AN ECOLOGICAL STUDY OF THE ANTS OF THE SOUTHERN DESERT SHRUB REGION OF THE UNITED STATES[1]

ARTHUR C. COLE, JR.,
Box 815, E. Lansing, Michigan

The study of desert ants in the United States, represents collection of material during two years by the writer in the principal desert states (Nevada, Arizona, California, and New Mexico). Not only were specimens collected but also detailed notes were made, covering such important points as the habits and habitats of the species. When sufficient time was accessible a study of the floral environment was undertaken in so far as the ants of the particular biota were concerned. So sure was and is the writer that certain species of ants occupy type habitats, guided by a set of rather prominent limiting factors, that he was particularly interested in determining them. Because a great deal more study is necessary before such a distinct classification can be made the writer has, in the present paper, only touched upon these type habitats.

To date no publication has appeared covering the desert ants of the United States as a group. The writer has attempted to fill this gap to a rather limited extent not only by listing the various species but also associating them with their habitats. This paper is intended to present the fundamental factors governing the existence of desert ants, and to relate the species as closely as possible to various habitats into which they migrate and in which they live and die.

The author appreciates the difficulties involved in attempting to discuss so vast a subject as the ants of a section of the United States. Furthermore, he realizes that such a study is always in a preliminary stage, in so far as the inability to thoroughly complete it is concerned. The writer wishes to present only the results of his own research on the group without attempting to offer more than a synoptic treatment of the species. To all those who have aided in making this study possible I am gratefully indebted.

[1]Part of a dissertation submitted as partial fulfillment of the degree of Doctor of Philosophy at Ohio State University, March, 1933.

PHYSICAL FACTORS AFFECTING SOUTHERN DESERT SHRUB ANTS

Mound Temperatures.—The temperature within an ant mound is of vital importance for the incubation and survival of the young and the necessary activity of the adults (1). The brood is raised and lowered within the mound with decided fluctuations of temperature. At night the brood of the majority of desert species is placed close to the surface of the mound, while during warmer periods it is carried to the lower recesses, where the temperature is decidedly lower. In other words, the movement of brood by the worker ants appears to be almost entirely a direct response to temperature fluctuations.

The writer has shown (11) that ant mounds tend to absorb more heat than do like areas of bare ground because of the greater intensity of the sun's rays on the mound faces. Thus the east-facing slope receives the morning sun and the west-facing one that of the afternoon. Temperatures as high as 180° F. are not uncommon on the faces of the mounds of true desert ants during the warmest part of the summer day. From the top of the nest downward, the writer has noted a gradual decrease in temperature to the base of the last chamber, fluctuating greatly, of course, daily and seasonally.

Temperature as Affecting Activities of the Ants.—During the hottest part of the summer day, usually from about eleven A. M. until 2 P. M., the activities of most species of desert ants are temporarily suspended and the insects undergo a short period of aestivation. During this time it is quite uncommon to see ants on or around their nests, and the formicaries appear to be uninhabited. If one digs into a nest, however, he finds that at a considerable depth below the surface (several inches to one or two feet or more) the ants are massed together in chambers and are in an almost inactive condition. The exposed ants usually do not attempt to pursue the intruder or even to venture forth from their nest, but instead, often dig deeper into the ground. Ants in this condition which were placed on the ground surface near the nest by the writer, did not appear to suffer from the intense heat as much as would be expected. They merely scurried to their nest as fast as they were able to travel.

The activities of desert ants, aside from those within the nest, are usually confined to the early morning and late evening hours. Many species may be commonly observed obtaining food at daylight and after dusk. *Dorymyrmex pyramicus bicolor* Whlr. was the only ant observed which did not show a definite mid-day period of aestivation, although a definite decline in activity was noticeable.

Temperature as Affecting Seasonal Successions of Ants.—Seasonal successions of desert ants are not of uncommon occurrence. Temperature, in combinations with moisture and other factors to a limited extent, seems to be the chief factor which causes and controls these successions. Many species of desert ants which are established in one area during a certain season may be forced to migrate to another or other areas when the temperature and moisture conditions reach a certain level. For example, during the spring of the year, many ants

migrate from the south-facing slopes to the desert plains; during the summer, from the desert plains to the north-facing slopes; during autumn, from the north-facing slopes to the desert plains, and at the approach of winter, from the plains to the south-facing slopes. Often, however, there are only two migrations—one from the slopes to the desert plains during cooler weather and another from the plains to the slopes with the approach of warmer weather.

Wind as a Factor in Destroying Ant Mounds.—Many nests of desert ants are destroyed partially or completely by the wind. The continuous westerly winds in southern Arizona keep many ant mounds in an unfinished condition, and sometimes "hollow out" the mounds. This also has been shown to be the case with many mounds of the Occident Ant (*Pogonomyrmex occidentalis* Cresson) in southern Idaho (8). Sand and debris carried by the wind exert all the more force upon mounds unprotected by natural barriers, such as rocks and vegetation.

Wind as a Stripper and Destroyer of Vegetation.—Wind indirectly affects desert ants by stripping the leaves and fruits from plants, or by completely denuding an area of its natural vegetation. The ants in such an area suffer in two ways: (1) because there is, in many cases, a limitation of the food supply; and (2) because the denuded area leaves the ant nests open to destruction by the sweep of wind over the bare area, unless, of course, some more stable barrier is present. Under conditions of wind pressure and scanty food supply, many colonies migrate to more suitable surroundings. It is an extremely uncommon sight to see ant nests in a totally bare area in the desert region.

Wind as a Factor in Directing the Establishment of New Colonies.—Strong westerly and northwesterly desert winds tend to partially limit the direction and concentration of new ant colonies. From the center of established concentration of a single species the mated females are transported in easterly and southeasterly directions. The establishment of new colonies is apparently directly proportional to the distance from the center; that is, the most new colonies are established close to, and in easterly or southeasterly directions from the original center of concentration.

Wind as a Transporter of Food.—While wind of a strong and continuous nature is usually a detriment to the existence of the desert-inhabiting ant, it is, however, of some immediate benefit. Insects upon which the ants feed, as well as various seeds, are carried and scattered widely. If one pauses beside a colony while a brisk wind is blowing he witnesses on all side an ever-changing array of seeds, insects, and spiders. The writer has observed many species of ants gathering food during such a time. Even the harvesting ants are without usual labor of cutting seeds from their bracts and transporting them great distances to their nests.

Wind as a Desiccator of Soil.—Wind indirectly affects desert ants by aiding in the desiccation of the soil through excessive evaporation. Rarely is this process advantageous to the ants, except after torrential rains which leave the ground in a more or less saturated condition. During most of the time the ants are forced to carry water with which

to moisten the nest chambers and protect the delicate brood from desiccation. Ants have been known to travel long distances for water, but most species obtain moisture from dew, and as the writer is inclined to believe, from food through their own metabolic processes.

Precipitation.—Although desert ants are accustomed to prolonged periods of drought, they are not, however, greatly affected by periodical showers. Even nests of *Atta versicolor* Pergande, which are usually in sandy washes of the desert region, are but partially destroyed by the torrential rivers which swirl through the "draws." When the water subsides, the ants reconstruct their mounds and the number of workers which appear for this function would seem to indicate that the colonies suffer no great mortality.

During periods of excessive rainfall or flooding desert ants retreat to their lower nest chambers and thus avoid possible destruction. The brood is lowered by the workers, and, in the case of harvesting species, seed is retrieved from damage by the water.

The writer does not wish to indicate by the foregoing paragraphs, however, that all ants escape destruction during torrential downpours. Such is certainly not the case. Workers leaving or returning to their formicaries are very often carried away in the swirl of water and many of them eventually drown. Those which do not drown usually die for they are social insects and cannot live for long periods without access to their colonies.

Evaporation.—Evaporation either directly or indirectly affects desert ants by limiting the available soil moisture and by almost completely desiccating the surface layer. As has been already pointed out, a certain amount of moisture is necessary for normal maturation of the brood and if this is not present in the soil constituting or surrounding the nests, the ants are forced to search elsewhere for it. On the other hand, evaporation is directly beneficial when it dries out the excessive moisture which would otherwise be in too large amounts for the ants to utilize.

Light.—Light affects desert ants by determining, in conjunction with temperature, the length of their daily periods of activity. On cloudy days, in spite of the slight reduction in average temperatures, many desert ants work continuously from daylight to dusk or after, while on bright days, as has been explained elsewhere, they undergo short periods of aestivation. The writer has repeatedly observed *Myrmecocystus hortideorum* McCook terminate its active food-gathering period at the onset of darkness although the atmospheric temperature remained almost as high as that of the light period just preceding.

Inasmuch as most species of ants lead a partially subterranean existence, light in any quantity is barred from the nest galleries and chambers. In spite of this some ants are more susceptible to light intensities than are others. For this reason we may classify desert ants into: (1) The sun-loving species; (2) the shade-loving species; and (3) the intermediate types, or those which are accustomed to live in either shady or sunny habitats. The sun-loving species are usually found in unshaded areas where light-protecting rocks and vegetation do not abound, while the shade-loving ones colonize shady places.

Cold Air Drainage as Affecting Desert Ants.—Cold air draining down a mountain gulch or ravine from snow fields above plays a decided and important part in limiting and directing the populations of desert ants on the plains below. It has been suggested to the writer by Dr. E. N. Transeau of Ohio State University that such a phenomenon may occur among ants in much the same manner as has been proved in the case of desert vegetation (22). The resulting limitation of the plants into two decided zones—that which supports the influx of cold air and that which is typical of the desert plains proper, has been explained by the process of cold air drainage alone. The writer is very much inclined to believe that the soil type at the base of the gulch has as much or more to do with the resulting organization of vegetation as the draining mountain air. The soil at the base is usually of a much coarser texture than that of the surrounding area, as must necessarily be the case from rock material washed or otherwise directed down the gulch. Furthermore, the moisture content of the soil at the base is noticeably higher than that of the outlying area.

The writer noted two abundant ant species in the area, *Pheidole desertorum* Whlr., which was dominant at the immediate base of the gulch, and *Pogonomyrmex barbatus rugosus* Emery, more common in the surrounding dry area. The former nearly always inhabits cooler and more moist areas than the latter.

It appears that the limitation of species is caused by a combination of factors and not by the action of any single one. Inasmuch as the limiting factors can not be separated adequately, it seems unwise to attribute such a limitation to any particular one of them or even to designate a dominant.

Desert Soils as Affecting Ants.—The type of desert soil has much to do in limiting the distribution of the many species of ants. While some ants, such as *Myrmecocystus melliger semirufus* Emery, live in all parts of the desert region irrespective of the soil type, most, however, demand a soil of a rather definite texture. Species which inhabit areas of sandy soil are not found generally in rocky or pebbly habitats.

Most species were found in areas of fine or coarse sand. Because the "playa" rarely supports vegetation, the number of species populating it is proportionately very low.

Desert Ants Related to the Topographical Divisions of Deserts.—The desert, from a strictly topographical standpoint, may be arbitrarily divided into three distinct units; (1) the desert plains, (2) the sandy or pebbly hillslopes and, (3) the dry washes and river bottoms.

By far the greater number of species inhabit the sandy-desert plains and the ants in such habitats are chiefly the exclusive and the characteristic ones, typical of the desert. As explained elsewhere in this paper, definite migrations occur at certain seasons of the year. Therefore, it is impossible to assign a definite habitat to a species on either an annual or a perennial basis.

THE ROLE PLAYED BY VEGETATION IN THE LIFE OF THE SOUTHERN DESERT SHRUB ANT FAUNA

The divers environmental extremes to which desert ants are at all times subjected limit their distribution into regions with more constant conditions. Long association of the species with certain variables of moisture and temperature, vegetation and food, permanently confines them to distinct and well-marked areas. Some species entirely or partially dependent upon the dominant or total vegetation are bounded only by regions in which these plants are unavailable. Thus a species, though it may be correctly termed a characteristic or an exclusive one, need not be present throughout the entire desert region.

Ants, like plants, arrange themselves in rather definite communities. Thus, if we observe a certain set of factors acting upon one species of ant in a given habitat, we can be almost certain that other species will be associated with it. Very likely, the same set of factors acting upon the one species will not be identical in the case of the others. For example, while the temperature and moisture requirements for three species of ants may be very nearly the same, the food requirements, on the other hand, may be uncorrelated. One species may feed upon seeds of plants, another upon insects, and yet another upon honey-dew. Thus it is that those ants which are directly dependent upon the existing vegetation are found in an area where the latter persists.

As we have a definite zonal arrangement of plants so may we also have a zonation of ants, the existence of colonies, in this case, being either indirectly or directly dependent upon certain degrees or fluctuations of temperature and soil moisture, or, in many cases, upon the dominant vegetation type which is itself chiefly dependent upon and a product of specific environmental conditions. While the ant species of one zone may not be exclusive to it, they are, however, rather characteristic, or if not, have such a divers number of food habits that they may extend their range into several or many vegetational zones.

The majority of ants are so dependent upon plants, or the insects and shade which they offer, that a careful study of them cannot possibly omit their plant associates. Should the entirety of the vegetation of a given area be destroyed, the number of surviving colonies of ants would be reduced to a minimum, this minimum being entirely dependent upon the life habits of the sum total of ants in the entire area.

SOME CHARACTERISTICS OF SOUTHERN DESERT SHRUB ANTS

Ants of the Southern Desert Shrub region may be arbitrarily divided into the exclusive, the characteristic, and the incidental species. The exclusive species are those whose distributions are confined to the Southern Desert Shrub region. These represent the most abundant desert ants and such forms are dependent upon the desert habitat for their continued existence. The characteristic species, on the other hand, are those which are most common to the Southern Desert Shrub but which may also extend their ranges outside of the true desert.

Familiar examples of these are *Myrmecocystus semirufus* Emery and *Dorymyrmex bicolor* Whlr. The incidental species are those which have been able to enter the desert domain in very limited numbers and survive. These latter forms are characteristic of some other type of habitat. An example of this type is *Myrmecocystus horti-deorum* McCook.

It is a significant fact that many of the true desert ants are harvesters (Pogonomyrmex, Novomessor, Ischnomyrmex, and Pheidole). Desert ants of the genera Camponotus and Myrmecocystus store water in the form of plant juices in specialized workers. Many ants adapt themselves to the desert seasons by becoming predators. This is true of some of the Myrmecocysti. Other species live upon fungi which they cultivate in their nests. Such species are greatly successful in deserts for they are not dependent upon the scant food supply. The Attine ants are of this type.

Many desert ants are supplied with specialized hairs, known as macrochaetae, on the clypeal, manibular, mental, or gular surfaces of the head (33). These hairs are characteristic of species in the genera Pogonomyrmex, Dorymyrmex, Novomessor, and Ischnomyrmex (33). The macrochaetae are probably used for the purpose of carrying water to the nests (33). Ants of desert regions usually secure water from dew and seeds. The writer believes that metabolic water is very likely produced by some of the desert species, especially among predacious forms which live in very arid sections.

The colors of desert ants are perhaps in some way the results of environmental conditions under which the ants live. The majority of desert ants are colored reddish grey, sandy, buff, or black. Many species tend to resemble the ground upon which they live, and so there is a preponderance of sand-colored forms.

AN ANNOTATED LIST OF THE ANTS INHABITING THE SOUTHERN DESERT SHRUB REGION, IRRESPECTIVE OF DESERT MOUNTAIN HABITATS

1. **Odontomachus haematodes desertorum** Whlr.—The writer found individuals of this variety foraging in the desert near Phoenix, Arizona, at 8:30 P. M. Only a few were discovered and it was impossible to trace them to their formicary. Apparently most of the foraging of this species is nocturnal. Wheeler (41) reports the ant from a dry arroyo near Tucson, Arizona, but was unable to locate the nest.

2 **Eciton (Acamatus) harrisi** (Haldeman).—This species has been reported from Nogales and Palmerlee, Arizona (35).

3. **E. mexicanum** (F. Smith).—Reported from Nogales, Arizona (35).

4. **E. arizonense** Whlr.—Reported from Las Cruces, New Mexico, and Nogales, Arizona (35).

5. **E. oslari** Whlr.—Reported from Nogales, Arizona (35).

6. **Monomorium minimum** (Buckley).—This ant was found by the writer in small numbers in the deserts of southern Arizona and to a limited extent in the Mojave Desert of California. It nests in the

ground, usually beneath stones. In rarer instances its small crater nests are in the open, directly exposed to the sun. This species cannot, however, be considered as a common desert ant.

7. **Solenopsis geminata** (Fab.).—Nests of *S. geminata* were of common occurrence in the deserts of southern Arizona, especially in the vicinity of Tucson. There the irregular crater nests are built in the open spaces between vegetation. The ants are granivorous but have been observed feeding upon live insects.

8. **S. geminata diabola** Whlr.—This is a much rarer ant than is the typical species. It was found in small numbers in the sandy soil along the Colorado River near Needles, California. It has also been reported from Tempe, Arizona (35).

9. **S. molesta** (Say).—This species has been reported from Las Vegas, New Mexico (35). It has been found by the writer in the desert near Phoenix, Arizona.

10. **S. xyloni** (McCook) (Fig. 3).—This species has been found in large numbers by the writer at Phoenix, Tucson, and Douglas, Arizona, and at Las Cruces, New Mexico. The ants inhabit rather rugged crater mounds in sandy desert "draws." The colonies are quite populous and the workers extremely aggressive foragers. Associated vegetation consisted of *Covillea tridentata, Franseria dumosa, Acacia greggi,* and *Opuntia* spp. at the Arizona localities, and *Covillea tridentata* and *Yucca* spp. at Las Cruces.

11. **S. xyloni maniosa** (Whlr.).—This ant is reported by Wheeler from Tucson, Yuma, Tempe, Yucca, Benson, Arizona, and from Needles, California. Other points outside of the Southern Desert Shrub region are also listed in its range (41).

12. **S. xyloni aurea** (Whlr.).—*S. aurea* is reported by Wheeler from Austin and Fort Davis, Texas; Magdalena, New Mexico; and Yuma, Grand Canyon, Phoenix, Casa Grande, Penaleno Mountains and Coyote Mountains, Arizona (41). Creighton (12) reports that the ant nests under stones. Apparently the nests are never of the crater type. The ants are nocturnal or crepuscular in habits.

13. **Pheidole militicida** Whlr.—*P. militicida* has been reported by Wheeler (41) as occurring in the desert near Hereford and Benson, Arizona (elevation 3,600 feet). According to this authority the small crater nests, three to five inches in diameter, are often covered with chaff, thus proving the ants' harvesting activities.

14. **P. virago** Whlr.—Wheeler described this species from soldiers and workers taken in the valley of the Santa Cruz River, near Tucson, Arizona (41). The crater nests possess large central openings half an inch in diameter.

15. **P. fimbriata** Roger (*P. rhea* Whlr.). Wheeler reports this species from Nogales, Arizona (41). Apparently nothing is known of its habits.

16. **P. kingi torpescens** Whlr.—The subspecies *torpescens* has been found at Tucson, Arizona by Wheeler who described it from a few specimens found in a small nest under a rock (41).

17. **P. californica** Mayr.—Workers of this species have been taken in large numbers by the writer in the desert near Needles, California.

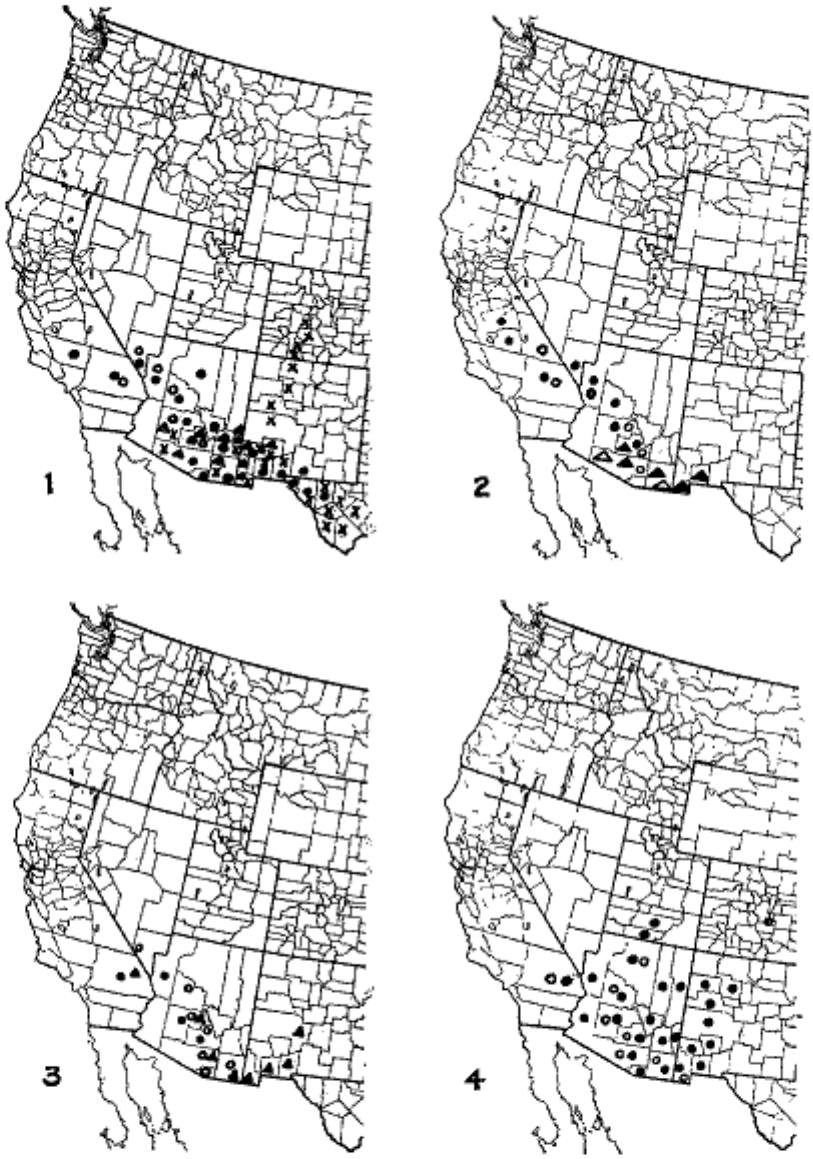

Fig. 1. Distribution of *Pogonomyrmex californicus* (●), *P. californicus estebanius* (○), *P. barbatus molefaciens* (▲), and *P. barbatus rugosus* (×), in the United States.

Fig. 2. Distribution of *Novomessor pergandei* (●), *N. andrei* (○), *Pogonomyrmex occidentalis maricopa* (▲), and *Aphaenogaster* (*I.*) *albisetosus* (△), in the United States.

Fig. 3. Distribution of *Aphaenogaster* (*I.*) *cockerelli* (●), *Pheidole desertorum* (○), and *Solenopsis xyloni* (▲), in the United States.

Fig. 4. Distribution of *Myrmecocystus melliger semirufus* (●), and *M. mexicanus horti-deorum* (○), in the United States.

The nests were small craters with single, central entrances in sandy soil. The ant is a true harvester, for seeds were stored in the nests and chaff surrounded the crater peripheries. Associated vegetation was *Atriplex polycarpa* and *Covillea tridentata*.

18. **P. californica oregonica** Emery.—*P. oregonica*, incidental to the Southern Desert Shrub region, occurs in very limited numbers in the rocky desert north of Phoenix, Arizona. Its nests and habits are almost identical with those of the typical form. The phytohabitat included such plants as *Covillea tridentata* and *Fouquieria splendens*.

19. **P. proserpina** Whlr.—Wheeler has reported taking individuals of this species "from a single nest under a stone on the banks of the Gila River at Tempe, Arizona" (35).

20. **P. xerophila tucsonica** Whlr.—The writer found many crater nests of this subspecies in the desert near Tucson, Arizona and as far north as Phoenix. They also occurred to a limited extent near Douglas. The colonies were usually quite populous and the ants active.

21. **P. xerophila tucsonica gilvescens** Whlr.—Nests of this variety were rather uncommon in the deserts of southern Arizona, but were found in small numbers in the vicinity of Tucson. The colonies seemed to be less populous than those of the typical subspecies which it resembles.

22. **P. barbata** Whlr.—This species has been reported by Wheeler from the Mojave Desert near Needles, California, where it builds small crater nests (35).

23. **P. vinelandica** Forel.—This species has been taken in considerable numbers by the writer near Douglas, Arizona. The ant extends its range north of the true desert region into the semidesert. The nests were commonly of fine sand and situated on exposed ground. Craters were usually present, although small and quite inconspicuous. The writer has collected numerous colonies from beneath stones and wood where nothing marks the presence of the nests but the very small entrances.

24. **P. desertorum** Whlr. (Fig. 3).—The writer has found ants of this species on the sandy desert plains beneath stones, near Phoenix and Tucson, Arizona. The colonies were usually very populous. The workers of this species are perhaps the most active of the entire genus in the United States.

25. **P. cockerelli** Whlr.—The writer was unable to locate this species in the desert region, although it has been reported from Tempe, Arizona by Wheeler (35).

26. **Crematogaster lineolata laeviuscula clara** Mayr.—Several individuals of this species were collected by the writer at Douglas, Arizona, and Lordsburg, New Mexico.

27. **Aphaenogaster (Ischnomyrmex) cockerelli** Ern. Andre. (Fig. 3).—*Ischnomyrmex cockerelli* is rather common in the deserts near Barstow, Ludlow, and Tehatchapi, California, and Phoenix, Tucson, and Douglas, Arizona. It constructs large and rude craters of pebbles, most of which are under four inches in height. The single nest entrance is large and irregular. Vegetation in association with *I. cockerelli* included *Covillea tridentata, Franseria dumosa, Opuntia* spp., and

Atriplex polycarpa at the California localities, and *Covillea tridentata*, *Carnegiea gigantea*, *Echinocereus* sp., *Fouquieria splendens*, and *Opuntia* spp. in Arizona.

28. **A. (Ischnomyrmex) albisetosus** Mayr. (Fig. 2).—A few colonies of *I. albisetosus* were found by the writer under large stones on the rocky desert plains in the northern parts of Cochise and Pima counties, Arizona. Many seeds were stored in one of the nests. This species is evidently much less common than is *I. cockerelli*. The phytohabitat was the same as that of *I. cockerelli*, at the same locality.

29. **Novomessor pergandei** Ern. Andre. (Fig. 2).—This is probably the most common species in the genus. It is quite widely distributed throughout southern California and Arizona. The nests are made up of one or more flattened and symmetrical craters, fifty centimeters or more in diameter, and perforated with from one to three very irregularly-shaped entrances. These entrances are often slit-shaped and as much as five or six centimeters in length. Galleries and chambers are excavated in dry compact soil or loose sand to a depth of about seventy centimeters. Seeds are harvested in great numbers, the kinds varying with the surrounding vegetation. A crescentic or circular ring of chaff borders the periphery of each mound and often many of the discarded seeds germinate, with a resulting circle of plants. Like other true desert ants this species confines its harvesting to the early morning and late afternoon hours and at these times long lines of workers may be seen actively engaged at harvesting.

N. pergandei is quite common in the vicinity of Barstow, California, in the Mojave Desert, where it inhabits the soil covered with an almost pure stand of *Atriplex polycarpa* (Desert Sage). Near Bakersfield, California it is associated with *Bromus* sp., *Salsola pestifer*, and *Atriplex polycarpa* and abounds in shady areas.

30. **N. andrei** Mayr. (Fig. 2).—*N. andrei* seems to be exclusively confined to the region of southern California and western Arizona, from Sacramento southward to the Mojave Desert and thence eastward to Williams, Arizona. It is of common occurrence on the desert plains near Bakersfield, California where its large crater mounds are built in the packed desert soil. Like *N. pergandei* it harvests seeds in great numbers and the nest chambers restricted to graineries are often filled to overflowing with seeds of *Hordeum* sp. The colonies are large and in July contain much brood and many winged forms. In the Mojave Desert, *N. andrei* is associated with *Atriplex polycarpa*, *Hordeum* sp., *Covillea tridentata*, and *Parosela spinosa* (Gray).

31. **Pogonomyrmex occidentalis** Cresson.—This species has the greatest geographical range of any in the entire genus. It is characteristic of, but not exclusive to, the short and tall grass plains and sagebrush semidesert areas of the United States. It was found in small numbers south of Prescott, Arizona, on the very edge of the desert.

P. occidentalis has attained such great interest and attention among myrmecologists that a detailed account of the species need not be presented here. The reader is referred to the excellent book by McCook (18) and shorter papers by Wheeler (27) and Cole (8 and 10).

32 **P. occidentalis subnitidus** Emery.—The writer collected a few individuals of this variety from a small mound on a gently-sloping hillside in the Mojave Desert of California. Little is known of its habits and habitat. It appears to be one of the more rare ants of the genus.

33. **P. occidentalis maricopa** Whlr. (Fig. 2).—This variety is present in considerable numbers in the region between Douglas, Arizona, and Lordsburg, New Mexico, where it inhabits large pebble mounds, especially along the Rio Puerto. The colonies are very populous. The habits and mounds of this variety seem to be very similar to those of the typical *occidentalis*.

34. **P. subdentatus** Mayr.—This species was collected by the writer from Arizona and California, and Wheeler states that it is confined to the deserts of Texas, New Mexico, California, Arizona, and northern Mexico (43). The colonies are small, widely scattered, and comprise only a few individuals. The ants build small crater nests and make no attempt to clear the surrounding vegetation.

35. **P. desertorum** Whlr.—The species *desertorum* nests from Texas to Arizona (43). The writer collected several individuals from small mounds twelve centimeters in diameter and two centimeters high. Each mound contained a crater and a single central entrance. The mounds were composed of coarse, loose sand in a community of *Yucca* spp. near Kingman, Arizona. One colony was also observed in the sandy soil along the Colorado River, near Needles, California.

36. **P. californicus** Buckley. (Fig. 1).—*P. californicus* is one of the more common ants of the desert states, especially California and Arizona. It has been collected by the writer from California, Arizona and New Mexico and has further been recorded from Texas by Wheeler (43). In California it replaces the Occidental harvester, *P. occidentalis* Cresson.

The ants construct nests of flat sand craters, or merely holes in the sand which lead to shallow subterranean chambers. The colonies are populous and the workers active. Seeds are harvested in great numbers.

The writer has already published detailed notes on *P. californicus* (9).

37. **P. californicus estebanius** Pergande (Fig. 1).—This variety of *californicus*, which is recorded from California by Wheeler (43), was found in various parts of the Mojave Desert and the deserts of Arizona by the writer. It appeared to be most common in the vicinity of Ludlow, California, but it was of much rarer appearance than the typical form.

The nests varied from mere holes in the sandy soil to large crater mounds with single central entrances, often irregular and eccentrically sloping. Brood chambers and seed chambers were interspersed throughout the mounds, and the first chambers appeared about four inches beneath the mound surfaces. Winged forms were present on July 18, 1931, with males predominating in numbers.

38. **P. (Ephebomyrmex) pima** Whlr.—This species is present in the succulent desert region in the vicinity of Tucson, Arizona, and

occurs less abundantly at Phoenix. The habits of the ant are apparently unknown, and, to my knowledge, winged forms have not been found. Associated vegetation consisted of *Carnegiea gigantea*, *Echinocereus* sp., *Fouquieria splendens*, *Covillea tridentata*, *Yucca* spp., and *Opuntia* spp.

39. **P. barbatus rugosus** Emery. (Fig. 1).—This subspecies is recorded from Arizona and California by Wheeler (43). The writer found it abounding in the desert region of southern Arizona. It is a characteristic ant of the Angel Plateau of the Grand Canyon, and of the adjacent dry boulder beds (31).

The nests are flat discs of gravel or sand and are often very rudely shaped. The ants clear the vegetation immediately surrounding their nests.

40. **P. barbatus molefaciens** Buckley. (Fig. 1).—*P. molefaciens* is of rather common occurrence in the region north of Lordsburg, New Mexico, and is found as far north as Pueblo, Colorado. It is also common in the western counties of Texas. The ants inhabit large bowled pebble mounds, whether grouped or scattered. The colonies are large and the occupants aggressive and vicious.

41. **P. huachanus** Whlr.—The writer found only one colony of this ant, in the Mojave Desert, near Needles, California. The nest was a rather minute crater mound in the sand. The colony was small and the workers were sluggish.

42. **Atta (Moellerius) versicolor** Pergande.—The writer found colonies of *A. versicolor* abounding in the deserts near Phoenix and Tucson, Arizona, and to a more limited extent in the Mojave Desert of California. The species has also been reported from Yucca, California by Wheeler (32).

The large crater nests of pebbles or sand are prominent in the sandy desert "draws." Single large, central galleries penetrate the craters and lead into numerous and irregularly-shaped brood and fungus chambers.

Catclaw bushes (*Acacia greggi*) are often defoliated in their desert habitats by leaf-gathering workers of *A. versicolor*. Wheeler presents excellent descriptions of the activities of this species in his paper entitled, "The Fungus-growing Ants of North America" (32).

43. **A. (Trachymyrmex) arizonensis** Whlr.—This species, which has been reported from Palmerlee, Cochise County, Arizona (32), has been found in small numbers by the writer near Douglas, Arizona. The nest of the ants was not located.

44. **Dorymyrmex pyramicus bicolor** Whlr.—The populous colonies of this form are numerous in sandy and pebbly soil throughout the Southern Desert Shrub region. The small and eccentrically-sloped crater mounds of *D. bicolor* are provided with single, central, and sometimes sloping, entrances.

45. **Iridomyrmex analis** Ern. Andre.—This species is one of the most common occupants of the Southern Desert Shrub region. It builds minute crater nests of fine sand, and unless the mounds are grouped, one experiences great difficulty in finding them. The small workers are very active.

46. **I. pruinosus** var.—An, as yet, undetermined variety of *I. pruinosus* was found in various parts of California and Arizona, especially in the vicinities of Needles, California, and Prescott, Arizona. The nests were much the same as those of *I. analis*. The colonies were always small and the ants active.

47. **Forelius maccooki** Forel.—This species has almost the same range as does *I. analis*, but is more limited and rather widely scattered. The nests are usually multiple craters of fine sand. The writer found colonies in various parts of the desert near Tucson, Arizona, which is perhaps the area in which it abounds.

48. **Prenolepis (Nylanderia) guatemalensis** Forel.—The writer found several individuals of this species in the desert south of Prescott, Arizona. The nest was not located.

49. **Lasius niger sitkaensis** Pergande.—This ant was found by the writer in small numbers along desert streams, especially in Arizona. The nests were usually beneath rocks, but occasionally a small crater nest was observed in a rather shady habitat. The colonies were quite populous.

50. **Formica subpolita perpilosa** Whlr.—This species is of quite common occurrence in the periodical river bottoms of the Mojave Desert and of the desert around Tucson, Arizona. It builds low mounds, often with craters, at the bases of shrubs. The colonies are rather large and the ants active.

51. **F. rufibarbis gnava** Buckley.—This variety is quite common in the eastern part of the Mojave Desert, especially in the vicinity of Needles, California. It also occurs, to a very limited extent in the desert area south of Prescott, Arizona. The colonies observed by the writer were all beneath large flat rocks, in shaded and rather moist habitats.

52. **F. cinerea pilicornis** Emery.—This subspecies was found by the writer in scattered, open nests on the sandy plains of the Mojave Desert, in the vicinity of Barstow, California. The low crater mounds were in the interspaces of creosote bush and Mormon tea (*Ephedra* sp.).

53. **Myrmecocystus melliger orbiceps** Whlr.—*M. orbiceps* is quite abundant in the deserts of southern Arizona, its range extending as far north as Phoenix. The nests consist of rather obscure craters built in gravelly or sandy soil, and possess eccentric and very large single entrances. The colonies comprise only a few hundred individuals, apparently none of which are repletes. The ants commonly feed upon termites and other insects, and have never been observed feeding upon the honey-dew of aphids. *M. orbiceps* builds its nests in the succulent desert areas of *Covillea tridentata*, *Echinocereus* sp., *Fouquieria splendens*, and various species of Opuntia and Yucca. The mounds are scattered in the bare areas between plants.

54. **M. melliger mimicus** Whlr.—This species is rather common and widely distributed through the Mojave Desert and the succulent deserts of southern Arizona, in the vicinity of Phoenix and Tucson. *M. mimicus* nests in both sandy and gravelly soil, the former habitat in the Mojave Desert and the latter in the deserts of southern Arizona. It constructs neat crater mounds about one inch in diameter and with

single, central entrances. The nests are not known to contain repletes, and the workers prey upon insects.

M. mimicus is found associated with *Covillea tridentata*, *Prosopis* sp., *Yucca* spp., and *Opuntia* spp. in the Mojave Desert, and with *Carnegia gigantiea*, *Echinocereus* sp., *Fouquieria splendens*, *Opuntia* spp., and *Yucca* spp. in the Arizona habitats.

55. **M. melliger depilis** Forel.—This variety of *mimicus* is apparently of occasional occurrence in the Mojave Desert, near Needles, California. It has been reported by Wheeler (34) but the writer has not been able to locate it.

56. **M. melliger semirufus** Emery. (Fig. 4).—*M. semirufus* is of common occurrence in the Mojave Desert of California and is less abundant in the desert about Tucson, Arizona. *M. semirufus* constructs small regular mounds about three inches in diameter in loose sandy soil. Each mound contains a deep crater and a single central entrance. At Hammett, Idaho numerous mounds were found by the writer on the sandy semidesert plains. Each mound contained winged forms of both sexes. The workers were very abundant but no repletes wereobserved among them.

The condition of the semidesert near Hammett approaches that of the Mojave Desert and many of the same plants are to be found. The vegetation of the former locality consists predominantly of *Artemisia tridentata, Sarcobatus vermiculatus, Chrysothamnus graveolens glabrata, Atriplex confertifolia,* and *A. canescens.* In the Mojave Desert the ant is common in a vegetational habitat of species of Yucca and Opuntia, and *Covillea tridentata,* and in Arizona is associated with *Fouquieria splendens, Covillea tridentata, Carnegiea gigantea, Echinocereus* sp., and *Opuntia* spp.

57. **M. melliger semirufus testaceus** Emery.—This variety Wheeler (34) believes to be merely a color form of *semirufus.* It is reported from the Mojave Desert as well as from the desert near Phoenix, Arizona. Nothing is known of its habits, but it presumably lives in pure sand.

58. **M. mexicanus horti-deorum** McCook. (Fig. 4).—This variety of *M. mexicanus* rarely occurs in the Mojave Desert. The writer, however, found one small colony in a rocky section between Needles, California, and Kingman, Arizona. Pebble mounds of this form are quite abundant in the area south of Prescott, Arizona, and an occasional one is to be found near Phoenix. The writer does not believe, however, that it can be regarded as a characteristic ant of the Southern Desert Shrub region. McCook, in his book (18), has covered this form so thoroughly that an extensive description of its habits and habitat is unnecessary in this paper. It is enough to state that this ant is the most common representative of the American Myrmecocysti.

59. **M. mexicanus navajo** Whlr.—Like *horti-deorum* this ant cannot be listed as characteristic of the true desert region. The writer found it in abundance near Hammett, Idaho in the sagebrush semi-desert region. Winged forms appeared on April 11. The mounds built by the ants were very small and consisted only of single entrances surrounded by scattered sand.

60. **M. mexicanus mojave** Whlr.—*M. mojave* is recorded from Ontario, California by Wheeler (34). Nothing is known of its habits.

61. **M. lugubris** Whlr.—This species is recorded by Wheeler (34) from the Mojave Desert, California. Repletes are present in the nests. Nothing is known of the habits of the ant.

62. **M. yuma** Whlr.—This ant has been taken by the writer from small crater mounds of sand near Douglas, Arizona. The colonies were rather large.

63. **Camponotus maculatus maccooki** Forel.—*C. maccooki* has been recorded from California by Wheeler. It has been found by the writer near Tehatchapi, California, and at various points between Prescott and Phoenix, Arizona. One nest was found near Douglas, Arizona. The ant inhabits nests beneath large rocks in moist habitats. The colonies are large and contain many soldiers.

64. **C. fumidus festinatus** Buckley.—*C. festinatus* inhabits the higher desert plateaus near Tucson, Arizona. The writer was unable to locate the formicaries.

65. **C. acutirostris primipilaris** Whlr.—This ant has been recorded from Nogales, Arizona by Wheeler (35).

66. **C. sayi** Emery.—*C. sayi* has been recorded by Wheeler (35) from Nogales, Arizona.

67. **C. hyatti** Emery.—*C. hyatti* is of very limited occurrence on the more moist slopes in the Mojave Desert, where a few individuals were taken by the writer. The formicaries were not found.

SUMMARY

The study of desert ants of the United States necessitated a survey of predominate vegetation and vegetation types as well as a knowledge of desert climate and soils.

Ants of the Southern Desert Shrub region are rather markedly affected by climatic conditions. Temperature affects activities outside the nests and is partially responsible for determining seasonal successions of ants. Winds alter, level and destroy mounds, direct the establishment of new colonies, transport food and desiccate the soil. Precipitation in the form of periodical showers and cloudbursts, destroys nests and kills the occupants. Evaporation determines the proportion of soil moisture which, in large amounts, is detrimental to ant colonies. Light in conjunction with temperature partly determines the daily periods of ant activity. Some ants are sun-loving species, others live in the shade, and some show no apparent preference to either type of habitat. Cold air drainage perhaps is partly responsible in determining ant distribution at the base of a desert gulch but soil texture and moisture seem to be more important factors. In many cases distributions

of the ants seemed to be correlated with topographical divisions and soil types. Vegetation plays a decided role in the existence of the colonies. The ants usually live in rather definite communities and these very often are associated with certain plant communities. Many desert ants are dependent upon seeds for food or upon plants for shade and moisture from dew.

Ants of the Southwestern deserts may be divided into the exclusive, the characteristic, and the incidental species. Many are seed feeders, others cultivate and live on fungi and a large number are predators or scavengers.

A list of ants of the desert region includes 67 species, subspecies and varieties which are discussed annotatedly.

LITERATURE SELECTED AND CITED

(1) **Andrews, E. A.** 1927. Ant mounds as to temperature and sunshine. Jour. Morphol. & Physiol., 44: 1–20.
(2) **Bailey, Vernon.** 1923. Sources of water supply for desert animals. Sci. Mo., 27: 66–86.
(3) **Buxton, A.** 1923. Animal life in deserts. A study of the fauna in relation to the environment. London.
(4) 1924. The temperature of the surface of deserts. Jour. Ecol. 12: 127–134.
(5) **Chapman, R. N.** 1931. Animal ecology with special reference to insects. N. Y., x + 464.
(6) **Cockerell, T. D. A.** 1899. Vernal phenomena in the arid region. Amer. Nat., 33: 39.
(7) 1900. The lower and middle Sonoran zones in Arizona and New Mexico. Amer. Nat., 34: 285–293.
(8) **Cole, A. C., Jr.** 1932. The rebuilding of mounds of the ant, *Pogonomyrmex occidentalis*, Cresson. Ohio Jour. Sci., 32: 245–246.
(9) 1932. Notes on the ant *Pogonomyrmex californicus* Buckley (Hym.: Formicidae). Ent. News, 43: 113–115.
(10) 1932. The relation of the ant, *Pogonomyrmex occidentalis* Cresson, to its habitat. Ohio Jour. Sci., 32: 133–146.
(11) 1933. Observations on semidesert ants. Ohio Jour. Sci., 32: 533–538.
(12) **Creighton, W. S.** 1930. The New World species of the genus Solenopsis (Hymenoptera: Formicidae). Proc. Amer. Acad. Arts & Sci., 66: 39–151.
(13) **Green, H. E.** 1931. Preliminary study of the ants of southern California. Jour. Ent. & Zool., 23: 25.
(14) **Kennedy, C. H.** 1927. Some non-nervous factors that condition the sensitivity of insects to moisture, temperature, light and odors. Ann. Ent. Soc. Amer., 20: 87–106.
(15) 1928. Evolutionary level in relation to geographic, seasonal and diurnal distribution of insects. Ecology, 9: 367–379.
(16) **Lutz, F. E.** 1927. Wind and the direction of insect flight. Amer. Mus. Nat. Hist. Novitate 291.
(17) **McCook, H. C.** 1880. The natural history of the agricultural ants of Texas. J. B. Lippincott & Co., Philadelphia.
(18) 1882. The honey ants of the Garden of the Gods, and the occident ants of the American plains. J. B. Lippincott & Co., Philadelphia.
(19) **Merriam, C. H.** 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. Nat. Geog. Mag., 6: 229–238.
(20) 1895. The geographic distribution of animals and plants in North America. Yearbook, U. S. D. A., for 1894. 203–214.
(21) 1898. Life zones and crop zones of the United States. U. S. Biol. Surv. Bul., 10: 1–79.

(22) **Shreve, F.** 1912. Cold air drainage. Plant World, 15: 110–115.
(23) **Sinclair, J. J.** 1922. Temperature of soil and air in a desert. U. S. Mon. Weather Rev., 50: 142–144.
(24) **Tulloch, G. S.** 1930. An unusual nest of Pogonomyrmex. Psyche, 37: 61–70.
(25) **Van Dyke, E. C.** 1919. The distribution of insects in western North America. Ann. Ent. Soc. Amer., 12: 1–12.
(26) **Webster, F. M.** 1903. The diffusion of insects in North America. Psyche, 10: 47–58.
(27) **Wheeler, W. M.** 1902. New agricultural ants from Texas. Psyche, 9: 387–393.
(28) 1902. A new agricultural ant from Texas, with remarks on the known North American species. Amer. Nat., 36:85–100.
(29) 1903. *Formica fusca* Linn. subsp. *subpolita* Mayr. var *perpilosa*, n. var. Mem. Soc. Cient. Ant. Alzate, Mexico, 17: 141–142.
(30) 1903. A revision of the North American ants of the genus Leptothorax Mayr. Proc. Acad. Nat. Sci. Phil., 55: 215–260.
(31) 1906. The ants of the Grand Canyon. Amer. Mus. Nat. Hist. Bul., 22: 329–345.
(32) 1907. The fungus-growing ants of North America. Amer. Mus. Nat. Hist. Bul., 23: 669–807.
(33) 1907. On certain modified hairs peculiar to ants of arid regions. Biol. Bul., 13: 185–202.
(34) 1908. Honey ants, with a revision of the American Myrmecocysti. Amer. Mus. Nat. Hist. Bull., 24: 345–397.
(35) 1908. The ants of Texas, New Mexico and Arizona. Amer. Mus. Nat. Hist. Bul., 24: 399–485.
(36) 1909. A decade of North American Formicidae. Jour. N. Y. Ent. Soc., 17: 77–90.
(37) 1909. A new honey ant from California. Jour. N. Y. Ent. Soc., 17: 98–99.
(38) 1911. The ant colony as an organism. Jour. Morph., 22: 307–325.
(39) 1911. Two fungus-growing ants from Arizona. Psyche, 18: 93–101.
(40) 1913. A revision of the ants of the genus Formica (Linne) Mayr. Bul. Mus. Comp. Anat. 53.
(41) 1915. Some additions to the North American ant-fauna. Amer. Mus. Nat. Hist. Bul. 34: 389–421.
(42) 1916. Guide to the insects of Connecticut. Part III: Formicidae Conn. Geol. & Nat. Hist. Surv. Bul., 22: 577–601.
(43) 1926. Ants: their structure, development and behavior. Columbia Univ. Press, xxv, 663.

BOOK NOTICE

A GENERAL TEXTBOOK OF ENTOMOLOGY, THIRD REVISED EDITION, by A. D. Imms. pp. i–xii and 1–727, 624 text figures. Published by E. P. Dutton and Company, Inc., New York. Price, $10.80.

Imms, now at Cambridge University, was recently Chief Entomologist at the Rothamsted Experiment Station and previous to that Forest Entomologist to the Government of India. Always he has been interested in the general problems of the biology of insects of which he has published much. Being in the British service with its far-flung colonies he has had continuously to adjust his ideas to a world point of view. It is this experience that helps account for the broad views of this volume. It is a general entomology for students in all the English colonies. As such it fits well into our American needs.

The volume is divided into three parts: Part I. Anatomy and Physiology, pp. 1–169; Part II. Development and Metamorphosis, pp. 170–210, and Part III. The Orders of Insects, pp. 211–693. Some few illustrations have been changed from the previous edition and a few added. Besides some expansions in Part III the revisional matter is confined largely to additional matter on anatomy and physiology which brings the text into line with the most advanced recent work. Imms appears to be particularly adept at keeping abreast of the times.

This well known text needs no further recommendation. We have recommended it twice before and it is now better than ever.—C. H. K.