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Roadside ditches as corridors for range expansion of the western harvester ant (*Pogonomyrmex occidentalis* Cresson)

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Abstract

The northeasternmost range extent of the western harvester ant *(Pogonomyrmexoccidentalis* Cresson) occurs just east of the Missouri River in North Dakota. The earliest known records (1882) of this species place it in the same general position as existed at the time of the first exhaustive survey in 1966. A 1990 survey reveals substantial eastward and northward range expansion beyond locations known to be stable between 1966 and 1978. This suggests that this species' range has not yet stabilized with post quaternary climatic changes. Field observations show that, near the expanding edge of its range, a strong relationship exists between anthropogenic modification of the landscape and locational propensity. Specifically, land uses which periodically disrupt the soil, such as row cropping, show a nearly absolute lack of occupancy, while the well-drained, sheltered roadside ditches are heavily populated by ***P.*** *occidentalis.* The roads themselves closely resemble bare-soil, post-nuptial landing sites known to encourage *P. occidentalis* ant colonization. This strongly suggests that the roadside ditches act as corridors for range expansion of the species. The similarity between road network density within and beyond the species range, combined with severe drought conditions during 1988 and 1989 indicate that climate, as a regional scale variable, is the stimulus for range expansion, while landscape level queues provided by the roadside ditches, are the mechanism by which it is accomplished. Of the site level factors examined, only roadside ditch azimuths and soil texture showed statistical significance as possible locational factors, but no causal mechanism can be assumed.

Introduction

As with most animal species some combination of climatic, biotic and edaphic factors governs the distribution of ants (Cole 1932, 1940). These governing factors are thought to be determined largely by overall adaptations of the species to large-scale conditions under which it evolved. When the range of a species extends beyond its absolute ecological limits one expects this range to eventually contract. Conversely, when its range is significantly within an area possessing favorable conditions, range expansion is possible. The geographic limit of this possible range expansion is determined by the minimum amount of the limiting factor which most affects the most sensitive developmental stage of the species (Udvardy 1969). The degree of response to limiting factors is highly variable and is often compensated for by behavioral adaptations allowing increased environmental elasticity.

As a taxonomic group the *Formicidae* have demonstrated an extremely high degree of such environmental elasticity. Even so, some ant genera have developed specific behavioral characteristics conditioning them to prevailing conditions.

mex occidentalis, a semi-desert, seed harvesting ant species, typifies such specific behavioral and ecological adaptations At a regional scale, this species does not occur in moist areas of North America and exhibits both behavioral and physiological adaptations to xeric conditions. This was corroborated by a regional model that demonstrated a marked species selectivity for high moisture deficit locations in North Dakota (DeMers **1980a).** Wheeler **(1962)** has suggested that, because of its selectivity to specific moisture regimes, changing wet and dry conditions might impact range expansion or contraction of *P. occidentalis.*

Alternatively, at the site level, Hess **(1958)** suggested the role of soil texture as a factor in ant locational behavior. Hess, citing Gregg's **(1944)** examination of ***P.*** *occidentalis* distribution, agreed that:

> **. . .** edaphic conditions, such as soil texture, are responsible, as these insects require soil of a consistency which enables them to build structures and hollow seed-storing chambers that will not collapse, especially if dried by summer heat.

Examining this premise, Holland and Cvancara (Wheeler and Wheeler **1963)** demonstrated that, in North Dakota, *P. occidentalis* is extremely selective of soil texture, at least for surfacing of the mound. More importantly, because of the critical nature of nest site selection prerequisite to proper nest construction and to the ultimate survival of the species, Cole **(1932, 1934, 1940)** showed that ants adapted to desert or semi-desert environments nest predominantly in areas of fine to coarse sand. Commenting on nest relocation of the related species *Pogonomyrmex barbatus*, van Pelt **(1976)** validated Cole's earlier work, stating that soil type could be a critical factor in nest site selection. Hess (1958), however, indicated that soil pH and salinity might also act, either independently or in concert with texture, to limit the range maximum of ants. Although no studies have examined the possible influence of slope orientation on western harvester ant distributions, aspect is known to impact plant distributions because of changes in local microclimates. It seems reasonable, therefore, that, in regions where an abundance of the ants occupy these microtopographic features, there might be some relationship between ant locations and aspect.

However, the selection of nesting sites for colony founding depends less on prevailing regional or site level environmental conditions than on landscape level behavior of the fertilized female after the nuptial flight (Hess **1958).** This behavior is most likely determined by landscape queues rather than site specific texture or regional climatic regimes. Based on work by Kannowski **(1959),** Nagel and Rettenmeyer **(1973)** studied landing-site selection during harvester ant colony founding. Their results confirmed that the newly fertilized queen prefers bare soil patches or areas with little vegetation to begin the nest. It is likely that landscape features exhibiting this visual signal, and occurring outside the existing range, may encourage range expansion of the species.

Anthropogenic landscape features, because of the rapidity with which they appear, may encourage greatly accelerated expansion of species queued to them. This would be especially true where linear features such as roads and their verges reach, in interconnecting networks, well beyond the species' range. If these networks provide suitable nest site clues within regions of appropriate environmental conditions or where viable microhabitats exist nearby, they may act as an extensive network of corridors supporting or even fostering range expansion.

Studies have already documented some impacts of roadways on animal populations. Buckner **(1957),** Oxley *et al.* **(1974),** Wilkins **(1982)** and Mader **(1984)** have shown that roads may act as barriers to movements of small mammals, and Merriam, *et al.* **(1989)** have shown that these barriers can even result in genetic isolation of small vertebrate populations. Road verges are known to provide access to food for white tailed deer (Bellis and Graves **1971)** and mule deer and Elk during critical weather periods (Rost and Bailey **1979),** supply waterfowl nesting habitat (Oetting and Cassel **1971),** encourage replacement of seed eating mammals by grass eating mammals (Baker **1971),** provide cover for nesting pheasants, and furnish habitat for many plant species, some of which are rare or endangered

(Joselyn, *et al.* **1968).** Although many of these studies examine the movements of animals along the roads or their verges, only one has concentrated on the potential for these linear features to act as dispersal routes. Getz *et al.* **(1978)** showed that roadsides do act as dispersal routes for a variety of small and medium sized mammals. In their study of two species of microtine rodents in central Illinois they demonstrated a range expansion for the meadow vole, *Microtuspennsylvanicus,* of between **90** and **100** km along interstate highways within a six year period. Because these mammals are very mobile, the rate at which they are able to extend their range is rapid; It remains to be seen whether such roadsides can act in a similar manner on other species, especially those which are not as mobile and do not generally extend their range over such short time frames.

The objective of this study was to examine regional, landscape and site level controls on range expansion of the western harvester ant. At the regional level, I examined the impacts of temperature and moisture regimes on the species range. Specifically **I** attempted to verify the potential of climatic cycles to determine range migration, as suggested by Wheeler **(1962).** At the landscape level, this research extends the work of Getz *et al.* **(1978)** to determine if *Pogonomyrrnex occidentalis* reacts in a manner similar to the meadow vole by extending its range by queuing in on the barren appearance of country roads and nesting in the adjacent roadside ditches. In examining the impacts of these landscape level queues, I hypothesized that, although roads and their verges provided avenues for range expansion, they were not the impetus. At the site level, I examined the possible effects of soil texture, pH, and electrical conductivity to further verify the work of Gregg **(1944)** and Hess **(1958.** Additionally, at the site level, I examined the potential impacts of roadside ditch orientation on ant distributions within its range because of the possible relationship between orientation and site-specific microclimate.

Methods

The rate of range expansion of harvester ants is notably slower than that of the rodents studied by Getz *et al.* (1978), additionally, the mated queen is the only member of the colony which can produce a new colony beyond the existing species range. Because the mating cycle is generally a slow and somewhat unpredictable process, the concomitant inability to trap mated queens and record their larger scale movements through time as was done in the rodent study complicates the analysis. Instead, the presence or absence of ant mounds must be used as surrogates for these colony founding activities; any analysis of range changes must have detailed surveys performed at large temporal separations. Fortunately, locational baseline information necessary for analysis of ant distributional patterns is readily available for North Dakota through a large collection of county-wide surveys produced under the tutelage of George C. Wheeler, ultimately resulting in a state-wide biogeography of North Dakota ants (Wheeler **1962,** Wheeler and Wheeler **1963, 1977).** Within these volumes, the first known sighting of ***P.*** *occidentalis* in North Dakota is considered to be McCook's **(1882)** in which he stated that the ant does not occur any distance east of the Missouri River. This was also the first indication of the northeasternmost range extent of the species. Later survey data, particularly that acquired during Moreland's **(1966,** Table **1)** research in Burleigh County, North Dakota demonstrated that *P. occidentalis* range and internal spatial distribution at its northeastern extent remained essentially unchanged. The existence of these surveys, and because they are the only two counties where the species occurs east of the Missouri River, Burleigh and Emmons Counties in North Dakota were selected as the study area for the present research (Figure **1).**

To determine whether range expansion had taken place, the northeastern range extent of the region known to be occupied in **1966** was again checked and documented by DeMers (1980b) in **1978** and **1979** and found to be, with only very minor differences in individual mound locations, identical to Moreland's observations. These locations were compared to a later survey undertaken in the sum-

Table 1. Comparison of Road Mileages within and Beyond ***P.*** *occidentalis* Range.

Roads within ant range		Roads beyond ant range	
North/South Miiles:	196.0	North/South Miles:	238.5
East/West Miles:	218.0	East/West Miles:	233.25
Northeast/Southwest Miles:	10.25	Northeast/Southwest Miles	4.0
Northwest/Southeast Miles:	18.0	Northwest/Southeast Miles:	16.0
Totals:	442.25	Totals:	491.75

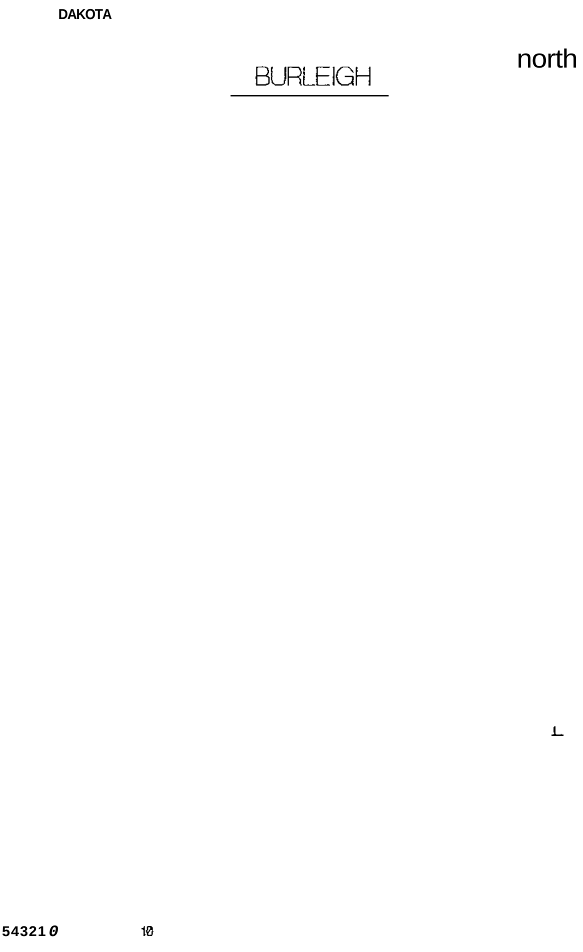

Fig. ***1. P.*** *occidentalis* range within Burleigh and Emmons Counties, North Dakota showing isochrones for 1990 and pre-1990 locations.

mer of 1990. All of these locational records were mapped as point locations. Isochrones were produced to show any major locational changes, and the hypothesis of co-occurrance of ant locations with roads in the region was examined by overlaying the map of ant locations with a map of roads in the region (Figure 1).

Regional climatic factors for range expansion, particularly as they relate to the behavioral adaptation of ***P.*** *occidentalis* to xeric conditions, were considered as possible causal mechanisms for range expansion. The Bismarck AP whether station records were selected as representative of the study region because of its complete set of records and nearly central location within the study area occupied by the species. Temperature and precipitation data for this location were collected from 1966, the oldest date with quantitative locational data, through 1990, the date of the last ant survey in the region. From these data a water budget was calculated using Thornthwaite's (1948) formula for potential evapotranspiration corrected for daylength, to ascertain first, whether any climatic anomaly might correlate with any range movements which might be detected, and second, if a long time build-up might account for such movements.

Landscape level examination of the hypothesis that roadside ditches constitute avenues of range expansion, but are not the driving force, the density of roads was examined by measuring differential linear miles per unit area within and beyond the species range. To do this, **30** random locations within the range and **30** random locations beyond the range were selected on the county road map (Scale 1:31,665), and a circle of 5.08 centimeter (2 inch) radius was drawn around each spot location. Separating the roads based on direction (i.e. north-south, east-west, northeast-southwest, and northwest-southeast), the length of roads was measured for each circle within each of the two test regions and then tabulated. The two sample groups were tested for similarity with the student's t test.

Because roads were hypothesized to provide range expansion corridors, but that they do not act as a driving force or impetus for any range expansion, site-specific factors, based on the behavioral characteristics of the species were examined to identify possible driving forces. Because of the close association between this species and soil characteristics, it was necessary to determine whether or not soil differences might be limiting factors to range extent of *P. occidentalis* if no range expansion had taken place, or whether significant differences between the soils within and beyond the range might contribute to range expansion likelihood. A total of 148 soil samples were collected, 118 at locations with ant mounds present, and 30 in locations where ant mounds did not occur, both within and beyond the species range, using random sampling stratified to include the largest possible numbers of soil classes in the region. The pH values for these soils were compared to detect any acidic or basic anomalies which might limit *P. occidentalis* range. Electrical conductivity was also examined to determine possible extremes of salinity. These two variables were compared within and beyond the species range using the student's t test for differences in variation about the mean. Finally, texture class determinations were made to look for non-sandy types of soils which are thought to limit this species' range.

To test the hypothesis that there are differential occurrences of *P. occidentalis* based on site-specific microtopographic variances, measurements of slope direction were made in the field at locations where the ants occurred. One hundred two such measurements were made and tabulated. The specific hypothesis was that the species exhibits preferences for azimuthal directions of the roadside ditch slopes. The latter corresponds to an assumption that if there were preferences for azimuth, there would also be an associated increased potential for range expansion where roadside ditch slopes of this direction are more prevalent.

Results

The final field survey during the summer of 1990 showed that, although the range of *P. occidentalis* had not significantly changed between 1966 and 1978, there was range expansion between 1978 and 1990. In its northernmost range extent, the species had extended its range by approximately nine miles, while there was a four mile expansion directly east of the pre-existing range maximum in Burleigh County and over ten miles east in Emmons County (Figure 1).

At the regional level, extremes of potential evapotranspiration (PE) and associated low precipitation (PPT) were found to have occurred several times between 1966 and 1990 with no appreciable expansion of the range being discovered until 1990. The most notable dry years were 1974 (PE = 58.37 cm, PPT = 27.07 cm), 1976 (PE = 64.01 cm, PPT = 28.28 cm), 1988 (PE = 67.13 cm, PPT = 25.84 cm) and 1989 (PE = 63.55 cm, PPT = 28.77 cm). The highest potential evapotranspiration of the entire 25 year period occurred in 1988 (PE = 67.13 cm), together with the lowest yearly precipitation for the same period (25.84 cm). April precipitation during that year was extremely low for regional norms as well, and occurred just as the potential evapotranspiration began to increase rapidly. Additionally, 1989 was easily as severe a drought year as 1976 and immediately follows the extreme drought year of 1988. Perhaps even more significantly, the 1988 and 1989 drought years immediately precede the known documented range expansion of the species in 1990.

The examination of landscape level factors found that, with very few exceptions, the species occurs in disturbed regions of Burleigh and Emmons Counties, with over 95% occupying positions very near the roads. All of the locations of the ants which were found outside the known 1978 range, that is, all those locations indicating range expansion between 1978 and 1990, were found in the sloping sides of roadside ditches. Examination of road network length data showed no significant difference between area within the range and those beyond (Table 1). A total of 442 miles of road were found in samples within the species' range and 492 miles beyond the range. Additionally, no significant differences were found between the amounts of roads in a north-south direction and those in an east-west, nor in the diagonal directions. In the

Table2. Summary soil pH and Electrical Conductivity statistics.

Soils with ant mounds			Soils without ant mounding		
	pH	EC		pH	EC
No. obs.	12373		No. obs.	2626	
Maximum	9	451	Maximum	8.8	215
Minimum	5.2	10	Minimum	5.8	6
Mean	*7.9	103.8	Mean	*7.5	87.27
Standard dev.	0.5	31.50	Standard dev.	0.6	47.20

*Geometric means used for soil pH values.

north-south direction, 196 miles of road were found in sample areas within the species' range and 239 miles beyond the range. East-west oriented roads were measured at 218 miles within the range and 233 miles beyond the range. Northeast-southwest roads measured 10 miles within the range, while 4 miles of road were measured beyond the range; northwest-southeast roads showed 18 miles within and 16miles beyond the species' range.

A Student's t score of − 1.31 (df = 55, p = 0.19) showed no difference between the overall numbers of roads within and beyond the species range. There were also no significant statistical differences between the percentages of north-south oriented roads (t = 1.96, df = **55**, p = 0.055) nor for the east-west roads (t = .73, df = 57, p = 0.47). Diagonal road mileage differences were found to be equally insignificant between the northeast-southwest roads (t = − 1.02, df = 34, **p** = 0.31) and the northwest-southeast roads (t = −.24, df = 55, p = 0.81).

Site level examination of the pH values for soil samples taken next to ant mounds as well as locations where they did not occur show a nearly identical pattern (Table 2). There was no significant difference between the geometric means of the two sets of samples; soils with ant mounds averaging 7.9 and those without mounds averaging 7.5. Only three samples had values below 7.0, pH's of 6.9 and 5.8 were found in samples where no ants occurred, and a value of 5.2 for one soil where ants did occur. Previous study indicated the high probability, because of the overall nature of soils in the region, that the anomalous value of 5.2 is either a measurement error or a typographical error. This cannot be proven; however, other soils located very near this anomalous sample show neutral to basic values, as do most of the other samples. The student's t test showed significant differences between the pH values for soils where the ants occurred and those beyond their range. **A** t value of 2.55 (df = 31, p = 0.016) does not support the null hypothesis that soil groups are essentially identical. Those soils which occur within the ant's range seem to be slightly more acidic than those which occur outside the range.

***Table* 3.** Within and beyond range comparison of soil texture classes.

	Within range		Beyond range	
Texture class	#	To	#	To
Sand	38	31.15	1	3.70
Loamy sand	24	19.67	5	18.52
Sandy loam	30	24.59	6	22.22
Sandy clay loam	20	16.39	1	3.70
Loam	10	8.20	1	3.70
Clay loam	0	0.00	7	25.93
Silty clay loam	0	0.00	6	22.22
Total	122	100.00	27	100.00

Site-specific electrical conductivity values measured for both soils with and without ants present also show no significant differences between the two soils groups. Average values of 103.8 micromohs for soils with ants and 87.27 micromohs for soils without ants show this similarity (Table 2). The student's t test value of 1.65 (df = 33, p = 0.0001) also supports the null hypothesis for soil group similarity. No significantly high values for electrical conductivity occurred in any of the 148 samples, indicating that soil salinity was generally low and relatively stable throughout the region.

Some significant site-specific differences between soil texture classes for soil samples taken in locations with and without ants (Table 3). For locations with ants nearly 92% of the soils were categorized as sand, loamy sand, sandy loam or sandy clay loam – all classes with significant percentages of sand present. While 8.2% of the ants were found in regions with loam soils, not a single mound was found in clay loam or silty clay loam soils. By con-

Table 4. Comparison of ant locational azimuths.

	Number	Percent
Northwest	0	0.00
Northeast	1	0.98
North	3	2.94
Southwest	**4**	3.92
Southeast	**4**	3.92
None	7	6.86
East	13	12.75
West	17	16.67
South	53	51.96
Total	102	100.00

trast, in locations which occurred beyond the ants' range only a single sample was classed as sand, and nearly one half **(48.15%)** of these soils were classed as clay loam and silty clay loam, both of which are low in sand content and high in clay content.

Site level influences on ant distributional patterns were also significant when slope directions were compared (Table **4).** Three directions contributed significantly to the locations of the ant mounds: **51.96%** of the **102** mound locations examined were found on south facing slopes, **16.67%** on west and **12.75%** on east facing slopes. Perhaps more significantly is the relative paucity of ant mounds on slope directions with a northerly orientation. Only **3** mounds were found on north facing slopes, **1** on northeast and none occurred on northwest facing slopes. This is possibly because of the extreme desiccation associated with northwest winds on northerly oriented slopes. There are no data to indicate that this is behaviorally driven. Rather, ant mounds newly developed in these locations probably do not survive the harsh winters.

Conclusions

A substantial northward and westward range expansion of ***P.*** *occidentalis* occurred in Burleigh County, North Dakota between **1978** and **1990.** Regional climatic variables, particularly the occurrence of an intense, but short term drought, appear to have provided the impetus for range expansion. Although relatively severe drought conditions had occurred several times at the margin of ***P.*** *occidentalis* range in North Dakota during the period **1966** to **1990,** none was as severe as that of **1988** and **1989.** Not only was **1988** the driest year during the **25** year period, but it was also succeeded by two additional years which were nearly as severe. During no other time during the 1966–**1990** time frame had such an event taken place.

Between **1966** and **1978** there was no substantial permanent range change, either expansion or contraction, of ant colonies from the existing range. Nor does it appear that any expansion occurred between **1979** and **1987.** A survey of the study area in **1979** yielded no such indications, and climatic extremes occurring between **1979** and **1987** were not nearly as harsh as compared to that for **1988–89.** Additionally, although there would have been ample time for the species range to expand beyond its **1966** extent and then retract without ant colonies being sited during subsequent field surveys, the existence of thatching ants living in and tending to abandoned ***P.*** *occidentalis* mounds, and the overall persistence of these gravel covered structures would leave clues of past occupation. There is no means by which ant locational records can be obtained for the intervening periods; however, the convergence of evidence overwhelmingly supports the contention that the range expansion occurred very near the severe drought event of **1988–89.**

At the landscape level, all of the post **1978** extra-range ant locations occur in roadside ditches, it is evident that this expansion has been accommodated by the microhabitat conditions along these ditches. Despite the presence of the visual queue of bare soil on the roads, and the known environmental advantages of colony founding in the roadside ditches, there is no evidence to indicate that the ditches themselves acted as an impetus for range expansion at all. The road network pattern in the study area had no changed substantially since **1966** when the first detailed survey of the ants was performed. Likewise the associated roadside ditches have existed since that time. Total road length within and beyond ant range, compared to determine if the amount of road and associated roadside ditch might have an impact on the likelihood of range expansion, showed no substantial difference. This result further confirms the hypothesis that, although the roadside ditches do accommodate range expansion of *P. occidentalis,* they are not responsible for it.

At the site level, substrate differences for sites with and without ants were found only in the soil texture and pH values. Only soils which were very high in clay and almost totally devoid of sand showed a total absence of ants. Within the two county study region such soils occur only in widely dispersed, small pockets of marshy conditions. Large expanses of high clay soils do not occur within the study region, but can be found well east of the species present range, in regions known to have experienced glaciation and underlaid by glacial till and exhibiting poor drainage. These regions may mark the potential maximum eastward range of *P. occidentalis,* as well as other animal types (Wheeler and Wheeler **1966),** but this has not yet been tested.

Some soils demonstrated a slightly higher alkalinity level where ant mounds were present than where they were absent. Although statistically significant, the minor difference is not likely to be environmentally meaningful, as the values were generally well within the necessary limits for survival of the species. Within the study area there are no indications that the range extent of *P. occidentalis* has been reached, at least as far as soil pH and EC are concerned. Range expansion is likely to continue well beyond Burleigh and Emmons counties until the limit is reached either due to soil texture or vegetative constraints.

Also at the site level, few ant mounds were found on northerly oriented ditch slopes, and none were found on northwesterly oriented slopes. This adds credence to the selectivity of the species to environmental conditions found in roadside ditches, at least during range expansion. Winter winds in western North Dakota come predominantly from the north and northwest and are both extremely cold and severely desiccating. Mounds located on northerly aspects would be subject to the full force of these winds, which would have detrimental effects on the ant colonies by severely reducing the mound temperature and drying out the colony. It might be expected that if ant mounds did located in these sites they would quickly be eliminated by the effects of wind. This indicates that the ants do not necessarily choose, through some visual queues, against northerly sloping surfaces, but rather that those which do, have a lower probability of survival, however, there are no empirical data that can confirm this.

In contrast, a very large proportion of the ant mounds were located in more southerly oriented ditch slopes. There are two major ecological advantages to this. First, there would be protection from the bitterly cold winter winds because the ditch slopes themselves would slow down the wind and allow snow cover to build up and insulate the mound during the winter. Second, more southerly locations would receive increased amounts and intensities of incoming solar radiation all year long. During the summer months this would operate to increase the temperature of the mound during the early morning hours, thereby serving as a stimulus for the ants to begin foraging for food before the hottest part of the day. I verified that temperature differentials of at least **4** degrees Fahrenheit occurred between the mound surface facing the morning sun and the adjacent horizontal mound clearing. No empirical evidence exists to indicate that the temperature difference causes early foraging. Further, there were no significant differences in the visual appearance of these locations that would significantly attract more fertilized queens, therefore, it is unlikely that the fertilized queens actively selected these slope directions. The higher numbers of ant mounds on southerly oriented slopes may indicate an apparent increased survivability, but this has yet to be proven by field data.

Discussion

It is important not to generalize the results of this study to include southern, northwestern or western range extents of the species. The northwestern extent of *P. occidentalis* borders that of another species of harvester and *(P. owyheei*), that was originally considered to be a variant of *P. occidentalis.* The major difference between the two species is whether or not the basalmost mandibular tooth is offset (Cole **1969).** Similarly, many species of ***P.***

Pogonomyrmex harvester ants border, and even co-occur with the western range extent of ***P.*** *occidentalis.* The southern range extent of *P. occidentalis* may have changed in recent years as indicated by records of several mounds of the species in Mexico (Schmidt *et al.* **1986).** However, there is some question about the validity of the identification of the Mexican records. Individuals in the Mexican sites exhibited one additional tooth on each mandible as compared to *P. occidentalis.*

One might assume that population pressure could account for the impetus for range expansion of ***P.*** *occidentalis* as the competition for food increases. Rather, it seems that the reduction in available food is more a function of reduction in seeds due to the intense drought. Examination of the species colonies in the study area, for example, showed that the distance between mounds in Burleigh and Emmons Counties was frequently as much as several miles even in regions occupied by the ants since the **1960's.** None of the locations showed concentrations even approaching those found west of the Missouri River in North Dakota, and none resembling the concentrations found in other parts of its range, for example in Wyoming.

Finally, if drought conditions account for the **1990** range expansions, one needs to ask whether increased precipitation might eventually eliminate these newly established mounds, resulting in range contraction. It is evident that the species has not yet reached the limits of such environmental factors as soil texture, pH or EC. This brings to bear questions originally voiced by Jeanette Wheeler **(1962)** and which have not yet been answered:

Does the limit of the range of Pogonomyrex occidentalis fluctuate with the wet and dry cycles? If so, what is the speed of the response? Does the food supply determine the edge of the range?

It seems evident that soil factors, especially texture, have an instrumental effect on the distribution of the species. Those soils with little or no sand do not have *P. occidentalis* mounds occurring on them. Additionally, the grassland vegetation which nurtures the species occurs some distance east of the existing North Dakota range, so it is also safe to assume that, if this limits its range maximum, it has not yet been reached. Yet the species has already reacted strongly and quickly to extremely dry conditions by expanding its range. A survey of the study area following wetter climatic conditions would show whether the reverse response occurs and would determine the response time.

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