THE RELATION OF THE ANT, POGONOMYRMEX OCCIDENTALIS CR., TO ITS HABITAT*

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INTRODUCTION

In spite of the obvious abundance of colonies of P. occidentalis in the western section of the United States, our knowledge of the species is somewhat limited. McCook (2) has written quite extensively on this ant and Wheeler (3) has added many bits of valuable information. It is hoped that the following data will bring a clearer interpretation of the species occidentalis to those interested, especially as to the relationships existing between the ant and surrounding vegetation.

GEOGRAPHICAL DISTRIBUTION

Pogonomyrmex occidentalis is widely distributed over the far western states with the exception of California, western Oregon and Washington. It is especially abundant in Idaho, Nevada, Utah and Wyoming and generally follows the area of the desert-shrub formation. In Oregon it becomes more scarce with westward progression and I was unable to find it in the western portion of the State. In California it is replaced chiefly by P. californicus, especially in the San Joaquin and Imperial Valleys and the Mojave Desert. In Arizona I found it abounding from the Grand Canyon northward. Wheeler (3, p. 565) lists it from Wyoming, Colorado, New Mexico and Arizona; McCook (2, p. 125) from Wyoming, Colorado, New Mexico, Arizona, Utah, Nebraska and Kansas. I have observed it at the following specific localities:

Idaho.—Twin Falls, Rogerson, Pocatello, Nampa, Boise, Blackfoot, Arco, Idaho Falls, Wieser, Mountain Home, Shoshone, Ketchum, Hailey, Redfish Lake, Hagerman, Hammett, American Falls, Dubois, Hollister, Shoshone Falls, Shoshone Canyon, Rock Creek Canyon, Malta, Bliss and Craters of the Moon National Monument.

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Oregon.—Echo, Pendleton, Ontario, Baker and La Grande.

Utah.—Salt Lake City, Delle, Tooele, Grantsville, Snowville,
Brigham, Ogden, Zion National Park and Kanab.

Arizona.—Grand Canyon, Williams, Cameron and Lee's Ferry.
Wyoming.—Cheyenne, Laramie, Rawlins, Rock Springs, Green
River, Kemmerer, Cody and Ten Sleep.

South Dakota.—Rapid City, Mitchell and Sioux Falls.

Other localities from which *occidentalis* has been reported are as follows:*

Parma, Idaho; 8-29-27; G. W. Haug.
Virginia, Idaho; 7-30-37; G. W. Haug.
Stockton, Kansas; 7-15-20; R. C. Smith.
Custer County, Montana; 7-31-29; R. E. Hutchins.
Woods County, Oklahoma; 7-3-30; R. D. Bird.
Capa, Mobridge, and Newell, South Dakota; H. C. Severin.
Keremeos, B. C.; E. R. Buckell.
Oliver, B. C.; E. R. Buckell.
Okanagan Falls, B. C.; E. R. Buckell.
Osoyoos, B. C.; E. R. Buckell.
Trinidad, Colorado; W. M. Wheeler.
Ash Fort, Arizona; W. M. Wheeler.
Grants, Utah; September, 1917; R. C. Shannon.

McCook (2, p. 126) states that "the vertical distribution of occidentalis is probably not much above the altitude of 6,300 feet, which is the height above sea level of the Garden of the Gods," where he studied its habits most closely. Although I have often found the ant above McCook's level, the mounds are always scattered and few in number. This vertical distribution is essentially the same as northward distribution inasmuch as the limiting factors are practically the same in both cases.

STRUCTURE OF THE MOUND

External Structure—Most mounds of occidentalis are irregularly conical in outline. McCook (2, p. 127) speaks of them as "elliptical cones," whose shorter faces are about one-half the length of the longer faces. Wheeler (3, p. 291) refers to them as "masonry domes." As a rule the base of the mound is of greater dimensions than the slopes, or faces, but occasionally mounds are to be found with the dimensions very nearly equal. The diameter of the base is usually significant of the size of the colony, but such is not always the rule. Weaker colonies sometimes inhabit larger mounds than those of stronger and more active relatives.

^{*}From the files of M. R. Smith.

Mounds of *occidentalis*, though primarily existing on somewhat level sandy or gravelly areas and exposed to the direct rays of the sun (Fig. 1), are often found on the tops of flat

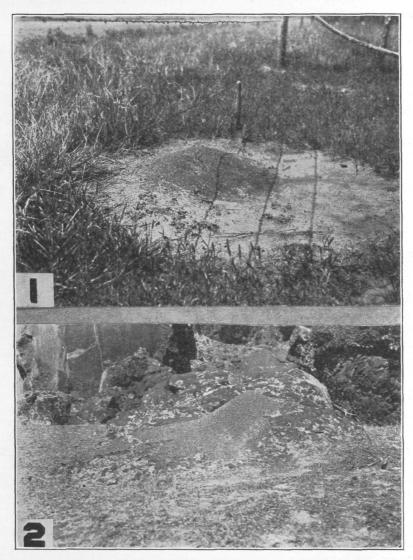


Figure 1. Typical mound of *P. occidentalis* in Western Wyoming, with small crater of *Dorymyrmex pyramicus* in the denuded area. (Original).

Figure 2. Pebble mound of *occidentalis* on rock near Twin Falls, Idaho. Note the nest entrance at the base of the mound. (Original).

rocks (Fig. 2), around rocks and around plants (Fig. 3). often compose part of the base of a mound and upon removing them the various nest chambers and galleries are brought into view (Fig. 4). The composition of the mounds differs greatly and consists of the following chief types:

Average or typical mounds

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- Pebble mounds.
 - a. Large pebbles. (Fig. 3).
 - b. Small pebbles. (Fig. 2).
- Sand mounds.

 - a. Fine sand. (Fig. 1).b. Coarse sand (small pebbles).
- Earth mounds.
 - a. Packed earth.
 - b. Loose earth.

Combination mounds

- 4. Earth and pebbles.
- 5. Earth and sand.
- 6. Pebbles and detritus. (Fig. 5).
- 7. Earth and detritus.

Divergent types of mounds

- 8. Cinders.
- Horse or cow dung (dry).
- 10. Bits of glass and pebbles.

The composition of the mound coverings may be classified as follows:

- 1. Cinder covering.
- Frass covering (from harvested seeds).
- Covering of bits of glass.
- 4. Covering of twigs or bark.
- 5. Covering of leaves.
- 6. Covering of dry horse or cow dung.
- 7. Covering of sheep, lizard or rabbit dung pellets.
- Covering of keys from trees (especially ash).

Wheeler (3, p. 202) states that "* * * in P. occidentalis the single entrance is situated at the base (of the mound) and almost invariably on the southern or eastern side." Upon examining five hundred mounds in the state of Idaho I obtained the following data:

Number of mounds with one opening	387
Number of mounds with two openings	109
Number of mounds with three openings	4
Number of mounds with opening(s) at base	486
Number of mounds with opening(s) at top	14

Number of mounds with opening(s) on south face 126 Number of mounds with opening(s) on east face 197 Number of mounds with opening(s) on north face 152 Number of mounds with opening(s) on west face 25



Figure 3. Incipient mound of large, limestone gravel around alfalfa plant near Twin Falls. The bordering vegetation is Salsola pestifer. (Original).

Figure 4. View of nest chambers of occidentalis under rock at base of mound. The white areas are termite galleries. (Original).

The size and shape of the nest openings vary greatly. Some are merely circular holes while others consist of several layers of packed material, giving them a "shelled" appearance.

McCook (2, p. 134) presents excellent descriptions of these openings, or "gates" as he terms them.

For further evidence as to the plasticity of occidentalis mound structure I offer the following data. A pebble mound was excavated for the purpose of collecting seeds from the various chambers both in the mound and below the ground level. At the end of six days, upon revisiting the mound, I found that it had been partially rebuilt. The only major difference between the rebuilt mound and the original architecture was the presence of two entrances, one on the east face and one on the west, whereas originally there was only one entrance and that on the southeast face.

Mounds of *occidentalis* do not always occur singly. There are many double mounds and occasionally a triple one. I have never observed more than three mounds within the same denuded area.

Internal structure—The position and numbers of the nest chambers are especially interesting (Fig. 4). The brood chambers vary in number and size according to the relative strength of the colonies. Invariably there are present one or more chambers near the surface of the mound where the brood is isolated during the day time (providing the temperature is not too high) and chambers at the base of the mound or under the ground level to which the brood is moved at night or on cooler days. This movement is apparently entirely dependent on temperature fluctuations and will be discussed later. The shape of the chambers varies between colonies and within the same colony as well. The chambers are usually fairly large, averaging 8.5 centimeters, and are irregularly domed with galleries leading to the various adjacent chambers.

The seed chambers are especially interesting for there is stored the fruit of the ants' labor. These, like the brood chambers, also vary in number and size, but as a rule they are not abundant and are more or less slit-shaped, being noticeably longer than high. I have found as many as seven and as few as one in a single mound, some overloaded with seed and others containing very little or none. A study of the various seeds harvested has proven interesting and will be dealt with further in the paper.

I have observed many cases in which both brood and seed were confined to the same chambers but this seems to be the

exception rather than the rule. The brood, however, is rarely isolated into separate chambers according to its age but is usually intermingled in the same chambers.



Figure 5. Combination mound of pebbles and detritus in an almost pure stand of sagebrush near Twin Falls. (Original).

Figure 6. Burned area of bromegrass and sagebrush near Ontario, Oregon, illustrating the protection of the mound by its denuded area. (Original).

Table I lists several typical mound temperatures. These temperatures, both inside and outside of the mounds, vary with atmospheric temperature and are never constant. From the data in the table we can recognize the correlation between these fluctuating temperatures and the movement of the brood. This movement is gradual as a rule, the brood being transferred from one chamber to another, the last position being the optimum for the maximum or minimum temperature concerned.

The temperature must not be too high for the delicate brood to withstand, neither must it be too low for proper incubation of the brood. Minor fluctuations are met with adjustments inside of the mound. As the temperature rises during the day, the workers move the brood from the deep recesses underground into the mound and often just under the surface covering. As the temperature decreases the brood is moved from the upper chambers and returned to the lower levels. That this process is gradual has already been pointed out.

THE DENUDED AREA

The cleared or "denuded" areas surrounding mounds of P. occidentalis are as impressive as the mounds themselves (Fig. 1). They represent "subseres," average about five feet in diameter and are more or less regularly circular in outline. They are due to the destruction, by the worker ants, of vegetation closely surrounding the mounds. The plants are literally "chewed-down," bit by bit, from the apex to the base. debris is either carried away by the ants or scattered by the wind. The rate and extent of denudation is proportional to the size and strength of the colony. I carefully observed occidentalis workers cutting down a large plant of wild lettuce at the base of a mound. Fourteen days of cutting were required for the plant, 12.1 centimeters high, to be reduced to a mere stump of 0.2 centimeters, only a few ants working at a time. Small grasses are often hewn by the sharp mandibles of a single The remaining stubble eventually dries out and is disseminated by the wind. The apparent tolerance of the ants toward some plants growing in the denuded areas cannot be explained. Peppergrass (Lepidium sp.) seems to be commonly tolerated in many sections.

As a rule the denuded areas are cleared of all vegetation, but occasionally there are a few scattered grasses, such as Agropyron and Stipa, growing near the periphery of the circle. Rarely do we find plants growing on the mounds themselves. Many annuals border the denuded areas, among the most common being Russian thistle (Salsola pestifer A. Nels.), mustards (Sophia parviflora (Lam.) Standl. and Sisymbrium altissimum L.) and bromegrass (Bromus tectorum L.).

One is not certain whether the denuded area is detrimental or advantageous to the life of the colony. The strong, prevailing, westerly winds of the west tend to "hollow-out" the mounds of *occidentalis* and related species which have denuded areas surrounding their mounds. This is detrimental to the

	•	TABLE	I.
SOME	TYPICAL	Mound	TEMPERATURES.

Temperature of*	Mound 1	Mound 2	Mound 3	Mound 4	Mound 5	Mound 6	Mound 7
Sun	97	97	**	**	**	**	**
Shade	88	88	69	69	69	69	69
Top of mound	106	91	70	70	70.5	70	70.5
Interior of base		93	71	70	70	71	70.2
In entrance		91	70	70.5	70	70	69.5

^{*}Temperatures in Degrees F.

continued existence of the colony. Such is not the case with adjacent mounds of Formica which are invariably protected by surrounding vegetation, no matter how short or scant it may be. In some localities occidentalis mounds are tightly packed and are composed of a material which resists the average winds to a great extent. Mounds composed of loose earth, sand or detritus are much less stable than pebble mounds for they are more inclined to be destroyed or at least damaged by the sweep of wind over the denuded areas.

Of what value is the denuded area? Near Ontario, Oregon, I observed a large sagebrush-bromegrass area which had been burned-over, completely destroying the vegetation and amplifying the preponderance of *occidentalis* mounds (Fig. 6). The large denuded areas surrounding the mounds had prevented the fire from coming into direct contact with them. That there was a slight mortality of the ants is obvious, but had there been no denuded areas, the destruction of at least a large portion of the colonies would have been inevitable.

^{**}Cloudy; no sunlight.

Occasionally occidentalis mounds do not have denuded areas. I observed full-sized mounds in large patches of annuals where the vegetation all but touched the sides. I observed two colonies in a huge area of Bromus tectorum L. (Bromegrass) which made no effort to clear areas around the mounds. Ants returning to the colony would continually weave to and fro, dodging stems of Bromus and often temporarily losing their loads of seed.

OBSERVATIONS IN THE TWIN FALLS, IDAHO AREA

"The Twin Falls Area, Idaho, is situated in the northern part of Twin Falls County. It lies in the southern part of

TABLE II. Ecological Distribution of Occidentalis in the Twin Falls Area.

A	NTS PRESENT			Ants Absen	T
	Vegetation	getation No Vegetation Vegetation		No Vegetation	
Abundant	Intermediate	Scarce	Wet	Dry	
Sagebrush Brome grass	Greasewood	Shadscale	Lake Margins	Sand dunes Old lake beds Plowed areas	Cultivated fields

the great inter-mountain valley known as the Snake River Plains." (1) Thus it forms a part of the Upper Sonoran Zone with its characteristic fauna and flora. The Twin Falls area covers approximately 350 square miles, or 223,360 acres.

"The climate of the area, like that of the greater part of the Snake River Plains, is characterized by a low annual rainfall, a dry atmosphere, hot summers, cold winters, and a large proportion of sunny days." (1) The average annual precipitation at Twin Falls is about 11.03 inches and the average annual snowfall 27.5 inches at the same locality.

In the Twin Falls area mounds of *occidentalis* are present only where there is vegetation. They are very abundant in greasewood communities, and occasional in regions of shad-scale. However, we do not find them in all vegetational areas.

In cultivated fields, where the soil is periodically disturbed, they are not present. Nor are they abundant in very wet tracts bordering streams where there is likely to be a luxuriant growth of plants. Colonies do not exist on active sand dunes nor on the old dry lake-beds. Plowed areas only support mounds when they are undisturbed for some time and until plants begin to grow. Table II summarizes these various points.

Occidentalis brood will not mature in soils of high mositure content. Excessive moisture germinates the seeds stored by the workers, making them utterly useless for food. After a shower, under normal circumstances, when the seeds become

TABLE III.*
Distribution in Relation to the Vegetation in the Twin Falls Area.

PLANT COMMUNITY	Locality	Number Mounds in One-tenth Square Mile		
		Established	Incipient	Abandoned
Sage-rabbitbrush Sage-brome grass Sagebrush Sage-greasewood Greasewood Greasewood-Shad Shadscale Brome grass	Twin Falls Twin Falls Hagerman Hagerman Hammett	7 6	5 4 2 4 5 4 2 9	0 0 0 0 0 0 0

^{*}The figures given are the means of three counts.

damp, the workers transport them to the surface of the mound where they are able to thoroughly dry. They are then returned to the seed chambers. In an area of very high humidity, if the seeds are taken to the surface to dry, they germinate instead. This is detrimental and may lead to the extinction of the colony. The result is the same when rain falls on the exposed seeds before the workers are able to carry them into the interior of the mound. Thus we occasionally observed sparse growths of annuals on the mounds themselves. The rarity of this occurrence has been pointed out in a preceding paragraph.

The relative distribution of *occidentalis* in regards to the vegetation is illustrated in Table III. Sagebrush and bromegrass areas support the greater number of colonies and shadscale communities the least. The abundance of mounds in the

bromegrass areas is explained by the harvesting habits of the ants, *Bromus tectorum* seeds being the chief seeds harvested.

Mounds of *occidentalis* are found on all types of soil in the Twin Falls area but occur most abundantly on gravelly soils. Perhaps this is due to the apparent preference for pebble mounds in many localities. Portneuf silt loam of wind-blown origin covers about 83% of the Twin Falls area (1). Table IV lists the types of soils present and the abundance of *occidentalis* mounds in these various soil areas.

TABLE IV.*

DISTRIBUTION OF MOUNDS ON VARIOUS SOILS IN THE TWIN FALLS AREA.

Soil	Locality	Number Mounds to One-tenth Square Mile
Portneuf silt loam		22 24
(Shallow phase) Portneuf silt loam	Castleford	$\begin{array}{c} 18 \\ 22 \end{array}$
Downey loam	Rock Creek	7 26 12
Rough stony land		28

^{*}See literature cited, (1).

HARVESTING HABITS

That occidentalis is graniverous is evidenced by the presence of seeds in many of the nest chambers. According to Wheeler (3, p. 282) occidentalis is one of the most characteristic of the American harvesting ants. Table V illustrates the many species of seeds found in various mounds. Seeds of Bromus tectorum were predominant, due to the wide expanse of this plant in Idaho.

May seeds which are present in the nest chambers do not abound in the surrounding area and are often at a considerable distance from the colony. From one mound I excavated several wheat seeds, while the nearest wheat field was two miles distant. It is possible, but not probable, that a few isolated wheat plants were growing in a nearby meadow and that these were harvested by the ants. From observations it is evident that seeds of sunflowers, thistles and other annuals have been transported great distances by the ants. In one

case the nearest sunflowers were 0.7 mile from a group of mounds, Canada Thistle, 0.4 mile, Alfalfa 1.35 miles, and Jim Hill mustard 0.25 mile. Long lines of workers were transporting the above seeds to their formicaries. The seed chambers of mounds in dense bromegrass areas often contain a greater quantity of other seeds and only a few colonies were located

TABLE V.
SEEDS HARVESTED IN THE TWIN FALLS AREA.

Seed	ABUNDANCE	
Carduus arvensis L. Robs	Abundant	
Bromus tectorum L	Very abundant Abundant	
Agropyron spicatum Scribn. & Sm	Moderately abundant	
Lubine sp	Scarce	
Salsola pestifer A. Nels	Very abundant Moderately abundant	
Sophia parviflora (Lam.) Standl	Moderately abundant	
Sophia longipedicellata (Fourn.) Howell		
Melilotus alba Desv		
Ambrosia trifida L	1	
Ambrosia artemisiaefolia L	Scarce	
Bursa bursa-pastoris L		
Thlas pi avense L	100000	
Amaranthus retroflexus L	Scarce	
Chenopodium album LPolygonium persicaria L	Moderately abundant	
Polygonium persicaria L	Scarce Scarce	
Avena fatua L		
Hordeum jubatum L	Abundant	
Lactuca scariola L		
Chaetochloa viridis L. NashSonchus arvensis L		
Iva axillaris Pursh		
Atriplex rosea L	Abundant	
Helianthus annuus L	Moderately abundant	

which seemed to harvest bromegrass seeds exclusively. It is safe to state, however, that seeds of bromegrass are more generally harvested than others especially in the Twin Falls area. This is due primarily to the predominence of *Bromus tectorum* in the semi-desert areas.

COMPOUND NESTS

One of the most interesting associations of P. occidentalis is its relationship to other ants, either intermingled with the

colony or existing in separate nests on or in the mounds or on the denuded areas. I observed several mounds in western Wyoming which supported small crater-mounds of *Dorymyrmex* pyramicus on the faces and on the surrounding denuded areas as well. (Fig. 1). Wheeler (3, p. 426) lists the genera Dorymyrmex and Forelius as compoundly associated with occidentalis. McCook (2, p. 155) lists Formica sanguinea, Dorymyrmex insanus (pyramicus) Buckley and Dorymyrmes flavus McCook.

In the Painted Desert of Arizona I observed several mounds of occidentalis which supported small craters of Lasius niger var. in their denuded areas. There is no apparent relationship between the two species except the tolerance for one another. There were apparently no connecting galleries and the individuals of the Lasius colonies were not found walking on the mounds. Such compound nests are apparently rare in Idaho.

McCook (2, p. 152) mentions Termes flavipes as associated with occidentalis. I, too, have noticed this relationship, and in a large area of greasewood I found fourteen nests which contained the termites and three which did not. Their position in the nest is shown in Fig. 4.

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