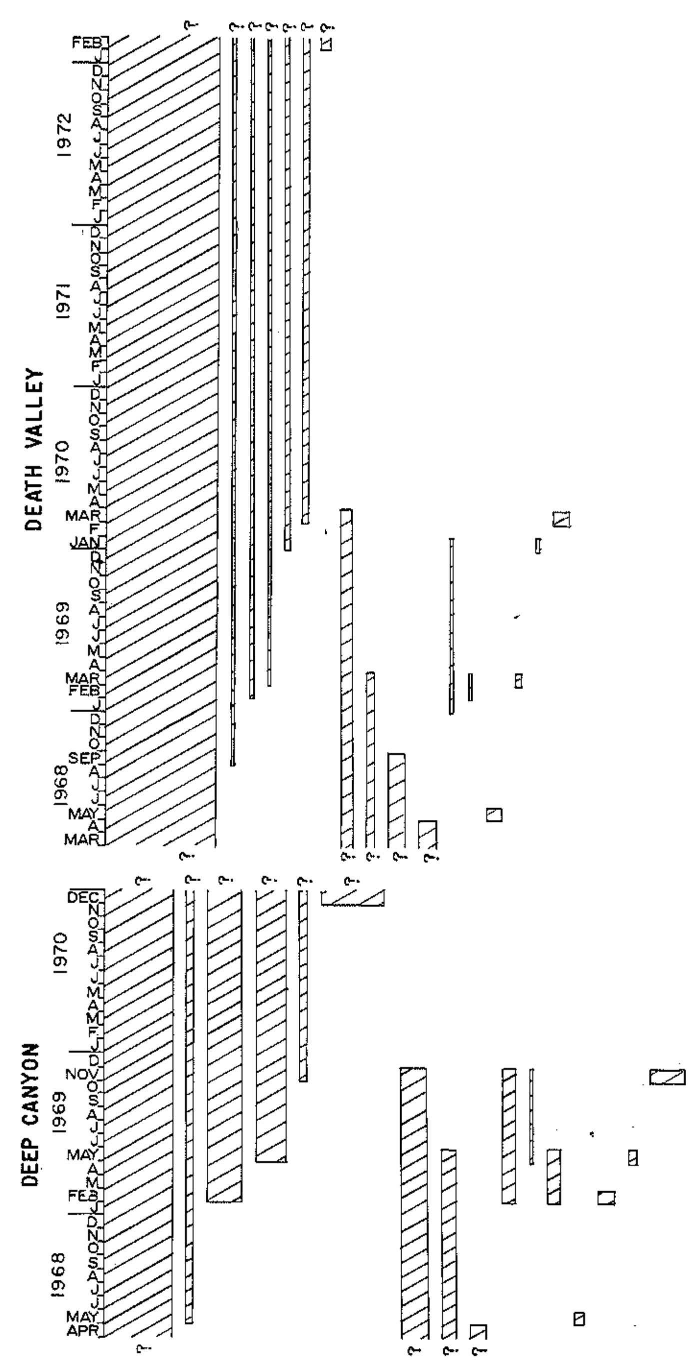

FIG. 6. Survival of colonies on the grids in Deep Canyon and Death Valley. Width of column indicates number of colonies; narrowest column represents one colony. Question marks indicate the colony was already established on our first survey or still thriving on our latest. Spelled-out abbreviations indicate months when surveys were made.

as still active if a crater or craters were found within, or adjacent to, the area of craters observed during the previous survey. A well established colony had numerous abandoned craters. An abandoned crater had no entrance, the rim was lower, the refuse pile was dull grey and and matted and could be picked up in large patches. A new crater was started almost as soon as an entrance was opened from below. A mature colony under favorable weather conditions had several entrances active at the same time; they appeared as described above under "Craters."

In Deep Canyon, April 1969, we made a survey of the grid. About a third of the nests were inactive and apparently extinct. However, a half-inch rain fell during the next night. On the following afternoon in the warm sunshine, workers were active at nearly all the colonies rebuilding entrances and craters.

DISCUSSION

All records for winged sexual forms of *V. pergandei* are for March and April. In June in Death Valley in 1973, we found numerous craters 25 mm in diameter, which we judged to be incipient colonies. At this stage these contained only the founding queen, nanitics, and a small packet of brood. Creighton (1953: 16) reported that the nest-founding queens made their first nests under covering rocks. In 1968 we found one incipient nest under a covering rock; all others have been in the open with small craters.

Mature colonies were reported by both Creighton (1953) and Tevis (1958) to have only one entrance active at any one time. We have found that this species may have as many as 8 entrances active simultaneously; 2 or 3 would be the average.

Tevis (1958) followed the spiralling main gallery of a mature nest to a depth of 4 m in the nearly pure sand of the Whitewater River terrace. He found shallow seed chambers, but no brood. In 1968–1970 we worked 16–32 km south of his area at elevations of 75–1220 m in Deep Canyon. Most of our nests were in outwash channels in sand, gravel and boulders (Wheeler and Wheeler 1973). Whereas Tevis was able to follow his gallery for nearly 4 m, we lost ours at about 1. The chambers and galleries were next to large boulders; when we moved them, we destroyed the structure of the nests. In Deep Canyon and Death Valley we tried slicing off the top or digging in from the side toward the center of the nest; even with the enthusiastic assistance of several students, we were never able to dig quickly enough to find any large concentration of workers. We did find superficial seed chambers, but never any brood.

We had tried several times with different substances to make a cast of a nest of *V. pergandei.* The cast reported in this paper is not that of an entire colony: To make such an extensive cast and excavate it would require energy similar to that involved in digging out an archeological site; and it would take the same kind of careful uncovering and mapping. The underground area of a single mature nest was estimated by Tevis (1958: 697) as about 15½ m (50 ft) in diameter, which he calculated from the area in which he found the entrances of a nest during one year. As is shown in Fig. 4, the entrances of the intensively studied nests in Death Valley do not cover such a large area. On the other hand, both Creighton (1953) and Tevis (1958) said that only one entrance was in use by each nest at one time. Perhaps the area in use in one nest is the same at any one time. We would like to see an entire mature nest excavated.

The underground structure of the portion of a nest of which we made a cast is an intricate system of anastomosing chambers and galleries. We had not expected to find the vestibule, thinking that the uppermost chamber was a seed-storage chamber. Tevis (1958: 697) said: "An inch or two under the surface, there was a store of unhusked seeds [= fruits], probably to be transported below by the ants after the removal of the chaff, and, at the seven-foot level, a small granary ($90 \times 50 \times 4$ mm) filled with seeds of Amaranthus." We had not realized that he was talking about two different stages in seed-handling. Now, with several casts of the upper portions of the nests, we can corroborate his statement. We also found the unhusked seeds in the topmost chamber, while the seed storage chambers are lower and are filled with cleaned seeds. We disagree on the kinds of seeds in a chamber. We found that seeds of several genera were mixed in each chamber and that the seeds were piled together in the seed chambers without any sorting. The plastic certainly reached these shallow chambers before the ants had a chance to carry the seeds away or mix them.

In the lower chambers, containing brood, the position of the larvae with seeds adjacent to their mouths certainly looked as if both larvae and seeds were in normal positions for feeding by the larvae. We have observed in artificial nests living larvae of *Veromessor* spp. and *Pogonomyrmex* spp. with seeds in similar positions. The further observation that the nanitic workers in the incipient colony placed seeds in the brood packet served to strengthen our hypothesis that larvae behave as a digesting link in the feeding of these harvester ants (Went, *et al.* 1972). This suggests that in *V. pergandei* the larvae are used as Wüst (1973) reported for *Monomorium pharaonis* Linnaeus, and as Ishay and Ikan (1968) reported for the Oriental wasp *Vespa orientalis* F.; the larvae digest foods and feed the mature workers with products of digestion. Wüst found that in *M. pharaonis*, the secretions from the larval labial glands which the workers imbibed contained amino acids, traces of proteins, and showed protease activity; the proctodeal secretions from the rectal bladder had a high water content and contained amino acids with traces of proteins. She found no trace of carbohydrates nor fats in either secretion.

Colonies near the northern limit of the range apparently last longer than those near the center: such would be the implication of our nest counts on the Deep Canyon and Death Valley grids. Roger Mauer (unpublished Master's thesis) found that the same species of desert rodents lived longer in Death Valley than in Deep Canyon. There is more cover and the variety of seeds is greater in Deep Canyon than Death Valley; so this observation is also peculiar. Why an organism (if one considers an ant colony as such) should live longer at the edge of its range than near the center is an intriguing problem.

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Sciomyzidae of Oregon
(Diptera)

T. W. FISHER AND R. E. ORTH
Division of Biological Control
University of California, Riverside 92502

INTRODUCTION AND BACKGROUND[1]

Sciomyzid flies, commonly referred to as swale or marsh flies, are found world-wide and most of the more than 500 named species occur in the northern hemisphere. The family Sciomyzidae is separated from other acalyptrate Diptera by the following characters: oral vibrissae absent, post vertical bristles diverging, costa entire, subcosta complete, one or more tibiae with preapical bristles. Body length within the family ranges from 2 to 12 mm and may be pale yellowish-brown to brown to gray to black in color. At rest marsh flies impart a grasshopper-like appearance because of the well developed hind legs and the head held higher than the abdomen. The more hygrophilous species of these rather slow flying Diptera are often seen resting head end directed downward on emergent rushes or grasses along the margins of ponds, lakes, and sluggish streams. However, genera such as *Limnia* and *Tetanocera* are commonly taken well removed from free standing or flowing water in rather typical mesic habitats.

Subsequent to the discovery by Berg (1953) that larvae of sciomyzid flies kill and consume aquatic snails, extensive biologies of nearly 200 species have been studied, mainly at Cornell University. It is now established that larvae of all species studied are obligate mollusk feeders. Some develop only on slugs or terrestrial snails, but most feed on freshwater snails. Certain species feed specifically on fingernail clams, and an eastern U.S. seaboard species is associated with a strandline marine snail. Host association or feeding habit of sciomyzid larvae varies among the species from saprophagous to overt predation to parasitoid. Certain species, mainly among the Sciomyzini are highly host specific. Certain species of *Antichaeta* (Tetanocerini) oviposit on the egg mass of the host snail, and the first-instar larvae feed obligatorily on snail embryos. Instars II and III require more food and in addition attack snails such as *Physa* directly. Biologies of nearctic Sciomyzidae include those published by Bratt, et al. (1969), Fisher and Orth (1964), Foote and Knutson (1970), and Neff and Berg (1962, 1966).

[1] This study was partially supported by University of California Agricultural Experiment Station Project 2037, "Biological Control of Non-marine Mollusks."