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## NEW DATA ON THE HABITS OF THE ANTS OF THE GENUS *VEROMESSOR*

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The major part of this paper deals with *Veromessor pergandei*, but it has been possible to include observations on the habits of four other species as well. The field work on which this paper is based is part of a survey of southwestern ants which was made possible by a Guggenheim Fellowship. I wish to express my sincere thanks to the John Simon Guggenheim Memorial Foundation for this opportunity and privilege.

It will avoid repetition to cite here certain characteristics shared by the species discussed in this paper. All these ants are remarkably docile. They will not sting, even when one tries to make them do so. They bite only on severe provocation. When a nest is broken open they show none of the frenzied excitement that marks many ants at such times. They attack the intruder methodically and without haste. If undisturbed they pay little attention to a person who is standing near the nest or close to a foraging column, and this makes them excellent subjects for field observation. But, despite this imperturbability, all the species are highly sensitive to damage to the nest. If the area about the entrance is no more than slightly altered, the ants are apt to abandon the nest. If the nest is broken open the ants will usually move to another site rather than repair the damage. When they move they do not always take all the stored seeds with them. Other harvesters (*Pheidole* and *Pogonomyrmex*) will often mine an abandoned nest for days after the *Veromessor* colony has left it. The colonies of *andrei*, *juliana*, *pergandei*, and *stoddardi* are large. When mature they may consist of several thousand

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workers. Those of *lariversi* are notably smaller, consisting of a few hundred workers at most.

### **Veromessor andrei** (Mayr)

The writer has been able to study 32 colonies of this ant at 11 different stations. The observations cover a period from May to September. They permit a much more satisfactory account of the habits of *andrei* than was possible in earlier publications.

The nesting habits of *andrei* are more flexible than is usually the case with a member of the genus *Veromessor*. The species is equally at home on the seashore, in lowland stream bottoms, or in mountain valleys up to an elevation of 3500 feet. The nests may be built in heavy clay, loam, sand, or gravel. *V. andrei* may or may not build a crater, but, when it does, the crater is low and obscure at best. When a crater is not present the excavated soil is spread around the nest opening in a circular disc or fan. The number of nest openings varies with the size of the nest. Small nests usually have a single opening. Large nests may have as many as eight entrances. The entrances are often an inch or more across and they may be very irregular in shape. Occasionally an entrance will lie at the bottom of a saucer-like depression. The construction of the chaff pile varies with the season. There is rarely any chaff pile present during the spring months. At such times the seed husks are scattered haphazard around the nest. But in late June and early July, when the seeds of various grasses ripen, the chaff pile often becomes conspicuous. It sometimes completely blankets the nest, but more frequently it has the form of a flattened band or ring which surrounds the nest but does not cover it. By the end of the summer the chaff pile has matted down to a thin carpet of hulls.

*Veromessor andrei* has morning and afternoon periods of foraging like *pergandei* (*q.v.*), but, unlike *pergandei*, there is little activity at the nest during the midday hours. At such times the nests of *andrei* appear to be deserted, for the ants retreat so far into the nest passages that they cannot be seen. The morning period of foraging usually terminates between 9 and 10 o'clock. The afternoon foraging is not begun until about an hour before sunset and continues during twilight and after it has become dark. Once the light has failed, however, the ants in the column are less certain in their movements. The column ultimately breaks up into scattered groups of workers trying to find their way back to the nest. The marriage flight of *andrei* occurs during the latter part of July. Latitude seems to make little dif-

ference in the time of the marriage flight. The females of *andrei* are frequently taken into established nests after the marriage flight.

A study of material taken in the area west of Jacumba, California, has shown that the subspecies *castaneus* Wheeler and Creighton is without validity. As may be recalled, Jacumba is the type locality for *castaneus*. The writer was particularly anxious to take *castaneus* at Jacumba, for the status of this form needed clarification. The area around Jacumba was collected for almost a month, but no colonies of *castaneus* could be found there. If the types of *castaneus* actually came from Jacumba the record is exceptional. On the other hand, the insect is abundant in Cameron Valley, about 20 miles west of Jacumba.

More than a dozen colonies of *castaneus* were found in Cameron Valley, and substantial series were taken from nine of them. The character of this material was disconcerting, for it showed that unjustifiable conclusions had been drawn from the limited type series of *castaneus*. On the basis of the types, *castaneus* was said to be lighter in color and smaller in size than *andrei*. It was also stated that *castaneus* has longer antennal scapes, a more feeble impression at the epinotal suture, and a less prominent ventral tooth on the petiole. When adequate material was examined, none of these distinctions held up, with the possible exception of color. It is now clear that they were the result of comparing the smaller workers of *castaneus* with the larger ones of *andrei*. When the two forms were compared size for size, the only difference was the uniformly light color of the Cameron Valley specimens. It may be added that this light color marked the females as well as the workers of the Cameron Valley colonies.

There is no reason why color should not distinguish a subspecies, provided that it can be correlated with a distinctive geographical distribution. As far as could be determined, the light-colored form is the only one in the Cameron Valley. But it should be remembered that, while all the workers in the Cameron Valley nests are light in color, those in colonies taken elsewhere are not always dark. Indeed, the number of colonies in which all the workers are dark seems to be comparatively small. Much more often there is considerable variation of color within the nest, and not infrequently the lightest workers in such colonies are so nearly like those of *castaneus* that no distinction would

be possible without considering the whole colony. These intermediate colonies occur at random over the entire range of *andrei*, except in the Cameron Valley. But, since this valley is only about 6 miles long and not more than 3 miles wide, it represents an extremely small part of the range of *andrei*. For the range of this ant parallels the Pacific coast for almost 1000 miles and at one point extends eastward to Arizona and Nevada. Under such circumstances it is impossible to attribute much geographical significance to the Cameron Valley colonies. A more acceptable view is that their light color results from some ecological factor (possibly aridity) which is more uniform in the Cameron Valley than in other parts of the range.

The range of *andrei* is more extensive than the older records indicate. The ant is surprisingly abundant in the Siskiyou Mountains of Oregon. Ten colonies were found in the mountains 6 miles west of Jacksonville at an elevation of 1500 feet. *V. andrei* also occurs in Baja California. The writer secured two colonies in a stream bottom 10 miles north of San Vicente, at an elevation of 600 feet. Two colonies were also found at San Antonio del Mar, on the landward side of the large dunes which flank the beach. Oddly enough no colonies of *andrei* were encountered in the Sierras of Baja California, although it might be expected that the vertical range of *andrei* would rise as it passes to the south.

#### **Veromessor chamberlini** (Wheeler)

Dr. M. R. Smith writes me that he has seen specimens of *V. chamberlini* that came from the California mainland. This is gratifying but scarcely surprising. As far as ants are concerned, there is little evidence of endemism in the case of the islands off the California coast. It is to be hoped that field observations on this species can be made, for at present nothing is known of its habits.

#### **Veromessor juliana** (Emery)

As far as the writer is aware, nothing has been published on the habits of *juliana*. It was, therefore, gratifying to discover three large nests of this species at Bahia San Quintin, Baja California. These nests were constructed in light, sandy soil at the edge of the bay and placed so that they were not more than 4 or 5 feet above high-tide level. The area in which the ants

were nesting was covered by a dense mat of *Mesembryanthemum crystallinum*. Through this mat the ants had cleared crooked trails about 1 inch wide. When foraging they kept strictly to these trails. There were several entrances to each nest, and these were often concealed by a *Mesembryanthemum* plant. There was no sign of excavated soil around the nest entrances nor any special arrangement of seed husks to form a chaff pile. Several of the entrances were partially blocked with seed husks which had been abandoned at the mouth of the entrance. In general the foraging activities of *juliana* are like those of *pergandei* (q.v.). It is interesting to note, however, that *juliana* will forage on days of heavy overcast, which *pergandei* seldom does. It is not likely that *juliana* could exist on the Pacific coast of Baja California unless it could adapt itself to considerable fog.

It appears that Bahia San Quintin lies near the northern end of the range of *juliana*. There are several areas farther north on the coast of Baja California where the environment is the same as that at Bahia San Quintin. If nests of *juliana* were present in these areas, they should be easy to find because of the characteristic paths which the ants clear through the *Mesembryanthemum* beds. No additional nests were found, despite considerable search. It also appears, since the range of *andrei* extends at least as far south as San Antonio del Mar, that somewhere between that station and Bahia San Quintin, a distance of about 50 miles, the southern end of the range of *andrei* may meet the northern end of the range of *juliana*.

#### *Veromessor lariversi* M. R. Smith

This species has been recently described from specimens secured by Dr. LaRivers near Pyramid Lake, Nevada. The writer has taken this insect near Lone Pine, California (elevation 4300 feet), Wagner, Nevada (elevation 4000 feet), and Goldfields, Nevada (elevation 5800 feet). Specimens from California were sent to Dr. M. R. Smith for comparison with the types of *lariversi*. I am glad to take this opportunity to thank Dr. Smith, who not only made the comparison, as requested, but generously sent me paratypes of *lariversi* as well.

Observations on *V. lariversi* were made in early May, in mid-July and in mid-October. Most of what follows is based on nests found 4 miles west of Lone Pine, California. This area is a part

of the plain that slopes upward from the foothills west of Lone Pine to the base of Mt. Whitney. During two visits to this station, six nests of *lariversi* were studied. All of these nests were built in fine, hard-packed gravel. Beneath this hard layer was a much looser layer of sandy gravel, but very few of the nest passages reached this lower layer. In May each nest was surmounted by a cluster of small, circular, steep-walled craters. Each crater was not more than 3 inches in diameter and each had a single entrance at the bottom. By July many of the craters had disintegrated and the soil that formed them had become a ragged pile above the nest. But in each case one or two craters had been kept in repair. The nest passages often extended as much as 2 feet beyond the area covered by the craters. The passages were remarkably shallow. Most of them were no more than 3 inches below the surface. At intervals along these passages elongate seed chambers occurred. The nests taken in Nevada did not differ significantly from those described above.

Little data on the foraging activity of *lariversi* could be obtained, for the ants kept strictly to their nests during the entire period when they were under observation. In May the nests were observed in the late afternoon and about nine o'clock in the morning. In July the observations were more extensive. They were made at suitable intervals from before sunrise (6:30 A.M.) until after dark (9:00 P.M.). The observations were discontinued after nine o'clock, for by that time it was clear that the ants were not going to forage. They were aestivating, and it was apparent, from the neglected condition of the craters above the nests, that this period of aestivation had been in progress for some time by the middle of July. While *V. andrei* and *pergandei* will sometimes suppress the afternoon foraging period during exceptionally hot weather, both species definitely do not aestivate. It seems entirely likely that this is also true of *juliana* and *stoddardi*, although the writer has seen too little of the last two species to be certain. But while the aestivation of *lariversi* may not be unique, at least this habit sharply separates *lariversi* from *pergandei*, for the latter species responds to high temperature in a totally different fashion. Since *lariversi* is more closely related to *pergandei*, on the basis of structure, than any other species in the genus, it is interesting that the two should have so little in common as far as habits are concerned. When additional studies can be made on *lariversi* in the early spring, the writer believes that it will prove to be a nocturnal forager.

### **Veromessor lobognathus** (Andrews)

This species remains as enigmatical as ever. Dr. Robert Gregg, who is in process of completing a very thorough survey of the ants of Colorado, informs me that he has not been able to discover additional specimens of *lobognathus*. The ant is either extraordinarily rare, or, as seems more likely, the locality labels on the four types may have been incorrect.

### **Veromessor pergandei** (Mayr)

In recent months the writer has been able to study the habits of this interesting ant at 57 stations. As will be subsequently shown, these stations cover most of the range of *V. pergandei*. The observations extended from early March to the middle of November. During the course of these studies certain experiments were made to determine the basis for some of the habits of *pergandei*. It will simplify matters to preface these experiments with an account of the behavior of *pergandei* at the time of its maximum activity.

Since much of what follows involves a clear idea of the nests of this species, it may be said that in a well-established nest of *V. pergandei* there is usually a single entrance which lies at the bottom of a low fan or crater of excavated soil. This crater is seldom more than 15 inches in diameter and ordinarily not more than 12 inches in diameter. At one edge of the crater is the chaff pile, a mass of discarded seed husks which sometimes forms a crescent at the periphery of the crater but more often forms a low and irregular band beyond it.

In the late spring and early summer *pergandei* begins its daily activity soon after dawn. Prior to sunrise the ants emerge from the nest entrance and spread slowly over the crater. At this time their movements are apt to be exceedingly slow because of the low temperature. After sunrise their movements quicken, and the spread of the ants away from the nest entrance is accelerated. Thirty to 45 minutes after the sunlight first falls on the nest the ants push out a foraging column which usually proceeds, without hesitation, to the seed supply. The area in which the seeds are gathered is often 75 yards or more from the nest. In such cases it may be 20 minutes before the first foragers reach the seed supply. During this period all ants in the column are outward bound. Presently, however, seed-laden workers, in-

ward bound, appear in the column, and soon they are bringing back quantities of seeds to the nest. This morning period of foraging ordinarily lasts from two to three hours.

About mid-morning there comes a time when the workers cease to leave the nest. This cessation is surprisingly sudden. At one minute workers will be leaving the nest two and three abreast. Five minutes later there will be only an occasional worker, outward bound in the column. This soon reduces the column to inbound workers only and shortly thereafter the column dwindles and disappears. Then follows what, for want of a better name, may be called nest work. The ants leave the nest entrance in short sorties which do not take them off the crater or beyond the chaff pile. Each ant carries a bit of gravel or a seed husk. The gravel is deposited on the crater, the seed husks on the chaff pile. This nest work may continue without appreciable change until the second daily foraging column takes off in the late afternoon. Usually, however, the number of ants engaged in nest work dwindles markedly towards noon. On very hot days the ants may terminate all visible activity and retire into the nest during the early afternoon hours. On most days this does not happen but, during the early afternoon, the nest work is often restricted to exceedingly brief sorties by very few ants. These ants barely get out of the nest entrance, hence this limited nest work is apt to be overlooked.

At some time in the late afternoon the volume of nest work begins to increase. This increase is also an abrupt one. In the course of a few minutes several dozen workers appear on the surface of the nest. With this increase in the number of workers comes an increase in the length of their sorties. As a result the ants begin to spread outward over the crater. At this time most of these workers are engaged in carrying out gravel or seed husks. But this nest work soon diminishes in a rush of workers who emerge onto the surface of the nest without carrying anything in their jaws. These ants push outward beyond the crater, and most of them take the direction in which the seed supply lies. More and more ants follow these leaders, and soon the afternoon foraging column is outward bound. It is seldom more than five minutes from the cessation of nest work to the formation of the foraging column. As a rule the afternoon foraging continues until early dusk (three hours, more or less), at which time the foragers straggle home for another period of nest work. This



nocturnal nest work may continue into the early hours of the following morning.

It is easy to suppose that this rhythmic behavior is controlled by the daily temperature cycle. For the morning period of foraging might be terminated by the rising temperature, which would first restrict the ants to the nest area and later force them into the nest passages. The reverse process could be expected as the temperature dropped during the afternoon. The ants should first show a limited activity near the nest and later begin to forage when the ground cooled to the proper surface temperature. It was, therefore, a surprise when attempts to measure these critical controlling temperatures showed that they do not exist.

The method used in the attempt to determine these temperatures was a rather crude one. The only thermometers with a proper temperature range which could be obtained were small, coil-spring type of instruments, enclosed in a metal case and provided with a rubber suction disc by which they are supposed to be attached. This disc was removed and the opening thus left was covered with masking tape to keep sand and gravel out of the case. The thermometer was then placed directly on the surface of the ground. In such a position the coiled spring was approximately 5 mm. above the surface. Dr. Charles Lowe, of the University of Arizona, who has read this article and generously given me the benefit of his experience with temperature determinations of desert animals, is of the opinion that the figures presented below as "surface temperatures" are more probably air temperatures 5 mm. above the surface. While this should make no difference in the explanation of the behavior of *pergandei*, it seems well to note that a more exact measurement of the true surface temperature may give figures somewhat higher than those presented in this article.

Daily observations were made on three nests of *pergandei* near Jacumba, California, from June 17 through June 29. During that time the morning period of foraging was observed to terminate at surface temperatures which varied from 88° F. to 112° F. A comparable latitude for temperature marked the start of the afternoon foraging. The column would form at temperatures which varied from 90° F. to 110° F. Since the identical response was forthcoming at temperatures which differed by as much as 30° F., it seemed highly improbable

that such responses could be the result of a temperature control.

Yet out of this mass of irrelevant temperature data certain significant temperature responses emerged. The speed of the ants is clearly determined by temperature. It increases with an increase in temperature over a range from 50° F. to 90° F. This range probably begins at 45° F., but below 50° F. the speed of the ants is so slow and their motion so lacking in direction that the writer could make no satisfactory measurement of it. At 50° F. the ants move at a speed of about 6 inches a minute. At 90° F. the speed has increased to 8 feet per minute. This appears to be the best speed of which *pergandei* is capable, for, while they will forage at surface temperatures up to 115° F., no further increase in speed was noticeable at temperatures higher than 90° F.

It also became apparent that a surface temperature of 125° F. restricts the ants to the nest. They never voluntarily expose themselves to such a temperature, and it was easy to find the reason for this behavior. In most cases workers placed on a surface where the temperature is 125° F., or higher, will scramble back to the shelter of the nest, or to some shaded area, within a few seconds after exposure. In such cases they are no worse for the experience. But if a worker of *pergandei* is picked up by one leg with a fine pair of tweezers, it can be held, uninjured but fully exposed, at one point on the heated surface. Under such circumstances the worker will die in a surprisingly short time. Minor workers will be dead in 20 seconds or less. Medias usually survive from 30 to 40 seconds. Majors are more resistant, but they succumb in a minute to a minute and a quarter. Hence, there is the best possible reason why the workers of *pergandei* avoid exposure to a surface temperature of 125° F. Such a temperature kills the ants in a short time if they are unable to get out of it. It may be added that this result occasionally occurs under natural conditions. Minor workers sometimes get too far away from the nest entrance, or a protective bit of shade, and die in consequence. Medias and majors are rarely killed in this way, probably because of their greater resistance, which gives them a longer time to get back to shelter. But, regardless of the size of the worker, it should be clear that if the ants waited until the surface reached a temperature of 125° F. to begin the avoidance reaction, they would run a serious risk of being killed. This risk is reduced to a minimum

because the avoidance reaction begins at a surface temperature of 120° F. At this temperature the ants are not restricted to the nest passages, but they confine themselves to the briefest of sorties from them. On such trips they rarely get more than an inch or two from the nest entrance and, unless they can take advantage of some bit of shade, they return to it with understandable alacrity. This is the behavior which occurs when limited nest work is done in the early afternoon hours. Thus this response, and the cessation of all external activity, are directly controlled by temperature. But this is quite a different matter from the foraging cycle as a whole.

After it became clear that temperature was not responsible for stopping the morning foraging or for starting this activity in the afternoon, the writer began to examine the possibility that light intensity might control the foraging rhythm. The daily cycle of light intensity has the requisite characteristics. There is a morning increase and an afternoon decrease comparable to that of the daily temperature cycle. After a few experiments with a light meter placed near the nest entrances, it was clear that it would be extraordinarily difficult to obtain significant readings for the critical light intensity, assuming that one existed. For the ants made daily alterations in the nest entrance and the nest area which defeated any attempt to secure uniform readings. One example may be cited to show the nature of the difficulties involved. At the time of these observations many of the seeds garnered by the ants possessed a terminal tuft of silky fibers rather like a tiny milk-weed seed. The ants would strip these tufts of fibers from the seeds, and they usually placed them on the chaff pile. But one colony occasionally left the tufts in the nest entrance itself, where they formed a loose, stopper-like mass which reflected so much light that the meter readings for that nest were temporarily doubled.

Nevertheless, it seemed possible that by shading the nests some effect should be observable if light intensity controlled the foraging rhythm of the ants. It was found that a card table made an excellent mask. By folding down two legs it could be set at a slant above the nest, where it produced a rectangle of shade 30 inches long and 20 inches wide. The shaded area was open on one side (north) to easy observation. This shading produced not only a decreased light intensity under the mask but a decreased surface temperature as well. As a rule

the surface temperature in the shade of the mask was at least  $30^{\circ}$  lower than that of the fully illuminated ground at its edge. But, as is shown below, this could be turned to advantage, for by removing the mask the light intensity could be immediately increased to full force, while the surface temperature rose much more slowly under such circumstances.

Since the cessation of the morning foraging and the resumption of the afternoon foraging are abrupt events, it seemed advantageous to try the effect of shading at such times. It was soon clear that shading the nest prior to the cessation of the morning foraging produced remarkably little effect on the behavior of the foragers. About the only observable difference was the confused response of some of the foragers when they entered the shaded area. A few of them would turn back into the sunlight but not many did so, and the morning foraging was not prolonged to any appreciable degree by shading the nest. This result might have been expected, for the critical light intensity would affect all the workers in the column and not merely those in the vicinity of the nest. Moreover, the morning foraging is always followed by a period of active nest work. As is shown below, this nest work was augmented when the nest was shaded.

If the mask was placed over the nest in the early afternoon some much more spectacular results ensued. Nest work immediately increased in volume. Instead of two or three workers hastily dodging in and out of the nest entrance, there were a couple of dozen workers on the surface at once, all busily engaged in bringing gravel and seed husks out of the nest. It was noticeable, however, that despite the large shaded area around the nest, very few of the workers left the crater. There were never more than three or four ants exploring the shaded area beyond the crater, and these explorers moved in a slow and desultory fashion. After an hour or more of nest work there was a sudden egress of several dozen ants onto the crater. These ants emerged from the nest entrance with empty jaws. They were, therefore, no longer engaged in nest work. These empty-jawed workers did not confine themselves to the crater and chaff pile but spread outward into the shaded area beyond the nest. In a few minutes the shaded area was crowded with hundreds of ants. These ants were very active, and they attempted to form a foraging column on the side of the shaded

area nearest the food supply. The ants at the head of this prospective column pushed out into the sunlight beyond the shade, but, as the surface temperature of the fully illuminated soil was above 120° F., they immediately returned to the shaded area. At this time there was extremely slight activity or no visible activity in the control nests. These unshaded nests did not start their foraging columns for an hour or more.

Since the ants were obviously trying to form a foraging column at the edge of the shaded area, there seemed to be no reason why they might not complete it if a "shade bridge" were furnished from the nest to the seed supply. This, however, they refused to do. When a strip of shade was provided from the nest to the seed supply the ants never went more than a foot or two on it. They then returned to the nest. Subsequent observations with patches of shade thrown onto a foraging column indicate that the ants need direct sunlight to orient themselves in the column. A patch of shade no more than 2 feet long causes many of the foragers to break out of the column and wander aimlessly about. It is interesting to note that this same lack of direction on the part of the foragers is usually encountered at the end of the afternoon period of foraging. As already noted this afternoon foraging usually extends past sundown and the workers straggle home at the approach of dusk with much less precision than they show when the column is in direct sunlight. If the ants ordinarily depend upon direct sunlight for orientation in the columns, this would also explain why the foraging columns do not continue after dark.

Having failed to produce a full-fledged foraging column under artificial conditions, the writer turned his attention to the abortive column which formed at the edge of the shade when a nest was masked. The surface temperature of the fully illuminated soil beyond the shadow of the mask ranged from 123° F. to 126° F. The surface temperature in the shade of the mask ranged from 87° F. to 94° F. If the mask was abruptly removed, all the ants in the previously shaded area rapidly returned to the nest. This response was surprisingly spectacular. As there were several hundred ants all trying to get into the nest at once, they formed an almost solid mass of jet-black, shining bodies at the nest entrance. This return to the nest, after the removal of the mask, never took more than five minutes and was often accomplished by the end of three minutes. During this period the

surface temperature of the previously shaded area never rose above 99° F. In order to make sure that there was no significant lag in the thermometers, they were tested and found capable of responding at a rate of 10° of change per minute. The greatest recorded rise in surface temperature after the removal of the mask was 11° in five minutes. It is clear, therefore, that the recorded surface temperature of 99° F. was due to the slow rise in the surface temperature and not to a lag in the thermometers. But the ants hurriedly left an area where the surface temperature was at least 20° below the point at which the avoidance response to heat begins. Since their rapid return to the nest is clearly not a response to temperature, it is reasonable to believe that this behavior resulted from the sudden increase in light intensity which followed the removal of the mask. Thus, if the light intensity is sufficiently high, it produces an avoidance reaction closely comparable to that which is caused by a surface temperature of 120° F. or more. But if this reaction to light intensity can be experimentally elicited, it must also occur under natural conditions, when the increasing light intensity during the morning hours reaches what may be called the avoidance level. Hence, as long as the surface temperature is below 120° F., the termination of the morning period of foraging is a response to light intensity and not to temperature. Conversely, the beginning of the afternoon foraging, at surface temperatures less than 120° F., is an indication that the light intensity has dropped below the avoidance level, again a response to light intensity and not to temperature.

Since shading the nests in the early afternoon had accelerated the time of foraging by as much as an hour, it seemed probable that an even greater acceleration might be expected if a nest were shaded as soon as the morning foraging had ceased. In the afternoon the abortive foraging column formed at the edge of the shade about an hour after the mask had been put in place. The writer expected a comparable situation to ensue as a result of late morning shading. This, however, was not the case. When the mask was put in place at the end of the morning period of foraging there was an increase in the volume of nest work which continued without significant diminution until well past noon. It then dwindled, but no column formed until 3:00 P.M. There was thus about the same period of nest work (four to five hours) whether the nest was shaded

or not. But, when the nest was shaded, the surface temperature and the light intensity in the shadow of the mask were both favorable to the formation of a foraging column. Since no column formed for a period of at least three hours, it would appear that the seed supply brought into the nest during the morning period of foraging is itself a factor which affects the foraging rhythm. These seeds have to be hulled and stored and, until this processing is completed, no new foraging column forms even though the external conditions may be favorable for it. The nest work done by the ants is the visible manifestation of this seed processing. Gravel is brought to the surface as the storage chambers are excavated. Seed husks are placed on the chaff pile as the seeds are stripped out. When no more seeds remain to be processed the ants appear on the surface of the nest with empty jaws, and it is not until then that a foraging column begins to form.

To summarize the above data, it may be stated that the foraging columns of *pergandei* form only when the surface temperature is below 120° F., when the light intensity is below its midday level and when the supply of seeds brought in from the last foraging period has been completely processed. There must also be a certain basic minimum of light, for this ant will not forage in darkness. A favorable combination of these controlling factors will ordinarily occur only in the early morning and the late afternoon hours. Conversely, the least favorable period on three counts would be the midday hours. Hence *pergandei* is held in, or close to, the nest during the dangerously hot hours at the middle of the day by a triple system of controls, any one of which will prevent the ants from exposing themselves to lethal conditions.

The success of this system of controls is obvious from the distribution of *pergandei*. The species shows its maximum abundance in the hottest and most arid regions on the North American continent. *V. pergandei* flourishes throughout the region around the head of the Gulf of California. In western Sonora it is frequently encountered as far south as Hermosillo. South of that station the incidence decreases, and the southern limit of the range appears to lie a little north of the latitude of Guaymas. In November of 1952 the writer observed many nests of *pergandei* in the area between Guaymas and Imuris. This was exceptionally easy to do, since at that time every

nest was surmounted by a large chaff pile of pale, yellow seed husks. Because of this conspicuous marker the nests could be noted many yards away. North of Hermosillo there were places where a dozen nests would be in view at once. Yet between Guaymas and Cocorit not a single nest could be found, despite much searching.

On the western side of the Gulf of California *pergandei* is abundant as far south as San Felipe. It has been taken at Santa Borja (C. D. Haines) which is approximately on the same latitude as Hermosillo. Hence, it seems probable that the range of *pergandei* in Baja California is similar to its range in Sonora. The writer believes that the northern end of the range of *pergandei* lies at or near the northern end of Death Valley. There are many nests present at Mesquite Springs, near the upper end of Death Valley and also at Beatty, Nevada, some 30 miles to the east. North of these stations the country rises steadily and the incidence of *pergandei* decreases sharply. The eastern limit of the range of *pergandei* is very irregular. The insect avoids the highlands of northwestern Arizona and also those which lie along the southern border east of the Baboquivari Mountains. The maximum eastward extension lies just north of these mountains and brings *pergandei* into the Tucson area. Whether *pergandei* should be regarded as occurring on the Pacific coastal strip or not is problematical. It certainly does not occur at sea level. But in southern California and in Baja California an occasional nest is encountered on the western slope of the mountains comparatively close to the coast. The incidence of such nests is exceedingly low in contrast to the abundant population which occurs east of the Sierras. All of the region outlined above is marked by intense summer heat. It is safe to say that nowhere in its range is *pergandei* free from lethal midday temperatures during the summer months. Yet, because of its beautifully adjusted responses, *pergandei* thrives in such forbidding areas. It even contrives to live at Bad Water in Death Valley. This station, 280 feet below sea level, is said to be the lowest point in the Western Hemisphere. In summer it is, undoubtedly, one of the hottest places on earth.

Before leaving *pergandei* it seems well to note that its marriage flight occurs in late March and early April. The nest-founding female of *pergandei* will often begin the nest beneath a covering stone. This behavior is noteworthy, since covering stones are



usually avoided by most xerophilous ants, presumably because they conduct too much heat into the nest.

### **Veromessor stoddardi** (Emery)

The writer has encountered only four nests of *stoddardi*. Two colonies were found at an elevation of 200 feet on a hill 1 mile east of San Ysidro, California. Another nest was taken in hills 4 miles south of La Mision, Baja California (elevation 700 feet). The fourth colony was secured on an upland plain 19 miles north of Ensenada, Baja California (elevation 1100 feet). The structure of these nests was remarkably uniform. Each nest was built in iron-hard clay soil. Each had two or three nest openings. Each nest opening consisted of an irregular aperture which was usually situated at the bottom of a shallow, saucer-like depression. In no case was there any sign of excavated soil around the nest. During May and early June the seed hulls are left in the depressions around the nest entrances. In July, when the ants appear to carry on more active harvesting, the seed hulls may be built into a flattened ring around the nest. No foraging column of *stoddardi* was encountered by the writer. Nevertheless certain deductions can be made as to the seed-gathering activities of this ant. From the quantities of seed hulls around the nest it is clear that *stoddardi* is an active harvester. It is also clear that *stoddardi* does not begin to forage when *andrei* does. Both species were simultaneously observed at the San Ysidro station. No activity of any sort could be detected in the nests of *stoddardi* at a time (about one hour before sunset) when *andrei* was actively foraging. This suggests that *stoddardi* may be crepuscular or nocturnal in its foraging. The former possibility seems more likely for, when these ants are exposed to light, they do not show the energetic avoidance response which marks most nocturnal species. When not foraging, the workers of *stoddardi* retire well into the nest passages. Their nests, like those of *andrei*, appear to be deserted at such times. The marriage flight of *stoddardi* occurs in early July. The females, which are rather strikingly marked with yellow, are comparatively small. It is worth noting that the worker caste of *stoddardi* is fully as polymorphic as that of *pergandei*. A contrary impression is apt to result from much of the material at present in American collections. All of this material that the writer has examined has lacked the smaller media and minor workers.

During the course of these studies two visits were made to San Jacinto, California, with the hope of securing topotypes of *stoddardi*. The second trip was undertaken after colonies of *stoddardi* had been secured elsewhere, hence the writer knew exactly what to look for. Despite this, no colonies of *stoddardi* could be found at San Jacinto, nor is this surprising. Extensive irrigation has greatly altered the character of the region around San Jacinto, and it seems probable that *stoddardi* may no longer exist in its type locality.