THESIS

HARVESTER ANT MOUNDS: UTILITY FOR SMALL OBJECT DETECTION IN ARCHAEOLOGY

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY LUCY ELLEN BURRIS ENTITLED "HARVESTER ANT MOUNDS: UTILITY FOR SMALL OBJECT DETECTION IN ARCHAEOLOGY" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF ARTS.

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Abstract of Thesis

Harvester Ant Mounds: Utility for Small Object Detection in Archaeology

Archaeological survey is frequently conducted at a walking pace at 10-m spacing. Under these conditions, detection of small (less than 5 mm) objects is extremely difficult. Unfortunately, time and financial constraints limit the amount of additional detailed survey that can be conducted so the presence of small artifacts is under or unreported. An alternative presented here is to inspect the highly-visible gravel nest mounds built by the western harvester ant, *Pogonomyrmex occidentalis*, for this small material. Present in much of the western United States, this ant was found to reliably detect and collect gravel-like material from distances as far as 20 m from the nest, although most collection occurred within 12 m. Collection occurred at low material densities and from all directions. Small local material deposits were less well detected than broad scale scatters. Offered three sizes and twelve colors of beads, medium beads (2.5-mm, 25 mg) were selected over smaller or larger beads at distances beyond 4 m from the nest. Color preference was not evaluated. In addition, in a large-scale study, ant colonies containing anthropogenic debris were neighbors to other colonies with this material more often than would be expected by chance. Colonies were aggregated so that foraging regions for most colonies overlapped within the 20-m foraging radius. Colonies were most frequently found in areas of disturbance such as arroyo or road edges. In combination, these results suggest that harvester ant mounds can provide an efficient indication of changes in exposure of anthropogenic material on the landscape surrounding these nests.

An attempt to resolve harvester ant nests in fine-resolution satellite imagery to aid in field survey of mounds was unsuccessful due to image seasonality and disk size relative to imagery resolution.

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> *"I followed it past clumps of dirt, a few discarded potato chip bags, and broken glass to the ant pile it called home. ... a mound that rose about four or five inches from the ground. The mound had one opening in the center, and around this opening, scattered about like planned landscaping, were small round rocks and beads. Beads of all colors. I remember the blue, pale green, yellow, red, and even the white beads that were scattered about the opening, childlike decorations or offerings to a god. I watched it enter the pile, and then I lost track of it. It had led me to what I wanted, and I forgot it immediately." (Red Shirt 1998:1-2)*

Chapter 1. Research Motivation

Archaeology seeks to understand and explain past human behaviors through interpretation of the modern day material remnants of those behaviors - the archaeological record. According to Shanks and McGuire, archaeology is a craft, comprised of both thinking and doing elements, that "manufactures archaeological knowledge" (1996:78). They use the analogy of a potter's need for both physical skill and material understanding to create an intended ceramic design. Compared to the potter, archaeologists have little control over the inputs of their work. The original cultural deposit will have undergone multiple unknown and potentially unknowable processes to reach its modern manifestation. A significant challenge facing archaeologists is to be able to reasonably recognize those processes and their impacts in order to establish an understanding of the original material and the behaviors that accompanied its creation, use, and eventual discard.

Schiffer (1987:7-11) separates these processes into cultural and non-cultural formation classes, where "formation" refers to the creation of the archaeological record. Cultural formation processes are those that are induced by human activity after a cultural object's initial period of use and include object loss, discard, reuse, and archaeological recovery or disturbance. Non-cultural processes are the result of natural events such as bioturbation, animal scavenging, decay, burial, weathering, and hydrologic activity. Schiffer stresses that these processes contribute to a transformation rather than a pure degradation of the original cultural deposit. In particular, this transformation, while complex, may evolve in and leave evidence of patterns or regularities that in turn can be recognized, described, and measured. Transformations can occur along dimensions of shape, space, relationship or association, and quantity. Understanding of these transformations is a key part of Shanks' and McGuire's (1996) "thinking" part of archaeology as a craft. Recognizing the footprint of these transformations at the towel's edge (to use an expression from Berggren and Hodder 2003:425) becomes an essential part of Shanks' and McGuire's "doing".

As will be illustrated below, knowledge of non-cultural transformations is often gained from disciplines outside of archaeology (Schiffer 1988:473). In particular, this paper which investigates the actions of a bioturbator, the western harvester ant (*Pogonomyrmex occidentalis* Cresson), draws heavily upon research from the fields of entomology, ecology, geospatial science, spatial statistics, range science, geologic exploration, and behavioral studies. It is through the integration of these studies that behavioral ecology of harvester ants can be evaluated for archaeological utility.

The western harvester ant constructs prominent gravel covered nest mounds in western North America (Figure 1.1). Although infrequently documented as such, these mounds are often checked for small bones by fossil collectors, diamonds and gold by prospectors, and small anthropogenic debris by archaeological surveyors (Bass and Johnson 2003:22-23; Galbreath 1959; Hőlldobler and Wilson 1990:373; Krajick 2001:95, 153, 202; Shipman and Walker 1980; and Wheeler and Wheeler 1986:29). As the introductory quotation from Red Shirt (1998) above indicates, ants manage materials on their mounds and are not simply passive agents that allow materials to become included in their nest structures. From an archaeological site formation standpoint, however, ant-based taphonomy has been poorly investigated. Schiffer (1987:208) in his discussion of formation processes characterized ants as surface foragers whose primary influence on the archaeological record is the creation of tunnels that form krotovinas. Further, while he recognized that birds and packrats displace surface objects, he did not make this same attribution to ants although he cites work by Nash and Petraglia (1984:140) which includes mention of displaced pressure flakes in an ant mound test area. Wood and Johnson (1978:321) and Bass and Johnson (2003:22-23) characterize ants as primarily soil and thus artifact mixers. In contrast, reports by Nagel (1969:69), Reynolds (1991), Krajick (2001:202), and Todd and Schoville (2001) stress that while some materials on ant mounds may be the result of nest excavation or soil movement much mound gravel is purposefully collected by harvester ants from exposed deposits on the surrounding land surface. So although it is known that ants collect materials and that materials of archaeological interest can be found on ant mounds, nothing can be said about the material's source location unless knowledge is available about the collection behavior of

Figure 1.1. *Pogonomyrmex occidentalis* nests and mounds. Left photo is a young colony while the center and right photos show various stages of maturity. (Photos courtesy of 2002 CSUAFS).

the ants themselves. Although extensive research has been done on the western harvester ant's seed foraging behavior, relatively little has been reported with respect to surface foraging for mound covering materials. An improved knowledge of foraging behavior may facilitate the structured use of harvester ant mounds as a tool for archaeological cultural resource assessment.

In arid and semi-arid areas like the American West where covering vegetation is limited, Phase I cultural survey (identification phase) for compliance with Section 106 of the U.S. National Historic Preservation Act of 1966 is often based on surface observation (often referred to as pedestrian survey or fieldwalking) without shovel testing or other excavation (Neumann and Sanford 2001: 97; Orton 2000:71). If significant cultural materials or features with good integrity are not identified in Phase I, it is likely the area will be exempt from further cultural evaluation and planned land use projects will proceed. A good faith effort at determining whether a location has significance or integrity is expected during Phase I, however, this effort must be balanced against project schedule and resource limitations. Investigation of harvester ant mounds may provide a means to increase survey effectiveness (or intensity using the terminology of Plog et al. 1978) for small objects without a significant change in methodology. For example, Bass' (2003:22-23) identification and salvage of Native American burial grounds prior to reservoir flooding in the 1950s and 1960s was predicated on the use of harvester ant mound inspection. In this case, ant excavated material was a primary indicator of sub-surface anthropogenic items, rather than surface deposits, but the concept is similar to the ideas explored here. Bass' ants, like the ones described below, favored previously disturbed areas - in this case grave sites which were otherwise undetectable.

Although governed by state-specific standards, archaeological survey is often conducted using 5-m to 15-m spaced transects examined by a multi-person crew at a walking pace (Banning 2002:41; Derry et al. 1985:17; Orton 2000:81; Wandsnider and Camilli 1992). At this spacing small and large low contrast objects can be difficult to detect but even small harvester ant nests can readily be seen (Burger 2002: 51; Dugas 2001:154; Todd and Schoville 2001; Wandsnider and Camilli 1992:Figure 3). Likelihood of object detection is determined by an object's obtrusiveness and visibility (Banning 2002:40; for additional discussion of object detection and survey effectiveness see Orton 2000 and Schiffer et al. 1978). Obtrusiveness is determined by size and contrast with the background materials, and is a function of the distance and viewing angle of the observer (Banning 2002:48,59). Visibility is a property of the environment and includes the type and resolution of the sensor (for example, the human eye) used to detect the object and the transmission of a signal to the sensor through the medium (i.e., soil, vegetation, pavement, air) between the sensor and the object (Banning 2002:46-47).

Visibility can be significantly impacted by object size and lighting conditions (Ammerman and Feldman 1978:736; Banning 2002:47). Since field lighting is often uncontrollable, Banning (2002:90) suggests that intersecting transects be walked from differing directions to change how sunlight impinges the survey surface.

There is no comparatively simple way to mitigate the issue of small object size, however. In controlled experiments, Wandsnider and Camilli (1992:Figure 3) found that detection rates of objects smaller than 10 mm were less than 25 percent when an average walking pace was used for survey. Detection rates improved with reduced speed but were still on the order of 50 percent. Object detection also improved with stronger contrast in either size or color of seeded objects against background materials. Based on these results some anthropologic materials like brightly colored beads or shiny metals are more likely to be identified than chipped stone flakes or debitage which may be very similar to background materials. Burger (2002:Figure 4.3) found that changing transect conditions from a 70-cm walk (arms-length spacing) to a zero spaced hands/knees crawl (shoulder to shoulder) increased object detection rates by 362 percent. Clearly an easily applied and improved method of identifying small objects and/or determining that small objects are unlikely to be on the landscape could be of benefit to archaeologists and cultural resource managers. Systematic examination of harvester ant mounds may provide such a method.

In addition to using foraging knowledge to determine the source of mound material, the potential exists to claim complete survey coverage if mound spatial relationships can be quantified and mound spacing is found to be sufficiently close. As a consequence, two scales of landscape use are considered in the research presented here:

the fine-scale use by particular ant colonies of the areas surrounding their nests and the broad-scale use of the overall landscape by populations of colonies. Within this framework, the research has two components: 1) determination of harvester ant mound material surface foraging behavior with respect to four specific questions: a) foraging distance, b) foraging direction, c) detection density, and d) deposition pattern using glass beads as surrogates for anthropogenic materials and 2) use of geospatial techniques to identify and examine the distribution of harvester ant nest mounds on the larger landscape. This thesis is organized as follows: Chapter 2) Colony Scale Landscape Use, Chapter 3) Landscape Scale Analysis, and Chapter 4) Remote Sensing Application. Chapter 5 concludes with an overall summary of the research and recommendations for further study.

Chapter 2. Colony Scale Landscape Use

This chapter presents a background of known foraging and behavioral patterns of the harvester ant genus, *Pogonomyrmex*, at the level of the colony and describes recent field research conducted to establish gravel foraging patterns in the species, *P. occidentalis*. As a caveat to the material presented below, behavioral research has not been consistent across all species within *Pogonomyrmex*. Where possible background information is based primarily on *P. occidentalis* studies and then supplemented with information from other species to show both the variety and similarity of behavior across the genus. It is hoped that based on the demonstrated species similarities, the field research described in this chapter can be extended across the genus.

Genus Description

Found only in the New World, the *Pogonomyrmex* or "bearded ant" genus contains about forty-four species (Taber 1998:132-134). Of these the most prevalent and therefore most useful species for North American archaeological survey are shown in Table 2.1. These species are all large bodied, build large or small graveled nests on dry clay loam soils with large colony populations when mature, tend to be aggressive, and to deliver painful stings if disturbed (Taber 1998:17, 139-140). In the U.S., *Pogonomyrmex* ants and their nest mounds can be found in southeastern coastal areas and in arid and semi-arid locations west of the Mississippi River at elevations below 2300 m (Gregg

Table 2.1. Common *Pogonomyrmex* Species Name and Distribution

Species	Common Name	Distribution
P. badius	Florida harvester ant	Florida, coastal regions of Alabama, Mississippi, Georgia, South and North Carolina
P. barbatus	Red harvester ant	Mexico, Texas, southern Arizona and southern New Mexico
P. californicus	California harvester ant	Southern California, Nevada, Arizona, and southern New Mexico, and northwestern Mexico
P. maricopa	Maricopa harvester ant	Northern Mexico, southern Arizona, New Mexico, and Texas
P. occidentalis	Western harvester ant	Western Great Plains and Great Basin including Montana, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Colorado, Wyoming, New Mexico, Arizona, and Nevada
P. salinus (also known as *P. owyheei*)	In older literature also referred to as a western harvester ant	Washington, Oregon, Nevada, Idaho, Montana, and northern California
P. rugosus	Rough harvester ant	Southern California, Nevada, New Mexico, Arizona, Texas, western Oklahoma, and Mexico

Note: Compiled from Taber 1998:104-116,132-134.

1963:331). Additional information on North American harvester ants is provided by Cole (1968), Johnson (2000, 2001), MacMahon et al. (2000), and Taber (1998).

In addition to small object collection, several other attributes of harvester ant colonies make them potentially useful to archaeologists. First, once established the colonies are persistent over time and space. It is estimated that fewer than one percent of queens are able to establish a colony and early mortality of colonies is common.

However, if the colony survives its first two years, it will remain viable through the life span of the queen (Gordon and Kulig 1996:2394). Generally, nests are not detectable by an untrained observer until a colony is at least a year old and during this time foraging is extremely limited. In *P. occidentalis*, colony survival has been estimated at between 20 and 50 or more years, in *P. owyheei* 17 years, in *P. barbatus* 15 to 20 years, and in *P. californicus* 15 years (Coffin and Lauenroth 1990:230; Gordon 1991:383; Keeler 1993:287; Porter and Jorgensen 1988:104; Ryti 1986:36). While queens may live this long and actual life expectancy of worker ants varies by task, individual forager ants have a life expectancy on the order of two to three weeks once they begin foraging (Gordon and Holldobler 1987:344; Porter and Jorgensen 1981:252).

Among *Pogonomyrmex* species, nests are infrequently recolonized by another colony and relocation is limited (Taber 1998:25). One percent of *P. occidentalis* colonies move each year (Cole and Wiernasz 2002:1435). Among *P. barbatus*, some colonies never relocate while some move each year (Gordon 1992a:45). *P. badius* is an exception to this generality in that most colonies will relocate at least once per year and some will move two or more times (Gentry 1974:1336). When movement does occur, regardless of species, the colonies move less than 10 m from their original location (Gentry 1974:1336; Gordon 1992:44; Van Pelt 1976).

Second, nests of mound-building species occur in relatively high densities where they are present (Figure 2.1) making them potentially useful for systematic rather than encounter sampling. Surveys of *P. occidentalis* have shown densities ranging from 6 nests/ha (nests per hectare) up to 75 nests/ha. Nests at the sparsest distribution would be roughly 40 meters apart while at the highest density nests would be 12 meters apart.

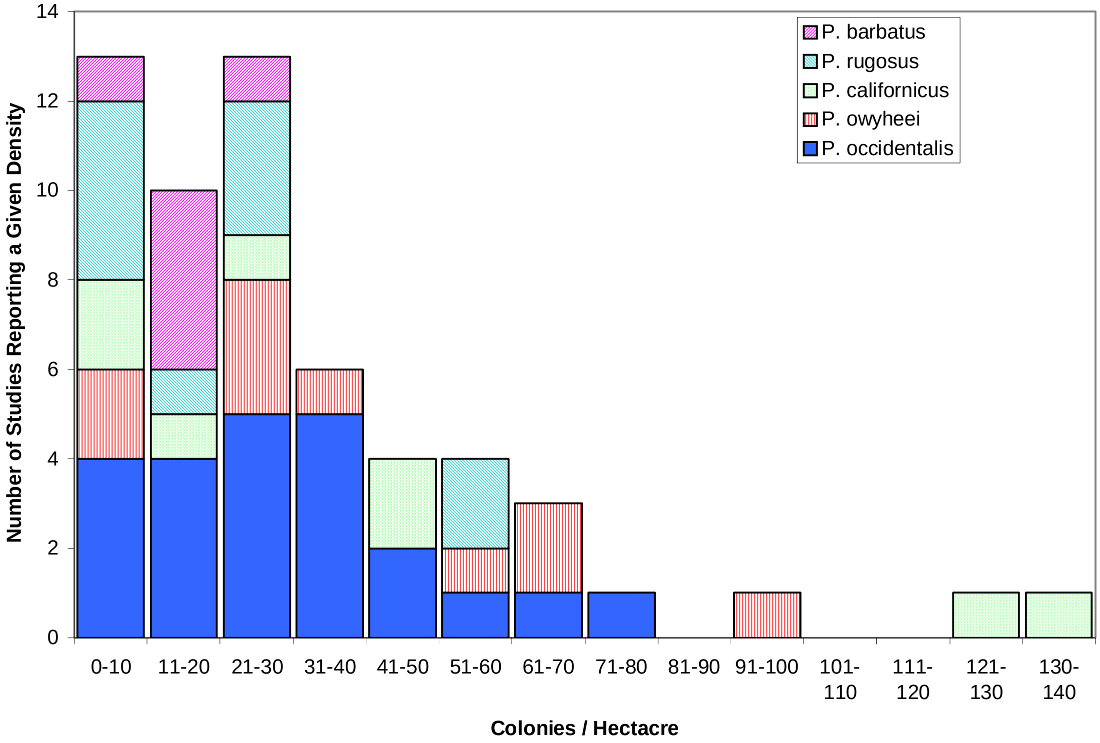


Figure 2.1. Reported *Pogonomyrmex* colony density per hectare by species. (Sources: Bernstein 1975:215; Bernstein and Gobbel 1979:935; Box 1960:382; Carlson and Whitford 1991:128; Clark and Comanor 1975:54; Coffin and Lauenroth 1990:230; Cole 1932a:144; Cole and Wiernasz 2002:1440; Crist and Wiens 1996:304; DeVita 1979:733; Dugas 2001:154; Giezentanner and Clark 1974:218; Gordon 1991:383; Headlee and Dean 1908:177; Holder Bailey and Polis 1987:441; Homburg 2000:171; Hopton 2001:211; Keeler 1988:481; Kirkham and Fisser 1972:57; Kretzer and Cully 2001:13; Mandel and Sorenson 1982:786; Melendez 1963:19; Nagel 1969:Table 58; O'Meilia et al. 1982:582; Parmenter and MacMahon 1983:Table 3; Porter and Jorgensen 1988:104-105; Race 1964:861; Rissing 1988:809-810; Rogers and Lavigne 1974:995; Ryti and Case 1986:446,448; Sharp and Barr 1960:133; Sneva 1979:Table 1; Snyder et al. 2002:407; Soule and Knapp 1996a:339, 1996b:162; Whitford 2003:282; Whitford and Ettershank 1975:Table 1; Whitford et al. 1976:127.)

Third, foraging (at least for food items) is extensive and thorough across a large area surrounding the nest. *Pogonomyrmex* use both foraging trails and individual foraging practices to obtain food at a minimum of 3 m and potentially much further from the nest (patterns vary by species with *P. occidentalis* using both approaches depending upon local conditions, Fewell 1988c:272). Foraging trails of *P. barbatus*, although relatively permanent during a single season, migrate through the colony's foraging range over the course of several years, which suggests that trails could eventually cover the entire area surrounding a given nest (Gordon 1995:655). Even in the absence of foraging trail relocation, individual *P. barbatus* and *P. occidentalis* ants deviate from the trail when they reach the foraging area at the trail's terminus (Fewell 1988c:266; Gordon 1991:Figure 2). Foraging patterns can be characterized as a random walk starting from a habitual direction (Crist and MacMahon 1991a:390). In colonies in which foragers do not use trails the likelihood of complete surface coverage seems even higher.

In addition to variation within individual foragers, the high turnover rate of foragers due to their short lifetimes suggests that any given part of a landscape around a nest will eventually be traversed since foraging memory will be no longer than the life span of an individual forager. Foraging trip duration varies by species but is on the order of 10 minutes (Jorgensen and Porter 1982:383; Morehead and Feener 1998:552). Given a foraging day length of six to eight hours, an active forager might make as many as 50 trips per day, for potentially 1000 trips over their foraging life span. Individual ants have a high degree of foraging direction fidelity during their lifetimes and so are likely to traverse their preferred sector somewhat thoroughly as long as foraging success is good (Bernstein 1975:214; Fewell 1990:49-50).

Fourth, as well as building graveled nests, harvester ants typically remove all vegetation from a broad disk surrounding the mound (Figure 2.2). The purpose of these disks is unclear and theories range from predator defense to prevention of moisture loss by plant roots to a drying area for seed or brood (Taber 1998:21). Whatever their primary purpose, they are easily observed by survey walkers, in aerial photos, in airborne

Figure 2.2. Mound with cleared disc. The mound consists of the large gravel covered central dome. The cleared disk consists of the circular, vegetation free flat area around the mound. (Photo courtesy of 2002 CSUAFS.)

video, and potentially in fine resolution satellite imagery (Crist and Weins 1996; Everitt et al. 1996; Fisser and Kirkham 1970; Todd and Schoville 2001). Due to the high visibility of these denuded areas and the harvesting of seeds, harvester ant seed foraging behavior has been broadly studied with respect to impacts on range land health. Since seeds and gravel-like objects are used for different purposes by the ants, it is unclear how much of this seed focused research can be applied to gravel collection.

Foraging Behaviors

For useful archaeological inference about objects found on harvester ant mounds, collection behaviors with respect to distance and direction need to be understood. Foraging behaviors in some harvester ant species have been studied more intensively than others. Although the information provided below is an incomplete comparison of food and gravel collection behaviors across the species mentioned above, it should be sufficient to show that common *Pogonomyrmex* ants exhibit broadly similar behaviors. To date the longest in situ behavioral studies have been conducted for *P. barbatus* by Gordon and others in the Sonora Desert beginning in 1981 with colony level tracking since 1985 and for *P. occidentalis* by Cole and others in southwestern Colorado since 1992 (see for example Cole and Wiernasz 2002; Wiernasz and Cole 1995; Gordon 1991, 1999).

Seed Foraging

Seed foraging experiments have shown that *P. occidentalis* and its close relation *P. owyheei* will routinely forage for seeds at a distance of 3 to 5 m from the nest and can forage as far away as 30 m (although maximum distances of 10 to 15 m are more common; Crist and MacMahon 1991a:383-384; Crist and Weins 1994:42; Fewell 1988a:404; Jorgensen and Porter 1982:383; Morehead and Feener 1998:552; Rogers 1972:77; Stevens 1965:Table 12; Willard and Crowell 1965:486). Crowell (1963:297) identified foraging overlap between colonies separated by 16 m. Willard and Crowell (1965:487) found that 1 percent of foraging occurred at a 30 m distance from the mound and no foraging (based on 593 observations) occurred at 60 m. Usnick (2000:202) found that foraging distance was significantly impacted by domestic cattle grazing level. Although foraging extended to 18 m (the maximum distance tested) in both grazed and ungrazed areas, in ungrazed pasture most foraging occurred within 6 m of the nest while in grazed pastures foraging levels were similar at all tested distances (6, 10, 12, 15, and 18 m). In comparison, *P. barbatus* forages to 20 m with foraging trail length determined by encounters with same species neighbors (Gordon 1992b: Figure 1). *P. maricopa* forages to 11 m while *P. rugosus* forages to 15 m (Hansen 1978:113; Zimmer and

Parmenter 1998:284). Maximum mean foraging trail length in *P. badius* colonies was found to be 12 m with an average of 7.3 m, although average trail lengths of 3.4 m have also been reported and experiments have been successful with foraging baits placed at 10 m (Ferster and Traniello 1995:674; Harrison and Gentry 1981:1468; McCoy and Kaiser 1990:Figure 6). Based on these reports, *Pogonomyrmex* ants generally forage within 3 to 20 m from their nests; they occasionally go as far as 30 m and it is unlikely that they forage any further than 60 m.

Seeds collected by ants do not necessarily reflect the seed distribution of the surrounding landscape indicating that ants discriminate in seed selection (Crist and MacMahon 1992:1773; Gordon 1993:484; Mull 2003:359). Although most seeds foraged by *P. occidentalis* range in mass from 0.26 to 0.50 mg, they can be as heavy as 5 mg (Crist and MacMahon 1991a:383; Crist and MacMahon 1992:1773). Crist and MacMahon (1991a:391) found that all items collected more than 2 m from the nest weighed less than 5 mg. In contrast, in a seed trial using a seed depot at 10 m, these same researchers found that ants preferred large (> 2.5 mg up to 27 mg) seeds over small ones (Crist and MacMahon 1992:1774). Broome (1988:47, Figure 9) found that seed selectivity varied with distance (up to 15 m) and time of year with increased selectivity at greater foraging distances and during the later part of the foraging season. A preference for retrieval of more valuable objects from farther distances may be explained by central place foraging theory, that is, a forager working from a central base will maximize the return on its foraging trip by bringing back the most valuable item it can retrieve (Hőlldobler and Wilson 1990:387). For a species comparison, the majority of seeds collected by *P. maricopa* averaged 1.5 mg, while the larger bodied *P. rugosus* collected seeds that averaged 2.7 mg (Hansen 1978:112, note correction of units from original publication). Interestingly, *P. occidentalis* foragers will switch to a new selection when a novel seed is offered even if it is a slightly less preferred seed based on food value; presumably this creates dietary diversity in the colony food stores (Fewell and Harrison 1991:382). This desire to maximize foraging return and to create variation in diet may carry over to a preference for variation in mound material collection, suggesting that since anthropogenic materials are novel and can be large, that they might be collected in preference to ordinary surface gravel.

Fewell (1988b:44) found a mean load (including all foraged items) for *P. occidentalis* of 8.1 mg or a burden rate of 2.34 where burden rate is given by load weight plus body weight divided by body weight. This corresponds well with the burden rate of 2.63 found by Crist and MacMahon (1991a:383) and is somewhat higher than the 1.9 value determined by Morehead and Feener (1998:550). Burden rates for other species are as follows: *P. barbatus*, 1.1; *P. maricopa*, 1.24; and *P. rugosus*, 1.19 (Hansen 1978:112; Morehead and Feener 1998:550).

P. occidentalis and *P. owyheei* have been shown to forage in all directions from the nest although individuals demonstrate preferred directions (Fewell 1988c: 267, 1990:49-50; Jorgensen and Porter 1982: 382; Willard and Crowell 1965:487). *P. owyheei* will also enter all types of surrounding vegetation although low vegetation is preferred (Willard and Crowell 1965:487). *P. occidentalis* uses both individual foraging and trunk trail foraging and switches behavior based on vegetation density (Fewell 1988a).

Crist and McMahon (1992) found seed density on big sagebrush steppe near Kemmerer, WY to be a function of yearly conditions and that undershrub densities were similar to interspace areas. Average density was assessed each month during the summer growing season with the lowest monthly average of 400 seeds/m^2 occurring in August within 7 m of ant nests (Crist and MacMahon 1992:Figure 1). During a more productive growing season the maximum seed density near nests averaged 2000 seeds/m^2 in July. Seeds were more abundant at distances between 7 and 12 m from nests. Mull and MacMahon (1997) at the same location tested for ability of ants to find seed patches at low and high density at given distances from the nest and nearest trunk trail. They found that, although ants took longer to find high density patches up to 2 m from a trunk trail and low density patches 100 cm from a trail, all seed patches were found. The average low seed density of 400 seeds/m^2 from Crist and MacMahon (1992) was used for the low density trials and continuous seeds were used for high density trials. In the short grass steppe of northeastern Colorado, the seed bank (surface plus 5 cm depth) averaged 780 - 1140 seeds/m^2 (Coffin and Lauenroth 1989:54). The sagebrush steppe seed bank (surface plus 5 cm depth) of southeastern Idaho averaged 1700 seeds/m^2 (Nowak et al. 1990:194). Reichman (1979:1087) found that ants only recovered surface seeds and failed to locate those buried at 1.5 cm. To summarize, harvester ants can maintain viability at surface seed bank densities as low as 400 seeds/m^2, collect surface seeds weighing less than 5 mg but this may vary by distance, and exhibit selectivity in seed foraging while foraging in all types of vegetation.

Gravel Foraging

As a secondary outcome of seed foraging studies, gravel collection has occasionally been recorded. Gravel collection rates for *P. occidentalis* have been reported at between 3 and 28 percent of all foraged items (Fewell 1988b:26; Crist 1990:166; Rogers 1972:Table 19, Table 26). Usnick (1999:75) found that non-food items (mostly gravel but also including insect and plant parts, and bird feces) accounted for 48 percent of foraged items and that this level was not effected by cattle grazing level. In *P. owyheei*, Jorgensen and Porter (1982:383) determined that rocks were retrieved in nine percent of foraging trips (n = 1,450 trips). In contrast, gravel collection by *P. californicus* accounts for less than two percent of foraged items (Ryti and Case 1988:2002).

In *P. occidentalis*, gravel foraging rates may vary by time of year although reports are inconsistent. Rogers (1972:Table 19, Table 26) found that most gravel was collected during June, July, and September with little collection in August. Usnick (1999:78) found a similar pattern with a peak in October rather than September. In contrast, Crist and MacMahon (1991b:272) found gravel foraging peaked in July and August and Eddy (1970:23) found most intense nest repair activity in March and April. These differences may be explained by variations in geography and local climate or may simply reflect idiosyncrasies between mounds in response to local disturbances or colony needs.

In a *P. owyheei* foraging study, gravel weight was reported to be 12 mg (Jorgensen and Porter 1982:383). In the same species, Reynolds (1991:121) found that native gravel in a rebuilt mound averaged 17.1 mg; his slightly heavier experimental aquarium gravel (22.4 mg) was not different enough to effect foraging behavior. Nagel

(1969: Table 33, Table 34) found that *P. occidentalis* mound gravel (based on three mounds) averaged 25 mg with an average length of 3.76 mm and width of 2.76 mm. Sixty-four percent of mound gravel was between 2.00 - 3.36 mm in size, smaller gravel between 1.00 - 2.00 mm comprised another 16 percent (Nagel 1969:70). Todd and Schoville (2001) found scavenged trail gravel on a mound to average 4.7 mm, while the average size of gravel on the trail itself was slightly larger at 6.7 mm. Mandel and Sorenson (1982:787) suggest that *P. occidentalis* will collect any sand particles that will fit within their mandible spread that exceeds 2 mm. *P. rugosus* mound gravel consisted of 4 mm material (Dugas 2001:154). For comparison, a fossil-bearing mound of *Messor barbatus* (an African harvester ant) had gravel ranging from 1.00 to 11.00 mm in size, averaging 3.67 mm (Shipman and Walker 1980:496). Maximum recorded single loads for *P. occidentalis* range up to 47.4 mg and 95.4 mg (Fewell 1988c: 274; Morehead and Feener1998:550).

Based on comparison with aggregates found on the mounds, Nagel (1969:71) speculated that gravels were selected based on size rather than weight. The absence of gravels from the adjacent soil surface or the mound subsurface material lead him to conclude that most of these materials were obtained from nearby man-made surfaces (Nagel 1969:81).

Few studies have recorded actual gravel foraging distance. In an experiment using colored aquarium gravel deposited in concentric rings around a deliberately destroyed mound, Reynolds (1991:120) found roughly equal collection of gravel from all rings starting at the mound edge and extending out to 2 m. Todd and Schoville (2001) deposited uniquely colored glass beads in nine concentric bands around a mound to a distance of 5 m (50-cm wide bands). Beads were quickly collected from all color bands. Beads from the 5-m and 4.5-m bands were found on a mound located 20 m from the 5-m band, suggesting a gravel foraging distance of up to 20 m.

Mound maintenance is an important activity for all harvester ants. In a set of mound destruction experiments, mounds were rebuilt in as little as 12 days and always in less than a month (Cole 1932b:246). Rebuilt mounds are often slightly larger than the original. Although variable by time of day, nest maintenance and midden work use about 50 percent of a *P. badius* exterior work force (Gordon 1984:408, Figure 2). Disturbances in the form of charcoal removal from middens in these colonies were repaired within seven days (Gordon 1984:405).

In aggregate, these results suggest that harvester ants actively forage for gravel over the same area that they forage for seeds (out to about 20 m), prefer gravels about 25 mg in weight and 3 to 4 mm in breadth, and are highly active in mound maintenance and gravel collection. An anthropogenic item on the surface with the appropriate form factor and weight will probably be collected for mound maintenance.

Foraging Investigation

To further explore and understand gravel collection patterns in *P. occidentalis*, a series of experiments was conducted during the summer of 2003. This section discusses those experiments and the results obtained. The design of the experiments was intended to identify gross surface foraging patterns that could be used as the basis for more extensive and comprehensive testing in the future.

Study Site

All experiments were conducted near the Hudson-Meng Bison Bonebed (25SX115) unit of the Oglala National Grasslands, in the Nebraska National Forest, United States Forest Service, near Crawford in northeastern Sioux county, northwestern Nebraska during the summer of 2003 (Figure 2.3). The 12-ha study site at an elevation of 1280 m is a mixed grass prairie / badlands dominated by western wheatgrass, needleandthread grass, and blue gamma with downy brome infestations as well as yucca, sagebrush, and prickly pear with adjacent ponderosa pine uplands (Johnson and Larson 1999:11). Average precipitation at Fort Robinson, Nebraska (about 32 km south of the site) between 1931 and 1960 was 45 cm (range 27 cm to 75 cm) and average temperature was 8.8° C (range 1.7° C to 46° C; Agenbroad 1989:3). Winters are characterized by cold temperatures and high winds. The early summer of 2003 was considerably wetter and stormier than prior years, particularly the drought year of 2002. However, during the later part of the summer, the weather was very hot and dry (author, personal observation). The surrounding area contains evidence of on-going occupation since Paleoindian times in the form of chipped stone artifacts, hearths, and ceramics; surface survey has been highly productive (Agenbroad 1989:17).

Gravel mound building harvester ants in the study area are limited to *Pogonomyrmex occidentalis;* a thatch mound building ant is also present as are many small bodied ground nesting ants. Only the *P. occidentalis* colonies were included in this study. Survey work during the summer of 2002 by the Colorado State University Archaeological Field School (CSUAFS) included a location and attribute survey of the surface harvester ant mounds on the 1200-ha area surrounding the study location

Figure 2.3. Photograph of study area. The 12-ha 2003 study area encompassed the grassy slope in the foreground to the gravel roadway detectable on the far left just below the tree line. (Photo by author.)

(Schoville et al. 2002). This survey indicated that the smaller 12-ha study site had sufficient mound density to facilitate experiments and minimize long-term contamination of the landscape.

Test mounds were selected from those in the eastern section of pasture 34, north of Forest Service Road 918. This area was disrupted by a two-track road (FS 918) and seasonal cattle grazing, and could be easily monitored during the experimental period. Although having no recorded cultural sites, the area did contain some ant mounds with chipped stone found during the 2002 survey and was easy to access for visitor demonstrations and monitoring. Further, the land surface in the area was relatively homogenous leaving the introduction of experimental materials as the major variable between ant colonies. The study area for the 2003 field season is shown in Figure 2.4. Three additional study areas (not shown) were established in high traffic areas near the research camp site, the public restroom building, and the bonebed enclosure. These additional study areas were used for preliminary evaluation and public demonstrations.

Materials

Beads. As a surrogate for gravel and anthropogenic materials, opaque glass beads were used for experimental materials due to the similarity of glass to gravel across a variety of physical factors (see Appendix A). A 2.5 mm glass bead (roughly cubic in shape) weighs about 25 mg, well within the size and weight ranges used by harvester ants as described in the previous section. In addition, previous experiments had shown that ants would collect beads, beads were easy to obtain, easy to disperse, and easy to observe in the field (Todd and Schoville 2001). Although fairly similar to gravel in shape, chunky cylindrical glass beads are a far from perfect surrogate for anthropogenic materials such as chipped stone which is often flat and thin. Beads may actually provide a worst case scenario for foraging since harvester ants generally avoid seeds with smooth outlines and very rounded shapes (Pulliam and Brand 1975:1163).

Depending upon the particular experiment up to twelve colors (black, white, yellow, red, orange, light green, dark green, light blue, dark blue, maroon, light purple, and dusty pink) and three sizes of beads (#10/#11, about 1.5 to 2.5 mm diameter weighing 11 mg; #8, 2.5 mm at 25 mg; and #6, 4 mm, 75 mg) were used. Aside from sorting beads to remove any without center holes, the beads were "as shipped" by suppliers from China (about 25 percent of beads) and the Czech Republic (75 percent). Field handling was minimized by prepacking beads into small plastic zipper bags of

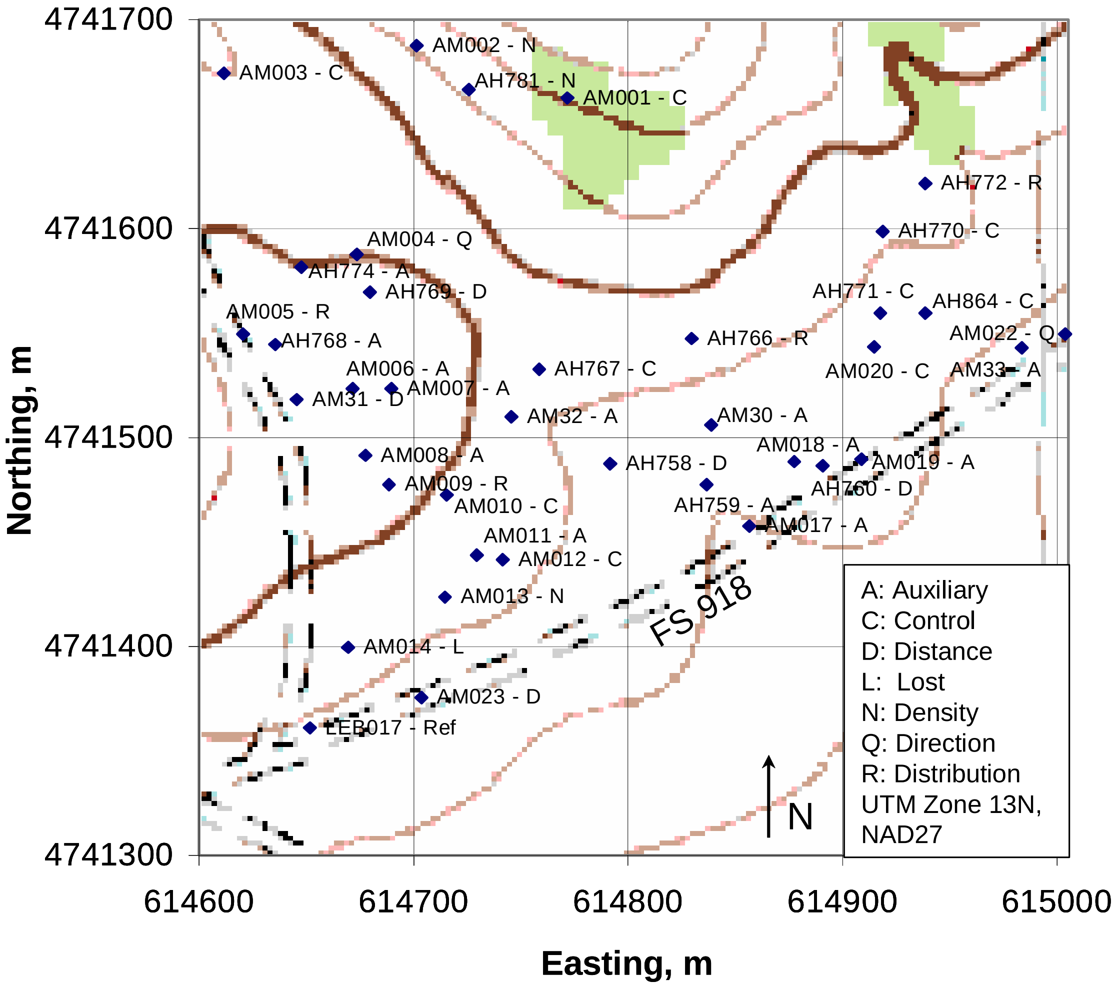


Figure 2.4. Map of study area for 2003 field season experiments. Symbols show mound location, identification number, and type. Bounding the study area are a gravel road seen on the left edge of the map and a two-track dirt road running from lower left to upper right center. Figure 2.3 was taken from upper right looking to lower left on this map. Topographic contour intervals are 6 m (20 feet).

roughly 900 beads of a single color and size (sufficient to cover the perimeter of a 4.25-m radius circle with a band 0.25 m wide with three bead sizes for a total of 400 beads/m^2) or 1200 beads (same coverage but with only two sizes of beads). For low density experiments, bags containing the required number of beads were prepared. Beads were apportioned to bags based on weight rather than count so there was some degree of variability in actual deposition. Where both suppliers of a given bead color were used, the ratio of China /Czech beads was held constant within each bag. All light green and maroon beads were sourced from China and all purple and pink beads were sourced from the Czech Republic.

Dispensers. All bead sizes were dispensed simultaneously using two or three plastic food storage containers with appropriately sized holes drilled into each lid. To dispense, the containers were turned lid side down and held away from the body as a field assistant walked a pre-defined circle around the experimental mound shaking the dispenser as needed. The circle was rewalked in the same direction if any beads remained in the dispenser after the first circuit. Dispensing was avoided during very windy periods. The desired dispense pattern was 0.25 to 0.5 m wide with a dispense rate of 400 beads/m^2. This deposition level was selected based on the lowest reported seed bank density information described earlier. To achieve lower dispense rates for testing with lower density an appropriate number of holes was blocked in the dispenser lids. For experiments requiring a small areal deposit of beads, beads were simply shaken out of the prepackaged zip bag onto the ground.

Experimental Design

Five experiments were designed to detect colony level foraging patterns of western harvester ants for mound material. These experiments were designed to determine experiment material acceptance and then using these results determine foraging distance, direction, density, and distribution responses.

Experimental mounds were defined as those mounds to which beads were deliberately applied in concentric rings or at a predetermined distance from the mound

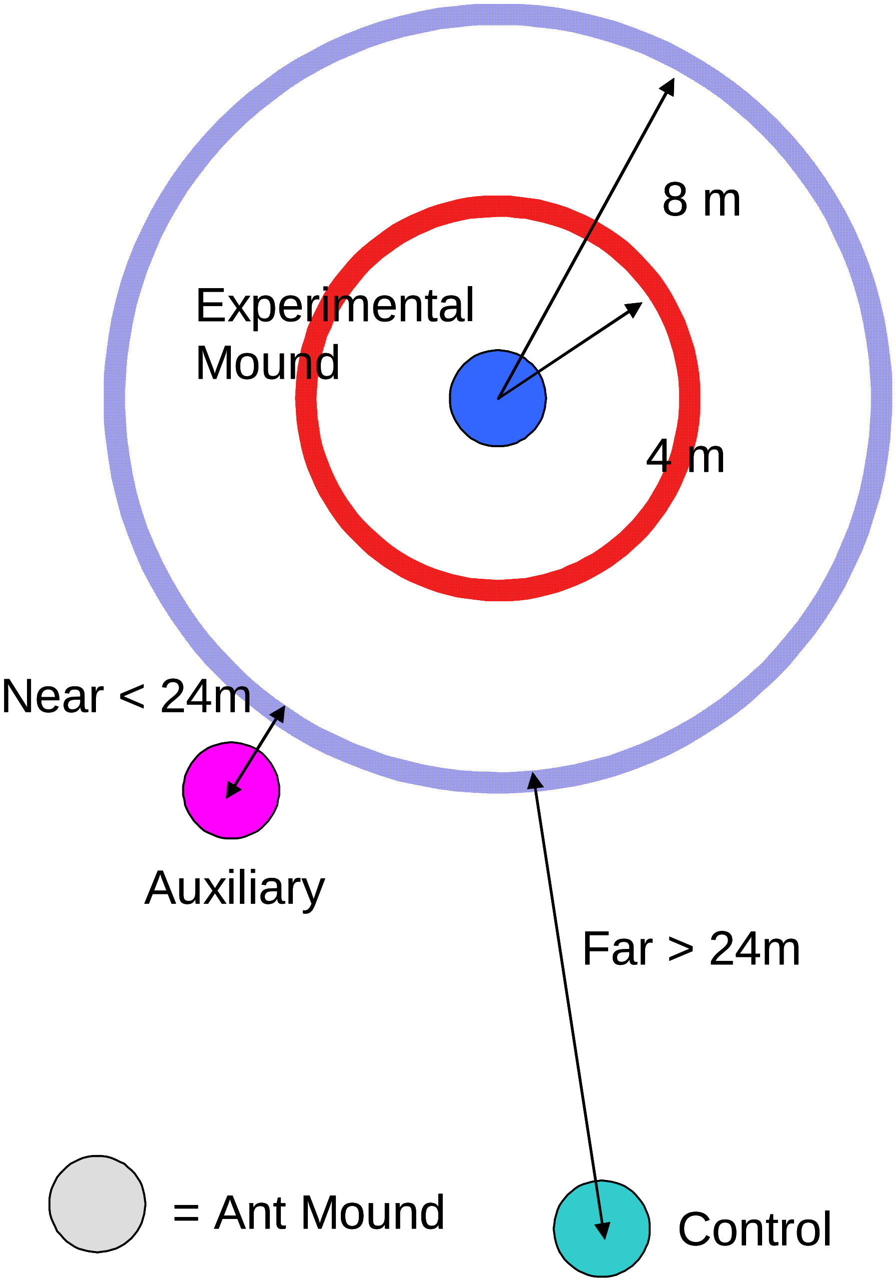


Figure 2.5. Mound definitions. Mounds farther than 24 m from a bead deposit (shown here as circles around the experimental mound) were assigned the status of "control". Mounds within 24 m of a deposit were assigned the status "auxiliary".

(Figure 2.5). Control colonies were those believed to be far enough away from any experimental bead deposits so that any beads found on them would have to be due to non-ant causes such as birds, wind, or cow transport. Mounds that fell within the sphere of influence of an experiment were designated as auxiliary mounds. After experiments were setup an arbitrary cutoff of 24 m was established to separate auxiliary and control colonies. It was possible for an experimental mound to also be an auxiliary mound for another experimental mound and for an auxiliary to be an auxiliary for more than one experiment. In total, experiments were conducted on 17 mounds, 15 mounds were strictly auxiliaries, 4 mounds were both auxiliaries and experiments and 8 mounds were counted as controls, excluding one colony which not be located after week six.

The following section describes each of the five experiments in more detail.

1. Qualification. Three mounds were treated with a combination of all twelve colors and all three sizes at a distance of 2 m (one mound) or 4 m (two mounds) at a density of 400 beads/m^2. Mounds were observed through the following day to determine whether the ants failed to collect any color / size of bead or whether any color / size was particularly difficult for observers to detect. These mounds were located near the public restroom building and near the research camp for convenience in early observation. Through the course of the study period, they were observed for activity and any obvious rejection of beads but were otherwise unmonitored. Due to their convenience, these mounds were used for demonstration purposes for training and visitors. A fourth mound near the bonebed enclosure was treated with 10 colors of medium-size beads and was used for visitor display. This mound too, was monitored for any significant changes in ant collection behavior during the study period but was not included in the results presented below.

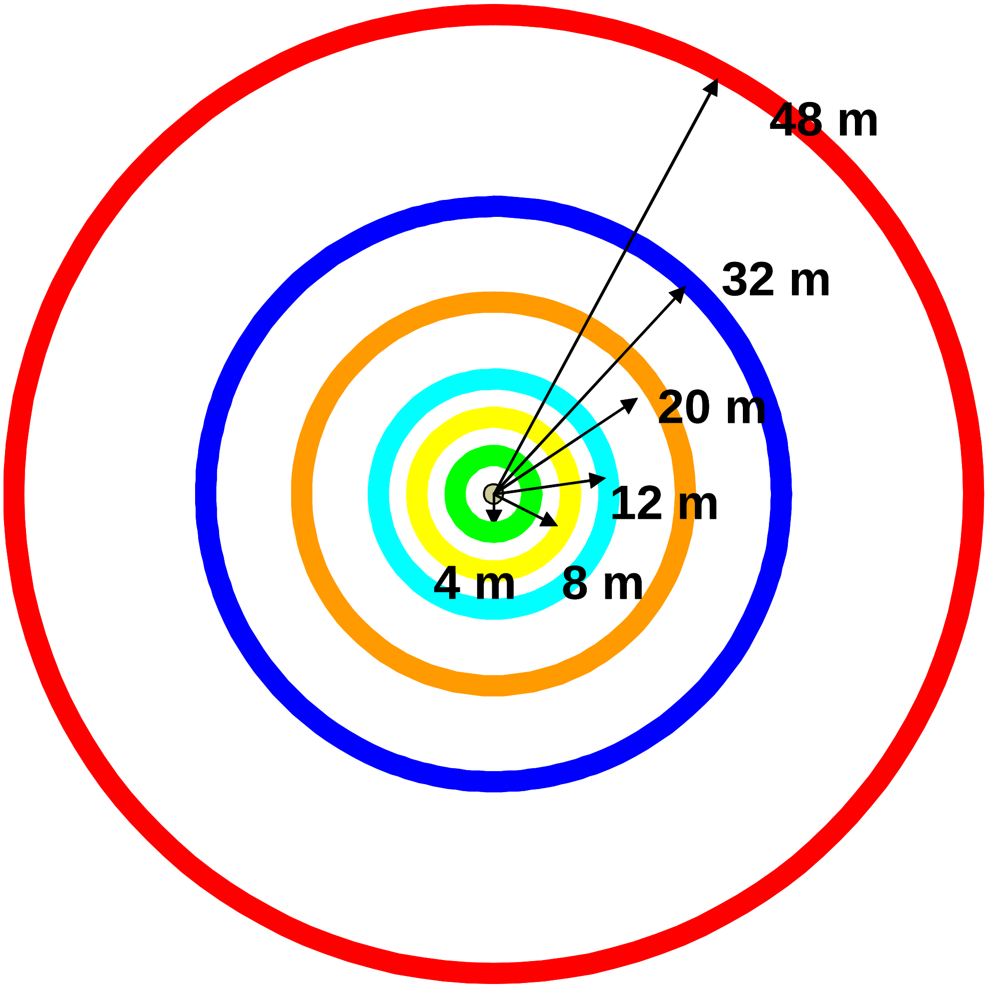


Figure 2.6. Distance experiment. The distance experiments consisted of a set of concentric rings deposited around the experimental mound. Beads in each ring were dispensed at a uniform rate of 400 beads/m^2. Only one mound included the 48 m ring.

2. *Distance.* Five mounds were set up with concentric colored bands of 400 beads/m^2 at distances of 4, 8, 12, 20, 32 and 48 m (1 mound only) from the mound (Figure 2.6). Bead dispensing for a distance experiment is shown in Figure 2.7. Color choice and order was randomized between mounds. Based on results from an early experimental colony near a two-track road, one distance experiment was configured with differing bead colors in vegetation and the nearby road. In another distance experiment,

Figure 2.7. Dispensing of beads for a distance experiment. Individual at extreme right is standing at the mound. Individuals at far upper left are 48 m away. Other individuals are spaced as shown in Figure 2.6. (Photo courtesy of Paul Burnett.)

some beads from the 12 m band were inadvertently deposited at the 8 m ring, so this mound essentially had beads only at four intervals 4, 8/12, 20, and 32 m.

3. *Direction.* Two mounds were set up with 4 colors of beads in each of four quadrants at a distance of 8 m from the mound (Figure 2.8). Quadrants were centered on the door orientation (Quadrant 1) and proceeded clockwise by 90° increments around the mound. Beads were deposited at 400 beads/m^2 in a combination of large and medium (one-half each) beads.

4. *Density*. Three mounds were treated with low density bead deposits at 8 m from the mound at one of the following deposition levels: 200 beads/m^2, 100 beads/m^2, or 50 beads/m^2.

5. *Distribution.* Four mounds were treated with a single randomly oriented deposit 8 m from the mound (Figure 2.9). The deposit consisted of 400 beads (200 large, 200 medium) of a single color dropped in within a circular area 20 cm in diameter.

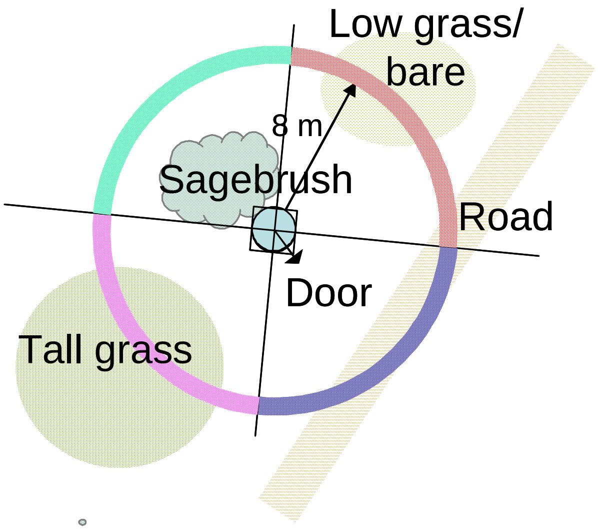


Figure 2.8. Direction experiment. Beads were deposited along an 8-m circle divided into quarters. A different color of bead was used for each quarter circle. The first quarter was centered on the mound door.

Experiments were setup during the week of June 2, 2003 with the assistance of the CSUAFS and by the researcher during the following four week period. Slightly more than 300,000 beads were dispensed around experimental mounds. Table B.1 (Appendix B) contains a detailed listing of each experimental mound and its associated treatment.

A survey at the start of the 2003 field season identified 24 previously unmarked nests and located 18 nests marked during the 2002 survey. Mound locations were recorded using a Garmin model 12XL GPS (global positioning system) unit with 3 to 4 m accuracy. Twenty-two mounds were measured by the CSUAFS with sub-centimeter accuracy using a Sokkia 4B electronic total station or EDM (electronic distance measurement). The root mean square error in Easting between the EDM and GPS coordinates was 1.4 m and 2.4 m in Northing. This is well within the estimated Garmin GPS accuracy of 3 m. Based on observed colony vitality and location relative to other

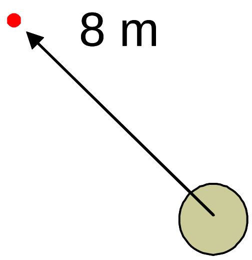


Figure 2.9. Distribution experiment. A local deposit of 400 total medium and large beads was dropped in a circular area 20-cm in diameter oriented in a randomly chosen direction from the mound door.

mounds and experiments, mounds were assigned to experimental treatment or control or auxiliary status.

Data Collection

All mounds were monitored on a weekly basis until week nine when monitoring shifted to every two weeks through week thirteen. Monitoring of experimental mounds consisted of observing each mound and its associated disk and collecting all surface beads or collecting until 5 or 10 minutes of collection time had elapsed and making an estimate of uncollected beads remaining on the mound. Only surface beads were collected, no attempt was made to recover beads that had become buried or embedded in the mound matrix, been taken inside the nest, or that had been moved near the nest but dropped in the surrounding vegetation. Beads were collected using tweezers and placed in a plastic Ziploc bag labeled with mound number, date, collection start and stop time, and subsequently sorted by size / color and counted. Beads were collected based first on uniqueness and then with an attempt to collect a representative sample of the remaining bead types during the collection window. Auxiliary and control mounds were observed each week starting in week three and bead counts by color and size recorded but beads were not removed until the final week of observation.

Status of all mounds was recorded as active or inactive during the observation period. Active mounds were those that had at least one ant outside the mound. If only a small number of ants were observed, the status was noted as "active(n)" where n indicated the number of ants seen. If no ants were observed, the status was noted as inactive. Door count was noted for mounds with low activity levels to monitor whether the colony was recently active.

During the final observation period (week 13), beads were collected from all mounds including auxiliaries and controls. As much as possible all surface beads were removed during the final period with no attempt to collect beads embedded in the mound matrix or retained inside the nest. Due to impending weather conditions, only partial collection was possible on the distance experiments. On these mounds all quantities of poorly represented beads were collected, and then either one-quarter or one-half of the mound, depending upon overall bead density, was cleared of all beads and an estimate of the uncollected beads made from this sample.

Results

As illustrated in Figures 2.10 and 2.11, the ants readily collected and returned beads to their mounds. Fifty-seven hundred beads were recovered from the mounds by the researcher during collection periods. An estimated 1600 beads remained on the mounds after week 13 (due to the time limit imposed by the collection window) but no attempt was made to determine the number of beads contained within the ant mounds themselves. Generally, no pattern was observed with respect to how beads were arrayed on the mounds. For example, there was no apparent preference for dropping beads on the door side and there was no indication of grouping beads by color or size on the mounds.

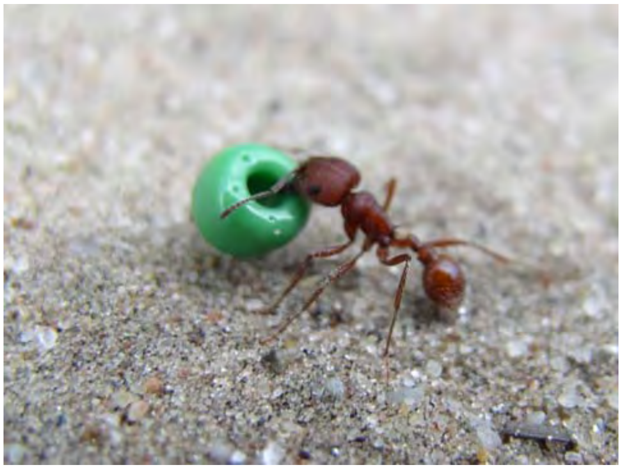


Figure 2.10. Ant carrying bead. (Photo courtesy of Paul Burnett.)

As a consequence of not collecting beads inside the mounds, the results presented here represent a lower bound on ant foraging quantities. Results are presented below in two sections. The first portion presents detailed results by experimental treatment and the second provides summary results.

Additional field data are available in Appendix B. Specifically, Table B.2 contains a detailed listing of each mound's activity status and bead presence/absence by observation week. Tables B.3, B.4, and B.5 contain listings of the final mound designations as well as relationships with other mounds. Table B.6 provides a record of mound physical attributes collected when experiments were set up. Table B.7 provides a listing of UTM coordinates for all mounds as well as three reference locations.

Significant uncontrolled events that occurred during the observation period included a severe wind (60 mph) and hail storm during week two with cool rainy weather continuing into week four. Hot and dry weather arrived by week five, which continued through the end of the observation period. Range cattle grazed in the study area between weeks three and week seven (about four weeks). Grasses started to go to seed (particularly needleandthread grass) by week four; by weeks eleven and thirteen grassy

Figure 2.11. Beads on a mound. Silver disk in lower left is a mound identification tag. Inset at right shows matrix detail. Small medium and large beads can be identified as can three of the colors used: orange, light blue, and light green. (Photos by author.)

vegetation had significantly dried. Throughout the observation period, dispensed but unforaged beads were noticed on the ground surface at the experimental mounds. This indicates that even though many beads had been retrieved by the ants, many more continued to be available for foraging for the full 13 weeks.

Results by Experiment

1. Qualification. No beads were collected from these mounds during the observation period. Instead, the mounds were observed for continuing signs of vitality and any obvious change in bead utilization such as beads being rejected in midden piles or at the edge of the disk. Beads were dispensed around mounds AH215, AH219, and LB01 during a mid afternoon period. Beads were found on these mounds within the hour. The quick recovery of beads suggests that *P. occidentalis*, unlike *P. barbatus*, does not rely on patrollers to set daily foraging patterns (Gordon 1991:390). All bead sizes and all bead colors were found on these qualification mounds within a short time. Although ants accepted all bead sizes and colors, human observation of pink, purple and maroon was difficult so these were eliminated from subsequent experiments.

Three days after AH219, an extremely large and vigorous colony, was set up a visual estimate of beads indicated that over 400 beads had been brought to the mound (out of 2700 dispensed) even though this mound was immediately adjacent to a pea-graveled roadway with very low vehicle traffic (fewer than 20 vehicles per day) which provided a rich source of gravel. By the end of the observation period, most of the beads remaining on the mound were large in size but no apparent bead dump was present around the nest indicating that many beads had been taken inside the mound or had become fully incorporated into the outer mound so that they were no longer visible on the surface. Unfortunately, without destroying the mound it is impossible to completely say how many beads were retrieved by this colony and what fraction was in turn taken into the nest. LB01 was located in a high foot traffic area and was stepped on within hours after being set up. Bead collection probably peaked before the disturbance since fewer new beads were seen on the mound when the ants were primarily involved in nest repair (removing dirt from collapsed tunnels). AM040 was set up to allow videotaping of ants handling beads. To facilitate bead retrieval, beads were deposited in the vegetation immediately outside the cleared disk. Vegetation was fairly thick and only after a significant rainstorm did large numbers of beads begin to appear on the nest. Throughout the observation period, ants continued to rearrange these beads on the mound surface, indicating that mound attendance is an on-going rather than strictly seasonal activity.

AH215 started out as a dominant mound with what appeared to be a relocation about 0.3 m away (but still on the cleared disk). Over the course of the season, the second location disappeared and ant activity remained at the original mound. Overall bead collection for this colony seemed low given the size of the mound and its vigor. Bead discovery may have been hampered by the dense vegetation surrounding the mound.

2. Distance. Beads were recovered from all distances on two of the five distance samples (AH760 and AM023). Two issues in the field confound the distance results shown in Table 2.2 and Figure 2.12. During setup of AH758, about half of the dark blue beads for the 12-m band were applied at the 8-m mark. All beads for both bands were considered 8-m beads for analysis although an estimate of the 8/12 split was made for Figure 2.12. AM031 (Table 2.2) was destroyed by unknown causes (the top of the nest was completely caved in, possibly by a deer which had been seen in the area; the mound was situated on what looked like a hillside animal trail) four weeks after setup so collection results represent only about one-third of the foraging time as the other mounds.

Mean bead counts and return rates by distance are shown in Table 2.2. Removing AH758 did not significantly change the summary values. Collection levels were fairly consistent between 4 and 12 m from the nest at about 1370 total beads although two mounds yielded over 1600 beads each and 4 beads were collected from as far as 48 m. Ninety-five percent of the collected beads on experimental mounds came from within 12 m of the mounds, 98 percent from within 20 m.

There is some indication that foraging distance increased as the summer season progressed. Excluding mound AM023 which was adjacent to a dirt two-track road, no

Table 2.2. Distance Results for Experimental Mounds

Collected Bead Count

Distance	4 m	8 m	12 m	20 m	32 m	48 m
Mound ID						
AH 758	293	591	-	30	0	-
AH 760	398	633	601	16	6	4
AH 769	608	657	339	9	0	-
AM 023	312	436	237	193	68	-
AM 031*	83	42	6	1	0	-
Beads Deposited / Band	2,700	5,400	8,100	13,500	21,600	32,400
Mean	403[a]	579[a]	392[a]	62[b]	19[b]	
(95 % CI of Mean)	(280 - 525)	(495 - 664)	(242 - 543)	(-12 - 136)	(-10 - 47)	4

Return Rate

Mound	4 m	8 m	12 m	20 m	32 m	48 m
AH 758	10.85 %	4.38 %	-	0.22 %	0.00 %	-
AH 760	14.74 %	11.72 %	7.42 %	0.12 %	0.03 %	0.01 %
AH 769	22.52 %	12.17 %	4.19 %	0.07 %	0.00 %	-
AM 023	11.56 %	8.07 %	2.93 %	1.43 %	0.31 %	-
AM 031*	3.07 %	0.78 %	0.07 %	0.01 %	0.00 %	-
Mean	14.9 %[c]	9.1 %[c,d]	4.84 %[d]	0.46 %[e]	0.09 %[e]	
(95 % C.I. of Mean)	(10.4 - 19.5)	(6.0 - 12.2)	(2.2 - 7.5)	(-0.1 - 1.0)	(-0.04 - 0.22)	0.01 %

Notes:

[*] Mound destroyed after 4 weeks, bead count and return rate are for this short period only. Excluded from Summary values.

[a,b,c,d,e] Differences between means with the same superscript are not significantly different ($p < 0.05$).

Collected Bead Count is the sum total of all beads removed from the mound during the 13 week observation period. Deposited Bead / Band is the number of beads dispensed during the experimental setup. Return Rate is the ratio of collected beads to dispensed beads.

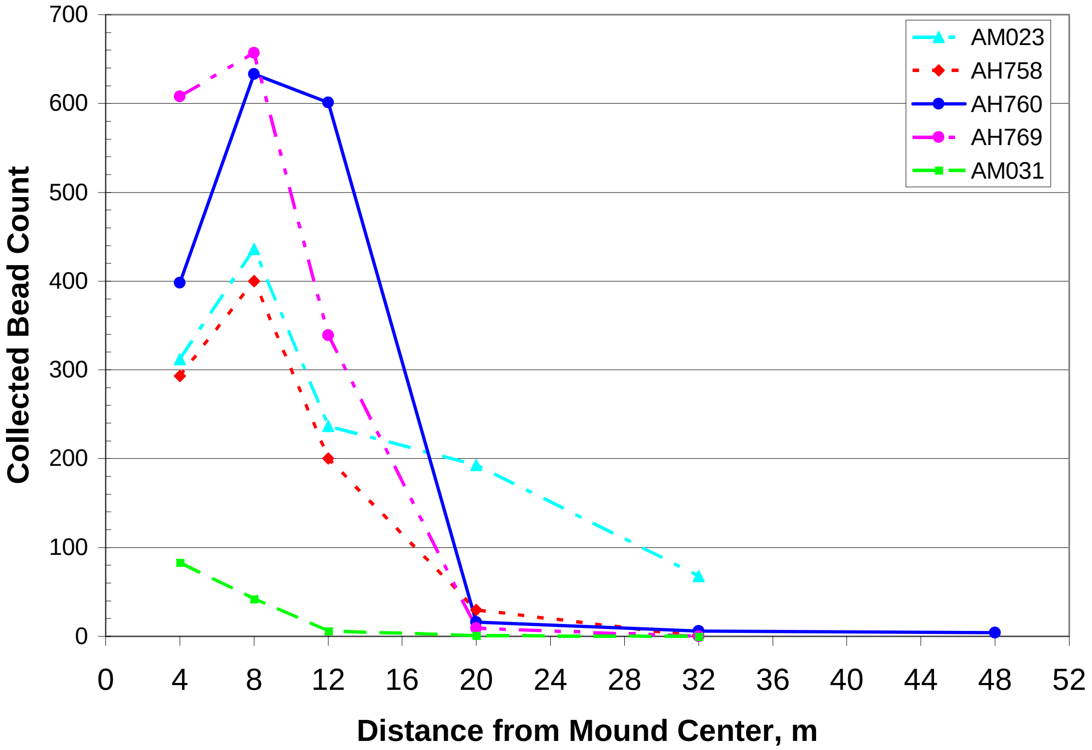


Figure 2.12. Distance results for distance experiments only. Mound AM031 was destroyed four weeks after experiment setup. Some 12-m beads on AH758 were misapplied at the 8-m ring, graphed line reflects an estimate of the beads at 12-m, Table 2.2 shows the actual values.

beads were recovered from distances greater than 19 meters before early July (5 weeks after dispensing) and most beads from this distance or greater were collected in August.

3. *Direction.* Beads were recovered from all four quadrants in both of the direction colonies (Table 2.3, Figure 2.13). AM022 was located immediately north of and adjacent to a 2-track dirt roadway; beads were retrieved earliest from the east quadrant even through the west quadrant had the same roadway exposure. AM004, completely surrounded by vegetation, retrieved beads most quickly from the southeast quadrant. Both mounds were originally small without a characteristic mound but with an organized gravel scatter within a cleared area (this was the typical condition for many of the mounds in the study). They were damaged by cattle during week four, but over the

Table 2.3. Direction, Density, and Disturbance Results

Experiment	Mound ID	Configuration Detail	Collected Bead Count	Deposited Bead Count	Return Rate [c]
Direction	AM 022	East	84	800	10.50 %
	"	South	16	800	2.0 %
	"	West	68	800	8.5 %
	"	North	20	800	2.5 %
	AM 004	Southeast	134	800	16.75 %
	"	Southwest	81	800	10.1 %
	"	Northeast	20	800	2.5 %
	"	Northwest	87	800	10.9 %
Density	AH 781	200 beads / m^2	85	1600	5.31 %
	AM 002	100 beads / m^2	83	800	10.38 %
	AM 013	50 beads / m^2	31	400	7.75 %
Distribution	AH 772	400 beads in a 20 cm pile	0	400	0
	AH 766	400 beads in a 20 cm pile	0	400	0
	AM 005	400 beads in a 20 cm pile	5	400	1.25%
	AM 009	400 beads in a 20 cm pile	85	400	21.25

Notes:

[a] Collected Bead Count is the sum total of all beads removed from the mound during the 13 week observation period.

[b] Deposited Bead Count is the number of beads dispensed during the experimental setup.

[c] Return Rate is the ratio of collected beads to dispensed beads.

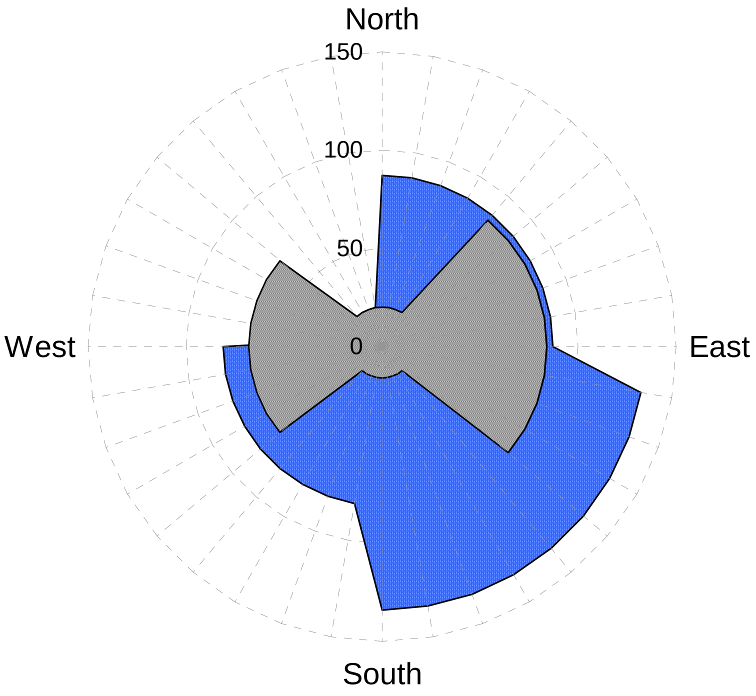


Figure 2.13. Direction results. Bead count radiates outward from center. Outer ring is 150 beads. Grey (lighter) wedges are for AM004, blue (darker) for AM022. Quadrant orientations are aligned to the door orientation of each mound.

following weeks repaired their scattered gravel and began to form nascent mounds. About 630 beads were collected from the surface of AM004 of which 320 were part of the direction setup, the remainder were from AH769, a nearby distance experiment. One-hundred eighty-eight beads were recovered from AM022.

Using a Rayleigh's test for randomness of direction, AM022 displayed collection rates that were not significantly different by quadrant ($z = 1.78$, $z_{0.01} = 4.6$, $p > 0.10$; Batschelet 1981:54) while at AM004 beads collection varied significantly by quadrant ($z = 49$, $z_{0.01} = 4.6$, $p < 0.01$). In examining AM004, the black beads in one quadrant inadvertently duplicated the black band used on the nearby distance experiment, AH769, so that beads from that experiment were available only 7 m away from AM004 (in other words at roughly 8 m from the direction experiment, the density of black beads was doubled). Since no experiments were conducted at higher densities, it is impossible to estimate the contribution of beads from the separate deposits but it is likely that had the double density of black beads not occurred, no directional difference would have been detected.

4. Density. Beads were recovered from all three density levels (Table 2.3, Figure 2.14). Although the number of experimental mounds was small and inference is risky, some observations can be made with respect to this experiment. Obviously, additional research will be required to determine whether these observations have inferential merit. It is important to recall that beads found on the mound are the result of a successful foraging trip. The number of beads found on a mound is a function of both the density of beads on the landscape and the number of trips made by ants that could have collected those beads. At very low densities of material, a large number of foraging trips will be required to encounter sparse materials. At some level of density, however, the number of beads returned will be limited by colony vigor or the number of foraging trips a colony can support. In these experiments at higher density levels, the same number of beads was collected (that is the bead count was not density related) and since these colonies were both small, collection may have been limited by colony size. At the lowest density, return rates may have been limited by density. It may be worth noting that the bead counts collected for densities of 200 beads/m^2, 100 beads/m^2, and one of the distribution mounds (AM009) were virtually identical suggesting that foraging success may have

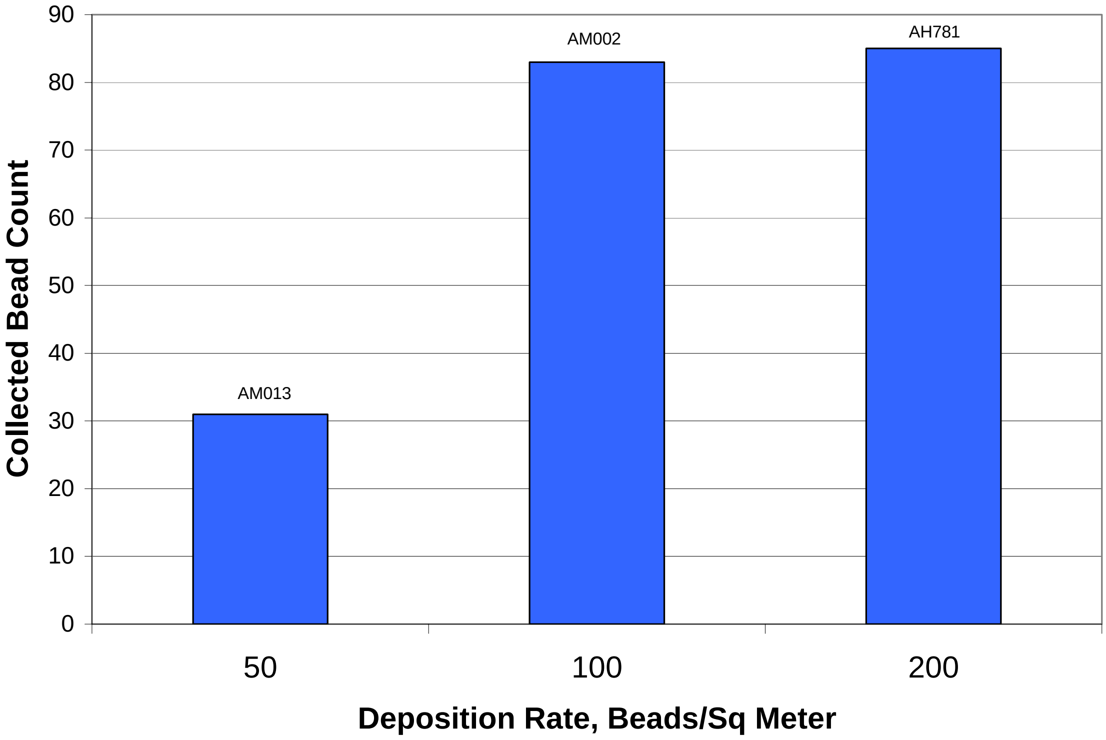


Figure 2.14. Density collection results. Mound numbers are given above each bar.

been forager limited. These colonies were all relatively small in size (holding positions 1, 2, 4, and 6 when all experiments are ranked by increasing mound length).

5. *Distribution.* Beads were recovered from only two of the distribution experiments, AM005 and AM009 (Table 2.3, Figure 2.15). Minimal ant activity was noted over the observation period at the remaining two mounds, AH772 and AH766. Lack of collection at these mounds may have been due to lack of colony foraging vigor or colony death. The smallest quantity of experimental beads was found on AM005 (n = 5, although this mound had a total of 25 beads due its also being an auxiliary). AM005 retrieved beads within a week of experiment setup even though it was located on the margin of a gravel road and had a ready source of small gravel within a meter of the nest. In contrast, AM009 (which recovered 85 beads) did not begin collection until four weeks

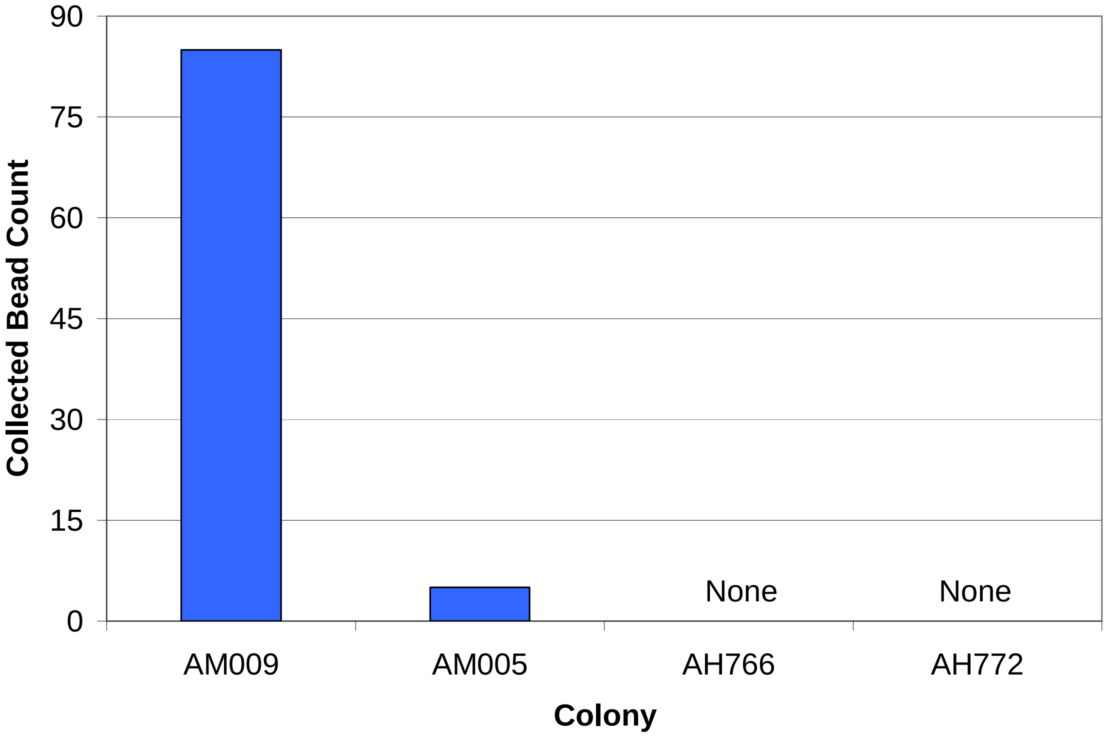


Figure 2.15. Distribution results. AM005 collected an additional 20 beads in its role as an auxiliary in addition to the 5 beads shown here. AH766 and AH722 were inactive during most of the observation periods.

after beads had been dispensed. These results suggest that localized sources are much less likely to be detected than are uniform scatters of material, even at low densities.

6. Controls and Auxiliaries. Over 900 beads were recovered from 11 of the 15 strictly auxiliary mounds and from auxiliary collection at two experimental mounds. Retrieval distances ranged from 1 m to 23 m from the bead source (Figure 2.16). This represents collection from 25 of the 51 auxiliary relationships. Ninety-seven percent of these beads were retrieved from within 15 m of the auxiliary mound. Only 22 beads were collected beyond 15 m. Two of the auxiliaries, AM018 and AM032, which collected no beads from any distance, were observed to be inactive during all observation periods.

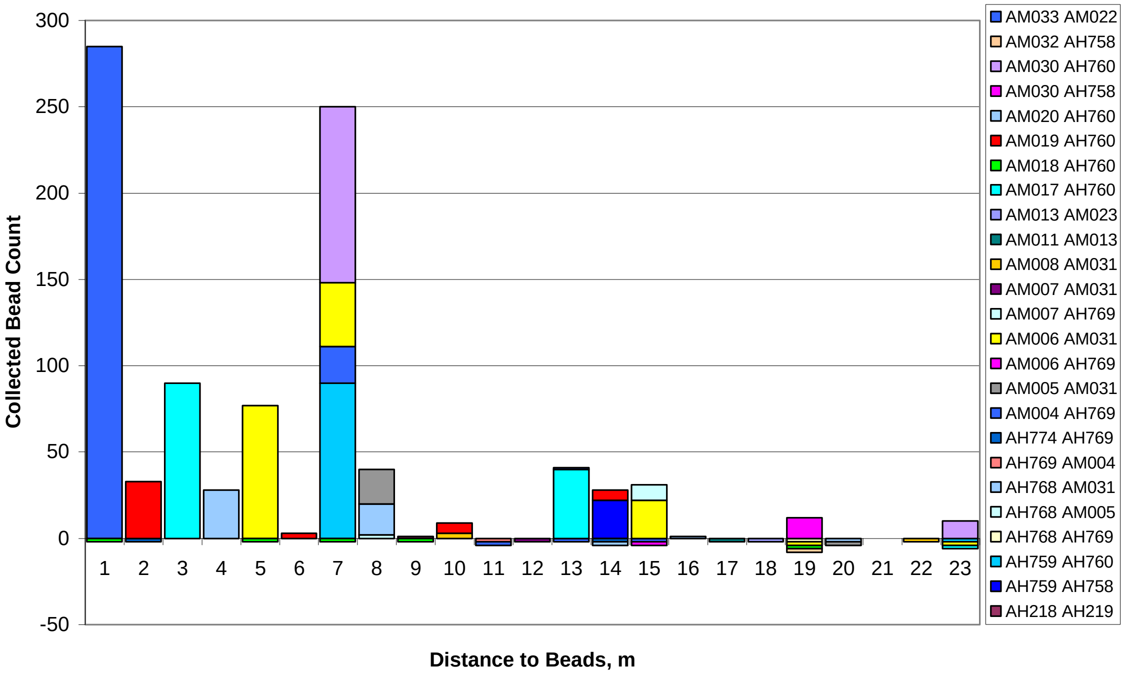


Figure 2.16. Auxiliary return rates by distance. Each color represents a unique auxiliary relationship (see Table B.4). Negative values indicate no beads were collected from that distance in the relationship. The majority of beads were retrieved from bead sources less than 17 m from the auxiliary mound.

Minimal activity was observed at AH774 and AM011, neither of which collected any beads. Of the nine original control mounds only one, AM010, contained beads. One control mound, AM014, could not be located after week six and was considered lost, leaving eight controls.

Three collected beads could not be explained as ant caused. Although the two yellow beads found on control mound AM010 could have been collected from a bead deposit located 45 m away (yellow band at AH758), this seems unlikely based on the poor recovery of beads from this distance at experimental mounds or auxiliary mounds. Since beads were not found on other control mounds, a feasible explanation for the presence of beads on a single control mound is difficult. If wind, cow, or bird transport was at work, it seems likely that other control mounds would also have been affected. Potentially these two beads were introduced by field error (dropping from the researcher's clothing or stuck in a boot sole for example). Regardless of cause, these beads are treated as valid data since the question of interest is whether the presence of material on a mound reflects the presence of material on the surrounding landscape. A priori, there would be no way to know that this control mound should or should not have contained beads. A small dark green bead was found on an experimental mound, AH023, whose nearest source (AH022) was 170 m away. This mound was immediately adjacent to a dirt road and the green bead deposit at distance experiment AH760 crossed the same road; a likely explanation is that the bead was transported by a vehicle to within foraging distance of AH023. It is also possible that this bead was inadvertently placed in a bag of light green beads (which were deposited at AH023) since the light and dark green beads were hand sorted prior to deposition. This bead was excluded from the analysis since two viable explanations exist for its occurrence.

Overall Results

Combining the experimental results presented above allows an assessment of bead size preference, distance patterns, and a determination whether experimental and/or auxiliary mounds differed from control mounds. In aggregate, less than 3 percent of the dispensed beads were recovered from mounds (7,300 / 310,000). However, 8.4 percent of the beads dispensed within 12 m of mounds were collected and 4.8 percent of beads dispensed within 20 m were collected when auxiliary collection is included. In one distribution experiment (AM009) 81 out of 200 available medium size beads were collected resulting in a 40 percent retrieval rate. Recall that collected beads represent only the materials remaining on the surface of a mound and thus provide a lower bound on the number of beads actually transported by ants to their nest.

Although all colors and sizes of beads were collected, there was a clear size preference. Sixty-six percent of the collected beads were of medium size, small beads comprised 22 percent while large beads made up only 11 percent of beads on the mounds (Figure 2.17). The only large beads retrieved from distances greater than 15 m were found on AH023, a mound adjacent to a dirt road which probably facilitated transport. Large beads were retrieved from as far as 14 m on five mounds (n = 66). Medium size beads were retrieved from distances out to 48 m by one mound and from distances between 20 m and 32 m on six mounds (n = 208). Five colonies collected small beads out to the same distance (n = 87). Since colors were not replicated in the experimental design it was impossible to determine any color preference pattern, however, all colors were collected.

At the end of the observation period, a total of 15 of the mounds with experiments contained beads while two did not. Twelve of the auxiliary mounds resulted in retrieved beads while 7 did not. One of the eight control mounds had beads while the rest did not. Based on a G-test (log-likelihood ratio test) for independence with Williams correction, the null hypothesis that beads appear on mounds independent of treatment or distance from beads can be rejected (Table 2.4, G adjusted = 13.2 tested against a critical value of $\chi^{2}_{.005,2}$ = 10.6, Sokol and Rohlf 1995:726).

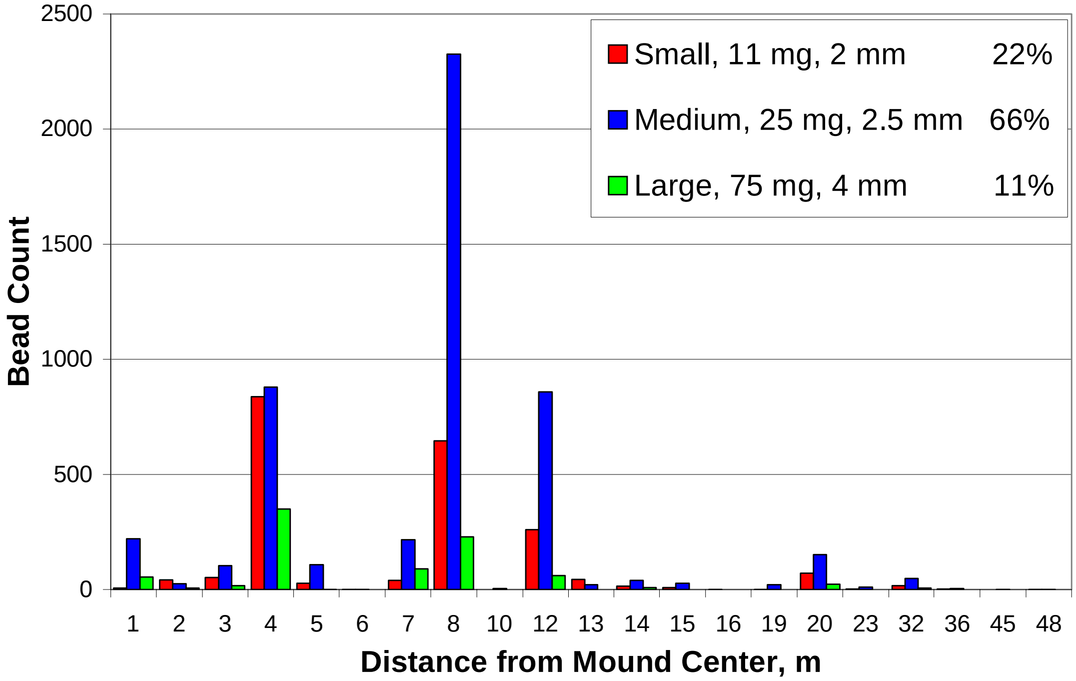


Figure 2.17. Return rates by size. Includes both experimental and auxiliary mounds.

The number of beads found on experimental mounds ranged from 0 (n = 2) to 1659 (n = 1), average number of beads per mound was 285 (95 percent confidence interval: 184 to 386, standard deviation = 193, using a square root transformation; Sokol and Rohlf 1995:415). The number of beads on control mounds ranged from 0 (n = 8) to 2 (n = 1), with a mean value of 0 (95 percent confidence interval: -.18 to 0.68, st. dev. = 0.62). The number of beads retrieved in auxiliary relationships ranged from 0 (n = 7) to 306 (n = 1), values intermediate between the experiments and controls. Since there is no overlap of confidence intervals for the means of experimental and control mounds, the null hypothesis of no difference between mean number of beads appearing on mounds by treatment can be rejected.

Table 2.4. 3 x 2 Contingency Table of Mound Condition and Bead Presence

Condition	Mound Count with Beads Present	Mound Count with Beads Absent	Row Total
Experiments	15 (bead count: 25 - 1600)	2	17
Auxiliaries (< 24 m from beads	12 (count: 1 - 285)	7	19
Controls (> 24 m from beads)	1 (count: 2)	7	8
Column Total	28	16	44

Discussion and Conclusion

Although glass beads are a far from perfect surrogate for other anthropogenic materials like chipped stone, the results presented here provide a baseline from which to continue research into ant foraging behaviors for non-food items. Clearly ants are active taphonomic agents with respect to small anthropogenic materials located near their nests, moving up to 8 and on rare occasions as much as 40 percent of nearby materials in their preferred size range. In particular, western harvester ants forage routinely for gravel-like material into vegetation within 20 m of their nests and may go considerably farther if conditions are favorable. If auxiliary data is included (Figure 2.16) it appears that the majority of foraging occurs within 15 m of the nest with minimal foraging beyond. These ants transport heavy and awkward loads (such as the large 75 mg beads used for testing) from as far away as 12 m. Given the three sizes of items offered, loads in a weight range and/or size range of 25 mg or 2.5 mm are preferred, although not exclusively, over either larger or smaller objects. Ants appear to be reliable collectors of materials around their mounds with densities as low as 50 items/m^2 but are less reliable at locating point deposits. Presence of materials on a nest site, is however, a good indicator of material on the surrounding landscape within an 18 m radius. In many colonies ants respond quickly to the arrival of new objects within their foraging range. When beads are placed within 4 m of mounds, they appear on the mound surface within minutes; when beads are several meters farther away, discovery can take several days to weeks depending upon distance. Although the sample size was small, there is a strong indication that ants forage in all quadrants around the nest, although they may display a directional preference.

Ants' preference for the medium over the small size beads used in this experiment at distances of 4 m and greater from the nest may confirm the previous reports that ants will bring back heavier items from further distances; in essence maximizing the return for their travel time expenditure. Since small beads were generally just as available as medium, it seems that the ants were rejecting small beads in favor of medium beads. The large beads were likely to have been too large to successfully return to the nest over great distances. This deliberate selection of medium size materials in the presence of both larger and smaller materials has the potential to help discern whether a small debris scatter encountered during archaeological excavation is intact or has been foraged by ants. Conceivably any debris scatter harvested by ants will be depleted in "medium" size materials relative to "large" and "small" materials. The nearby harvester ant mounds in contrast will be enriched in medium materials. The present research does not have enough resolution to identify a truly preferred "medium" size material although the medium beads used correspond well to the reported gravel sizes found on mounds. A preferred "medium" size is likely to be on the order of 25 mg rather than much larger or much smaller. In addition, since the number of large beads dropped off with distance at a rapid rate, potentially the ratio of small:medium:large anthropogenic materials on a mound can provide some indication of how far the anthropogenic source deposit is from the mound. For example, if "large" materials are on a mound the source is very likely to be less than 12 m away. Both of these areas offer opportunities for future research.

Although not measured in this study, it is likely that colony vitality also affects the ability of the colony to detect small isolated deposits. A smaller or less vital colony will have fewer foragers who in turn will have fewer opportunities to encounter objects on the landscape compared to a more vital colony. As a consequence, a lack of material on a nest does not necessarily imply a lack of material on the landscape. Poor colony vigor, dense vegetation, or severe weather may limit foraging opportunities. It is worth noting here, that these phenomena may be transient - during this research it was observed that foraging by all colonies virtually stopped while the colonies focused on mound repair after cattle trampling only to resume when repairs were sufficient. Finally, there is some indication that in a mixed-grass prairie, foraging range increases as grasses and forbs mature and more ground surface is exposed between plants.

This research has confirmed and extended the understanding of western harvester ant gravel foraging behaviors. In particular it has confirmed a typical foraging distance in mixed-grass prairie conditions and the gravel size estimates made by previous researchers.

These results are directly applicable to archaeological survey. Observation of an object of anthropological interest should immediately stimulate a more intense survey of the area focusing within 12 m and potentially extending up to 20 m of the nest. While it is important to recognize that materials on the nest are out of context, these materials can provide an easy way to assess if additional search of the area or excavation below the mound for subsurface material is warranted.

This research was limited to a single season, a single species, and a single ecological setting. Additional research is required to determine how extensible the results presented are to a larger variety of natural conditions as well as to materials which are of additional archaeological interest such as chipped stone or metal objects.

Chapter 3. Landscape Scale Analysis

In Chapter 2 it was shown that materials on ant mounds are likely to be the result of ants foraging up to 12 m and possibly as far as 20 m from their nests and that ants reliably detect seeded materials under experimental conditions. While there is significant value in the knowledge obtained in those experiments, it is also important to know whether foraging reliably and efficiently reflects the presence of material on the surrounding landscape under non-controlled conditions. Reliability can be reflected in two patterns: 1) whether mounds with anthropogenic materials tend to be nearest neighbors more often than would be expected by chance and 2) whether mounds with anthropogenic materials are the nearest neighbors to cultural deposits. Mound inspection has the potential to be an efficient tool for archaeological survey if mound distribution on the landscape is such that mounds occur in a pattern that will assure overlapping foraging areas that are still maximally far apart. Ideally this would be a uniform pattern with a separation distance slightly less than twice the foraging distance. If mounds provide a reliable signal of material on the landscape and density is sufficiently high, then the possibility exists that mound survey can also be considered a complete survey of an area since foraging ants will have completely canvassed the surrounding landscape for materials in their collection size range. Further, if the mound/disk clearings are sufficiently large, remote census of mounds may be feasible and allow for development of an a priori sampling scheme in lieu of a full field survey. This study (Chapter 3) investigates the spatial patterning of approximately 700 *Pogonomyrmex occidentalis* ant colonies found in the 2001/2002 Colorado State University Archaeological Field School (CSUAFS) survey at Hudson-Meng as previously described in Chapter 2 and evaluates the relationship of colonies to one another and to known cultural sites from a circa 1973 survey of the Hat Creek drainage. Chapter 4 investigates the utility of remote detection of colonies in satellite imagery.

Spatial Patterns in *Pogonomyrmex* Colonies

Harvester ant colony spatial patterns are described in a variety of ways. Most common is the overall pattern whether uniform, random, or aggregated as determined by measures such as the Clark and Evans nearest neighbor index. Distance between colonies as measured by the nearest neighbor distance and overall colony density per unit of area are also reported. Results from the literature for each of these are described below.

The Clark and Evans (1954) nearest neighbor index (NNI) compares the nearest neighbor distances between randomly sampled members of a population to the distance that would be expected between neighbors if the population were randomly dispersed (Reich and Davis 2000:62). An index value near 1.0 suggests that a population is randomly distributed; an index significantly greater than 1.0 indicates a uniform distribution while an index less than 1.0 suggests population aggregation or clumping. Although widely used, this measure is subject to error due to edge effects and region shape (Donnelly 1978; Sinclair 1985). *Pogonomyrmex* harvester ant colonies have generally been found to be regularly distributed (also described as over dispersed or uniform) although random and even clumped distributions have also been noted. To illustrate, Crist and Wiens (1996) found the colony distribution pattern of *P. occidentalis* colonies in eastern Colorado to be a function of observational scale (see Chapter 2 for a more complete description of the *Pogonomyrmex* species). For large areas, colonies appeared clustered while for small areas the pattern was regular. In contrast, Wiernasz and Cole (1995:522) found that *P. occidentalis* nests near Fruita, Colorado were uniformly distributed regardless of spatial scale. *P. badius* colonies have a regular distribution (Harrison and Gentry 1981:1469). In comparison, the desert species, *P. barbatus*, with low inter-colony interactions has shown clumped and random spacing (Gordon 1991:383) while *P. rugosus* has shown both regular and random distribution (Schooley and Wiens 2003:188; Whitford et al. 1976:127). In Levings and Traniello's (1981: 300-301) summary of 13 studies reporting colony relationships among seven *Pogonomyrmex* species, all indicated overdispersion (uniform) or random relationships with a tendency toward overdispersion.

Reported colony densities of *P. occidentalis* range from 0.43 to 75 colonies/hectare, and although based on fewer studies, *P. owyheei* has similar densities (Figure 2.1). These density statements generally reflect an assumption of homogenous coverage of ant colonies across the studied area. Many studies, however, have indicated that within study areas, local heterogeneity results in patchy distributions. In particular, Crist and Wiens (1996:304) found that *P. occidentalis* colony density in northeastern Colorado varied by grazing regime, soil, and topography. Highest colony densities occurred in lightly grazed areas with lowest densities in heavily grazed pasture. Higher densities were found on upland slopes with well-drained sandy loam soils unless heavily grazed. Although based on less extensive sampling of the same study area, Snyder et al. (2002:407) continued to find a similar relationship of lower mound density on more heavily grazed areas. Succession stage was found to be important in Costello's (1944:324) study of colony density on abandoned plowed lands in northern Colorado. Colony density was highest during a late stage with large numbers of forbs and short-lived perennial grasses. McIntyre (2003:Figure 1) found mound densities were highest in native grasslands of the Texas Panhandle; reseeded areas with both native and Old World grasses had fewer colonies.

Harvester ant response to burrowing rodents is inconsistent. Hopton (2001:210) in northeastern Colorado, found that ants preferentially located new colonies on old pocket gopher mounds regardless of grazing regime in the shortgrass steppe setting. However, Kretzer and Cully (2001:13) found that more *P. occidentalis* colonies were found on Kansas short grass prairie sites without prairie dogs than appeared on sites with prairie dogs. In contrast, O'Meilia et al. (1982:582) found that colony density did not vary with the presence or absence of prairie dogs on an Oklahoma grassland. Likewise, Schooley et al. (2000) found little difference between ant populations on kangaroo rat mounds and the surrounding areas in the Chihuahuan Desert. If, however, a tendency does exist for harvester ants to colonize old rodent mounds as found by Hopton, then the possibility exists that they can be surveyed for larger subsurface debris excavated by the rodents as well as the smaller materials discussed in the previous chapter.

Relative topography may also be important for colony location. DeMers (1993) and Dugas (2001) found that ant mounds were more prevalent along roadside ditches in North Dakota (*P. occidentalis*) and along arroyo edges in New Mexico (*P. rugosus*), respectively. Todd and Schoville (2001) also observed that *P. occidentalis* mounds were more prevalent along arroyo edges in northwestern Nebraska. Rissing (1988:810) found that *P. rugosus* nests were more frequently located at ravine upper edges in the Mohave Desert when compared to table lands or ravine bottoms.

Along with overall density, a another reported measure of colony relationship is nearest neighbor distance (that is, the distance from one colony to its closest neighbor of the same species). Four studies have reported this parameter for *P. occidentalis* (Cole and Wiernasz 2002:1435; Crist and Wiens 1996:Table 3; Homburg 2000:171; Keeler 1982:245). Values ranged from 9.2 m to 20.3 m with a mean value of 14.2 m.

The research just discussed does not provide a universal conclusion as to the spatial distribution of harvester ant colonies on a landscape. In a addition to the scale of study, factors such as grazing condition, soil type, land form, competition from other ant species, and the assessment method used determine both the actual locations of colonies and how those locations are assessed by common measures of dispersion. It is clear from the research that *Pogonomyrmex* colonies seldom appear as remote isolates, but rather in some type of aggregation based on local habitat extent. Given the heterogeneous nature of many habits, the scale dependent measures just described may be unreliable as the wide range of results presented suggests. Reich and Davis (2000:121) suggest the use of Ripley's K-function to examine scale dependent spatial patterns. No reported research has applied this technique to harvester ant colonies.

In the remainder of Chapter 3, the measures described above are applied to field data from a survey of almost 700 *P. occidentalis* colonies to further evaluate colony spatial patterns in the context of the research just presented.

Spatial Analysis

Study Site and Field Methods

The study site included the full 1200 ha surrounding the 2003 study site of Chapter 2 - the Hudson-Meng Bison Bonebed on the Oglala National Grassland near Crawford, Nebraska. During the summers of 2001 and 2002, the Colorado State University Archaeological Field School (CSUAFS) conducted a systematic survey of the area under the direction of Dr. Larry Todd (CSU) and Benjamin Schoville (CSU). The 10-m spaced transect survey encompassed the enclosed areas in Figure 3.1 (Forest Service pastures 33B, 33C, and 34). A two pass technique was used. During the first pass a team of three to six individuals canvassed a designated portion of the study area and recorded each ant colony (extinct or viable) using a Garmin 12XL GPS unit and assigned the colony an identification number (AHnnn). On a subsequent pass, the GPS coordinates were used by a second team (often different individuals) to relocate the colony and record attribute data such as size, air temperature, activity level, presence of anthropogenic material - particularly chipped stone, and so forth (see Schoville et al. 2002 for a more extensive data collection description). Many colonies were subject to third pass where the GPS coordinates were again used to relocate the colony for tagging and photographing. Due to time constraints roughly 470 colonies received this third visit. Field data were logged onto a paper worksheet which was then loaded into a Microsoft Excel® worksheet. Positional data was downloaded from the GPS unit and converted from WGS84 to NAD27 UTM13N (World Geodetic System spheroid 1984, North American Datum of 1927, Universal Transverse Mercator Zone 13 North) coordinates

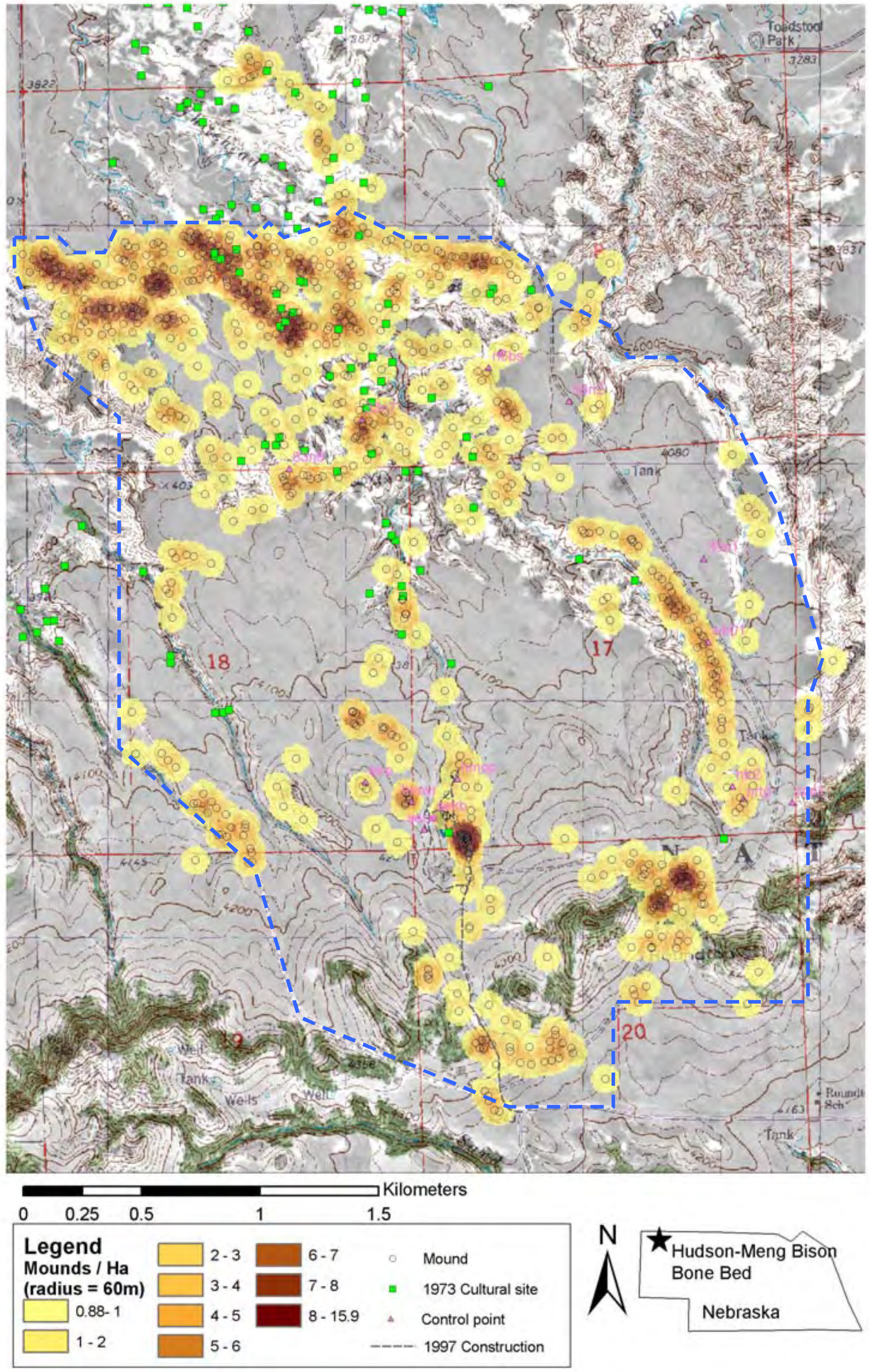


Figure 3.1. Study site with mound and 1973 cultural resource sites shown. Dashed blue line shows 2001/2002 survey coverage. Control points are from Burger 2002. Gray areas in background photo are grassy locations, light/white areas are exposed soils or roadways.

and then merged with the field attribute data by mound number. The resulting database contained over 800 line items, however, any attribute data or GPS coordinates that could not be matched to form a complete record of mound number, location, and attribute data were discarded during further analysis leaving 677 mounds which were included in this study. During the 2003 survey, it was discovered that the GPS coordinates for mounds in the 2003 study area described in Chapter 2 had been recorded using an incorrect datum during the 2002 survey that resulted in a systematic shift in the position of these mounds relative to the rest of the mound population. Since the coordinates of these mounds were internally consistent and the mounds were isolated from the rest of the mound population by more than 400 m the incorrect global positions were deemed acceptable for use in the Chapter 3 analysis (correct positions collected in 2003 were used in Chapter 2).

Data representing the cultural sites recorded during the 1973 survey were obtained from the Nebraska State Historic Preservation Office (NSHPO; Larry Todd, personal communication). The cultural site survey consisted of walking the Hat Creek drainage (which includes the Hudson-Meng locale) and identifying surface deposits of fossils, sites, and artifacts (Agenbroad 1989:17). Locations were determined using 9" x 9" aerial photographs at a scale of 1:17,000, topographic features, and compass bearings. These locations were then converted to latitude-longitude coordinates by NSHPO (L. Todd, personal communication). Materials recorded included 148 projectile points, 133 scrapers, 208 knives, 23 ground stone tools, 9 ceramic sites, and 108 hearths (Agenbroad 1989:17). The number of these sites that actually contained small artifacts that might be collected by harvester ants was unknown. In addition, recent attempts to relocate these sites have not been successful (Schoville et al. 2002). Given the limitations of this data set and the length of time since the survey (30 years) relative to the lifespan of *P. occidentalis* colonies (20 years), the likelihood of finding that extant ant colonies containing chipped stone correspond to cultural sites is low, however, the methodology is developed here in anticipation of use with higher correspondence cultural and harvester ant colony data sets. Locations in the 1973 cultural survey data set that were outside the 1200 ha 2001/2002 CSUAFS survey areas were excluded from the analysis.

Analysis Methods

For comparison with research described above, density (colonies/ha), nearest neighbor distance, and Clark and Evans nearest neighbor index were computed for the 677 colonies in the reduced data set. Two additional parameters, the index of dispersion and Pielou's index of non-randomness were also computed to determine the consistency of the Clark and Evan's NNI result. Ripley's k-function was used to evaluate the change in distribution with changes in scale (Reich and Davis 2000:122). To test whether spatial pattern of colonies found in the field with anthropogenic materials differed from a pattern caused purely by chance, a Monte Carlo simulation was run with colonies randomly assigned to contain chipped stone or not. Resulting nearest neighbor pairings were compared to the field data set using a log-likelihood ratio or G-test (Sokol and Rolf 1965:559). A similar procedure was applied to the 78 cultural sites from the 1973 survey. For visualization, a map was created using ESRI® ArcGIS 8.2 to provide both a visual display of the nature of colony patterns and to determine the degree of overlap between colony foraging areas. Specifics of each analysis are described below.

1. Density and nearest neighbor distance. Density was computed by dividing the number of mounds surveyed by the approximate survey area. In retrospect (see the GIS map discussion below), this appears to be a simplistic measure of density since colonies, based on visual inspection, are not present in large portions of the study area.

2. Clark and Evans Nearest Neighbor Index (NNI). This index was computed using the S-Plus library function "cenn" created by Reich and Davis (2000). The method compares the distance between randomly selected members of the population and their nearest neighbor against the distance that would be expected if the population followed a Poisson distribution across the area under consideration. Since each computation of a nearest neighbor index is itself a random sample, the NNI was computed 1000 times to assess the likely value of NNI. Fifty point pairs were evaluated in each calculation.

3. Index of Dispersion. This index was computed using the S-Plus library function "quad" created by Reich and Davis (2000). The method is based on a random sample of fixed size and shape quadrats pulled from the population and the comparision of the resulting ratio of sample variance of unit count per quadrat to the mean count per quadrat against the index test value of 1.0. The index is based on an assumption that randomly distributed units will result in a Poisson count of units per sample area. For a Poisson distribution the variance and mean are equal so a test ratio of 1.0 indicates randomness. An index less than 1.0 indicates a smaller variance than expected and an aggregated population. An index greater than 1.0 indicates a larger variance than would be expected and a regularly distributed population. Like the NNI, each computation of the index of dispersion is a random sample so the index was computed 1000 times to establish a sampling distribution for the index. The index was computed using both a 50-m diameter circular quadrat and a 100 m circular quadrat. Fifty sample points were evaluated during each calculation. Quadrats were permitted to overlap.

4. Pielou's Index of Non-randomness. Somewhat similar to Clark and Evan's nearest neighbor index, Pielou's index of non-randomness is based on a comparison of expected distance to test distance between points. In this case, a sample of random locations is drawn from the study area and the distance to the nearest population member is computed. The index reflects the degree of deviation of the distance results from the distance distribution that would be expected if the population was randomly dispersed. An index of 1.0 indicates randomness, less than 1.0 indicates regular spacing, and greater than 1.0 indicates aggregation. The S-Plus spatial library function "pielou" (Reich and Davis:2000) was used to compute 1000 values of the index. Fifty sample points were evaluated during each calculation.

5. Ripley's k-function. In comparison to the previously described measures of dispersion that consider the population as a whole, Ripley's k-function examines the relationship of each member in the population to all other members that allows an assessment of spatial pattern with scale (Reich and Davis 2000:121). As a consequence, variations in pattern with scale can be identified. Reich and Davis's (2000) S-Plus function "kfunc" computes the distance from every point in the population to every other point with correction for edge effects and establishes a cumulative distribution function (CDF) for the resulting distances. This distribution is compared to a simulated model distribution of the same population size. If the CDF falls within the envelope of the model CDF (mean value bounded by a 95 percent confidence interval) then the population can be taken to be match the model at that intermember spacing. If the CDF falls above the model envelope the population is aggregated at that spatial separation. If the CDF falls below the model envelope, the population is regularly dispersed. Tested models included a Poisson distribution and a simple inhibition process (SSI) distribution (selected because it allows for a minimum separation spacing between members of the population, a situation which was true for the mounds under evaluation).

6. Monte Carlo simulation of association using S-Plus. A Monte Carlo simulation was performed using S-Plus 6.0© for Windows (scripts are presented in Appendix C). During each of the 1000 iterations, each mound location was randomly assigned a status of chipped stone or no chipped stone in a ratio of 134:543 (as found in field survey for the 677 colonies). Average distance to the nearest neighbors within a radius greater than 1 m and less than 100 m was determined by paired categories: both mounds containing chipped stone, both mounds without chipped stone, and one mound with chipped stone and the other without. A lower limit of 1 m separation eliminated comparision of a mound to itself (since no mounds were found in the field that were actually this close together). Based on the field results described in Chapter 2, an upper limit for nearest neighbors was set at 100 m. In Chapter 2, maximum foraging distance for a colony was found to be 48 m (although foraging to this distance was extremely rare). If two colonies both foraged to this distance, their combined mound-to-mound separation would be about 100 m. Mounds any further apart than this distance would be foraging from non-contiguous areas and would not be expected to have similar chipped stone presence. In other words, the tested hypothesis was that if colonies were foraging in overlapping areas, then their collected materials should be similar. A log likelihood ratio or G-test of goodness of fit was used to determine the significance of the results. The G-test was selected over the more well-known Chi-square test due to its ease of use, ability to create a sampling distribution from which to determine a test statistic, and its lack of an assumption of independence (Meagher and Burdick 1980; Sokol and Rohlf 1965:560). The 95 percent critical value was established by ranking the 1000 G-values from the simulation and identifying the G-value which corresponded to the 95th percentile position.

7. Monte Carlo simulation of colony association using GIS. As in the previous analysis, the mound population (n = 677) was randomly separated into two groups; with and without chipped stone in the ratio of 134:543. Distance to the nearest neighbor (in either group) was computed using the ERSI ArcGIS 8.2, ArcToolbox, Distance to Point function. A Monte Carlo simulation (n = 50) was then conducted assigning mounds randomly to either group in a ratio of 134 (with):543 (w/o) and nearest neighbor distances recomputed within a maximum distance of 200 m. Only 50 simulations were run due to the time required to process each run. At the time that the ArcGIS simulation was executed, foraging data from Chapter 2 was not yet available. The arbitrary cutoff of 200 m between "neighbors" seemed a reasonable limit based on prior research. Only 5 percent of the mounds of the 677 were more than 100 m from their nearest neighbor. As a consequence, although the two simulation approaches used slightly different definitions of what could constitute a neighbor, the sample sizes are substantially identical and the simulation results comparable. A sampling distribution of frequency of nearest mound type was created.

8. Monte Carlo simulation of colony to cultural site. The distance from 1973 cultural survey sites (n = 143) to the nearest mound was computed using both ESRI ArcToolbox (50 iterations) and S-Plus 6.0 (1000 iterations) as described for the mound association analysis. Using ArcToolbox, an upper limit on nearest neighbor distance was set at 100 m, resulting in a test sample of 78 cultural deposits. Based on better information from the field foraging experiments in Chapter 2, in S-Plus 6.0, this limit was reduced to 50 m, resulting in a test sample of 36 cultural deposits. The Monte Carlo simulations were repeated (assigning the mounds randomly to either chipped stone or no chipped stone in a ratio of 134:534) to determine nearest mound type relative to each cultural site. A sampling distribution of frequency of nearest mound type to site was created.

9. GIS Map. Using ArcGIS 8.2, a map of the study area was created using background layers consisting of the USGS 7.5 minute Roundtop, Nebraska topographic quadrangle and a National Aerial Photograph Program (NAPP) black and white aerial photograph obtained from USGS EROS Service Center that had been georeferenced. Road features not present in the topographic layer were digitized. All colonies and cultural sites were plotted. Colony density was calculated based on a radius of 60 m, areas surrounding colonies were color coded yellow to dark brown by increasing density. The resulting map is shown in Figure 3.1. Discussion of this figure will be deferred to the next section.

Results

Mound Density and Nearest Neighbor Distance

Given the sample set of 677 colonies and a survey area of 16 km^2, the overall colony density was 42 mounds/km^2 or 0.42 mounds/ha. This value falls at the low end of the range of reported densities. Looking at Figure 3.1, however, it is clear that colonies are absent from large areas of the survey area and are clustered along areas of disturbance such as arroyos, roads, and drainages. Due to the aeolian nature of the sediments, in the black and white background image exposed soil such as dirt roads and arroyos appear as white/light areas and mixed grass pastures appear as gray areas. In Figure 3.1, it is important to note that all areas within the dashed outline were surveyed using 10-m transects within roughly a four week period during 2002. None of the colony densities described in previous research have encompassed an area comparable in extent to Figure. 3.1. It is likely that those counts were conducted within areas like those shown in yellow/brown in Figure 3.1, that is the population counts were made in areas that contained high densities of ant colonies. A visual estimate from Figure 3.1 suggests that colonies are present in only about one-half of the present survey area. Considering this area in isolation, the average colony density is about 0.8 mounds per ha and can be as high as 16 mounds/ha in local areas; these values are more consistent with those reported in the previous section. Average nearest neighbor distance was determined to be 30.7 m when colonies further than 100 m from a neighbor (5 percent of total) were excluded. Eighty-seven percent of the total colonies were within 60 m of their nearest neighbor while 73 percent were within 40 m and 45 percent were within 30 m. Based on the greater than 12 m and less than 20 m foraging distance determined in Chapter 2, almost half of all colonies have overlapping foraging ranges (or a separation distance of 24 m). If foraging distance is as high as 20 m, almost three-quarters of colonies have overlapping foraging areas (40 m separation distance). This suggests that where colonies are present in some abundance, their foraging patterns will traverse most of the inter-colony areas.

Clark and Evans Nearest Neighbor Index (NNI)

Based on 1000 iterations, the Clark and Evan's nearest neighbor index for the population was 0.467 (95 percent confidence interval: 0.3699 to 0.6248; p value = 0 for NNI = 1). Since the index is significantly less than 1.0, the NNI indicates that the population is aggregated. The computed nearest neighbor distance was 37.8 m compared to an expected distance of 80.7 m if the population had been randomly distributed. Referring back to Figure 3.1, recall that within the study area, mounds are frequently located in fairly narrow corridors along disturbed zones. The Clark and Evans NNI bases its comparison of distance on a random distribution across the entire sample area, it is not surprising then, that the NNI resulted in a prediction of aggregation. This illustrates a limitation of the NNI index - it is dependent upon a certain degree of dispersion of sample units across the study area. Unfortunately, the NNI is also subject to edge effects, so it is unlikely that partitioning the study area into smaller test regions which circumscribe mounds areas would improve the NNI results.

Index of Dispersion

Using a 50 m quadrat radius, the index of dispersion was 2.64 with 90 percent of the 1000 results falling outside the critical region for acceptance of 0.644 to 1.433. Using a 100 m quadrat, the index of dispersion was 6.09 with all values falling above the upper critical value of 1.433. Since the index of dispersion was significantly greater than 1.0, the hypothesis of complete spatial randomness can be rejected in favor of aggregation.

Pielou's Index of Non-randomness

Pielou's index of non-randomness was 24.01 (95 percent confidence interval: 14.4 to 36.46) with a critical region for acceptance of complete spatial randomness between

0.74 and 1.29. Results of all iterations were greater than 1.29. Since Pielou's index of non-randomness was significantly greater than 1.0, the population can be taken to be aggregated.

Ripley's k-function

Figures 3.2 and 3.3 show the cumulative distribution function for the population data plotted against a comparision Poisson distribution (a substantially similar plot was created for the SSI model and has been omitted). Figure 3.2 shows spatial patterns to a separation distance of 100 m while Figure 3.3 shows the leftmost portion of the X-axis between 0 and 20 m. From Figure 3.2 it is clear that for most of the separation distances the observed (i.e., population) values fall above that expected under a hypothesis of complete spatial randomness (CSR). Looking more closely at the region between 0 and 20 m in Figure 3.3, it is clear that no mounds are closer than 1 m (as would be expected based on knowledge of the data set). Colonies at all scales are closer together (that is aggregated) than would be expected by complete spatial randomness.

Monte Carlo Simulation of Colony Association

Mounds containing chipped stone had nearest neighbors that also contain chipped stone much more frequently than would be expected by chance based on either 50 GIS simulations (Figure 3.4; $G = 28.2$, $G_{critical} = 5.85$, following Sokol and Rohlf 1965 and Meagher and Burdick 1980) or 1000 S-Plus simulations (Figure 3.5; $G = 34.7$, $G_{critical} = 6.89$). This suggests that chipped stone containing mounds are forming clusters on the landscape that may provide a reliable signal (although not a strong one - note the large number of mounds that have chipped stone but a neighbor without in Figure 3.5, upper left) of the presence of anthropogenic materials nearby. In contrast, there is no apparent

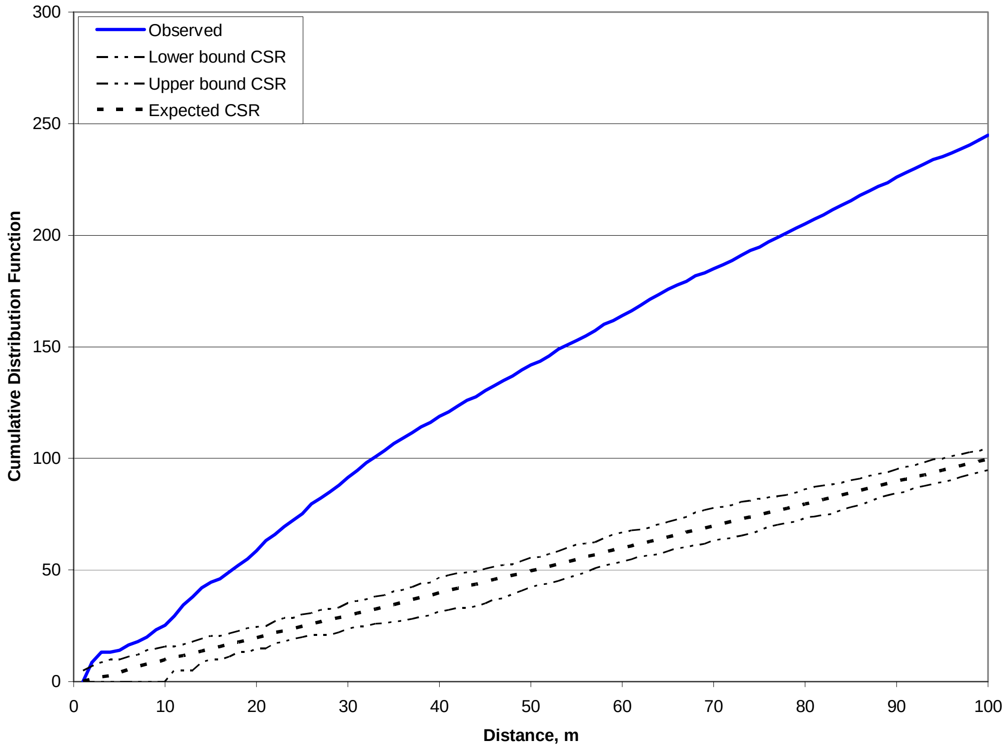


Figure 3.2. Ripley's K-function for spatial separation up to 100 m.

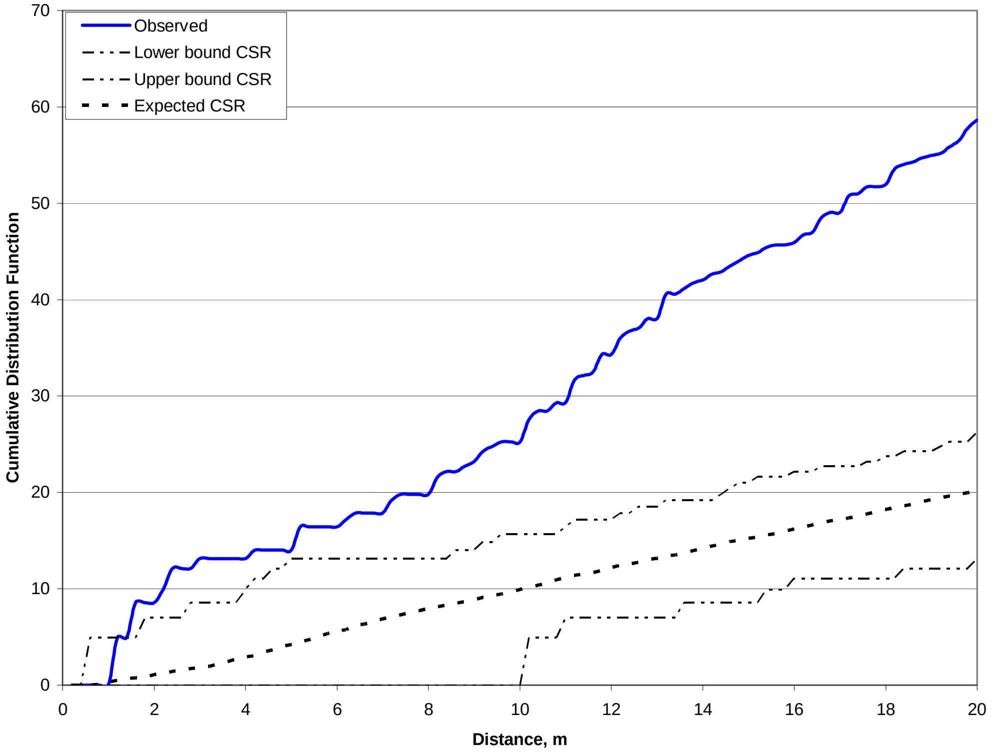


Figure 3.3. Ripley's K-function for spatial separation of 20 m (detail of Figure 3.3).

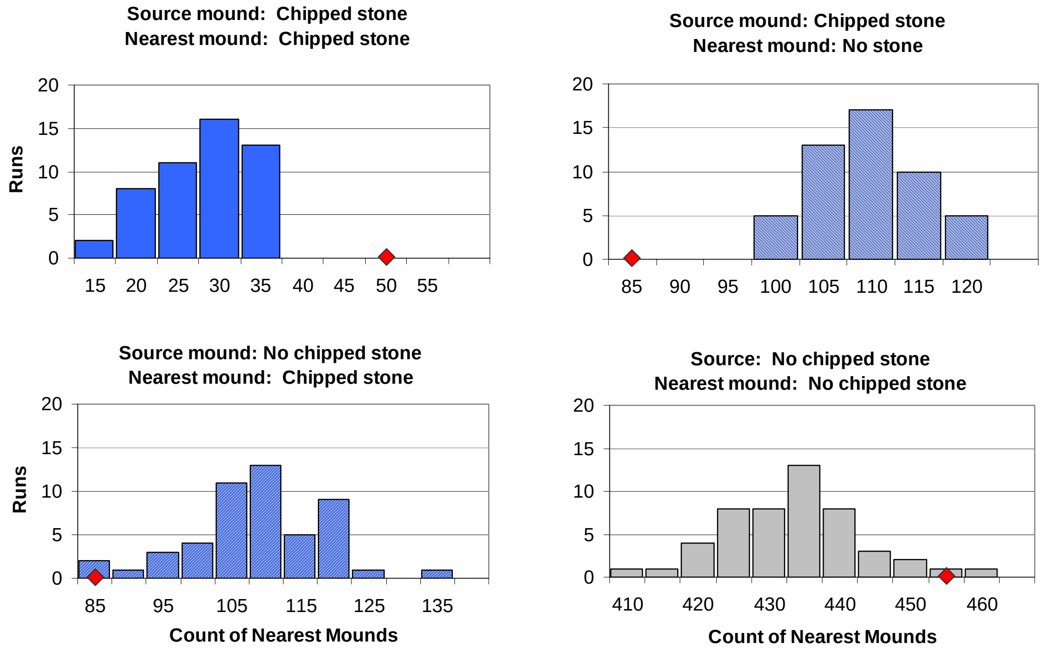


Figure 3.4. Monte Carlo Simulation, 50 GIS runs. Red diamond indicates field observations. X-axis values are maximum of bin and range from 11-15, 16-20, 21-25, etc.

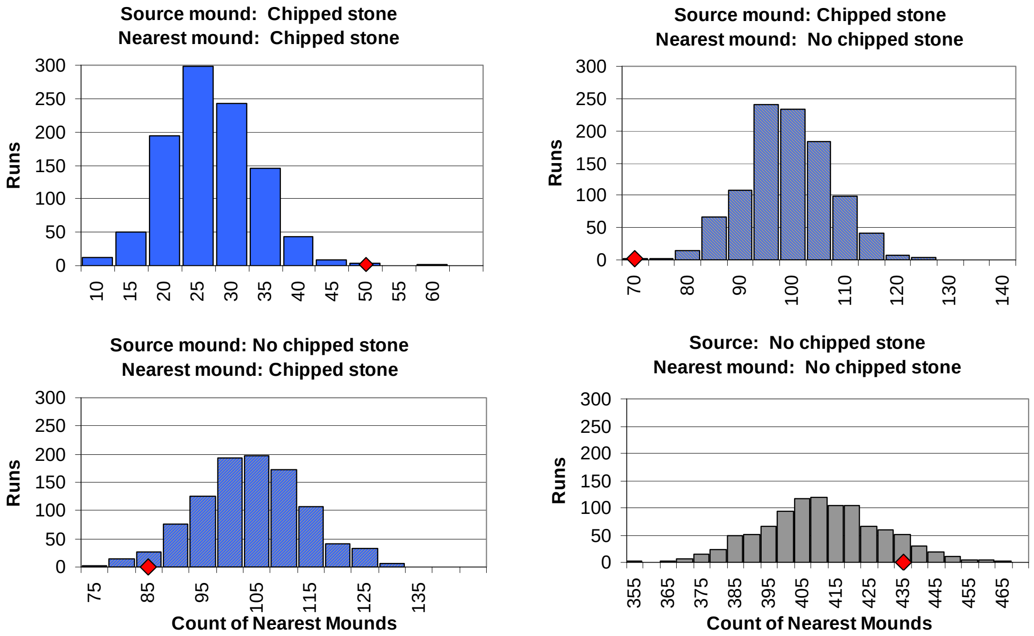


Figure 3.5. Monte Carlo Simulation, 1000 S-Plus runs. Red diamond indicates field observations. X-axis values are maximum of bin and range from 5-10, 11-15, 16-20, etc.

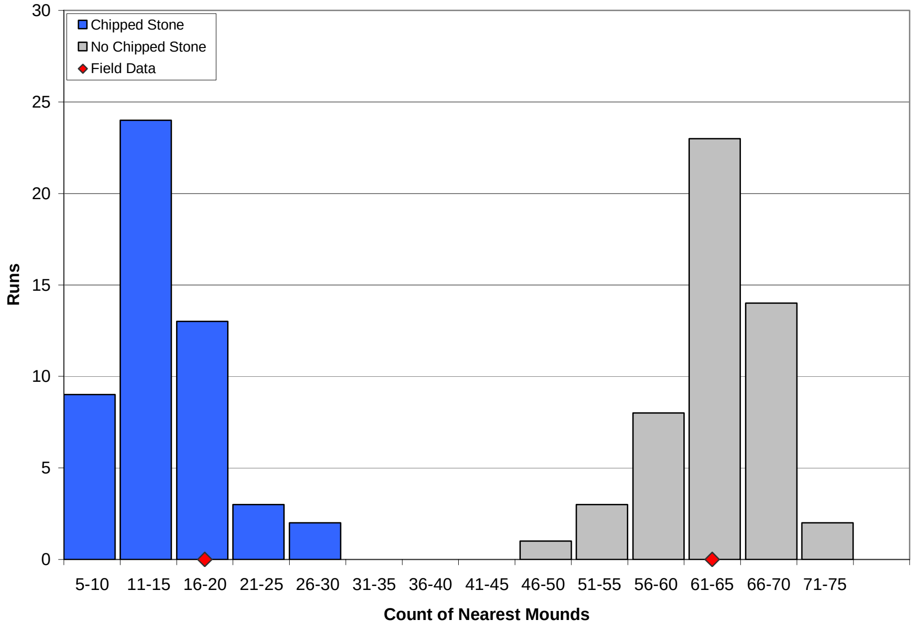


Figure 3.6. Cultural Resource Simulation: 50 GIS runs. Red diamond indicates field observations.

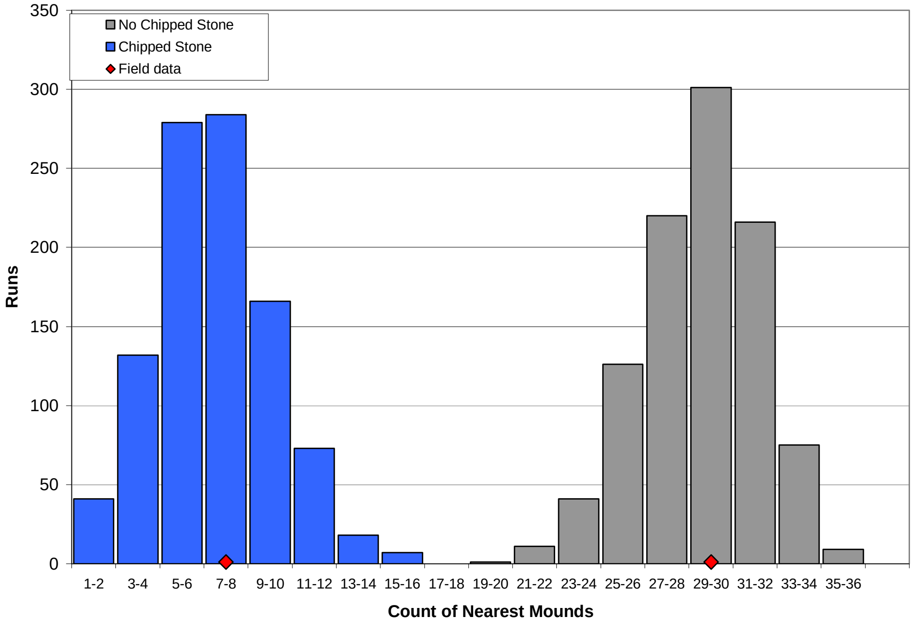


Figure 3.7. Cultural resource simulation: 1000 S-Plus runs. Red diamond indicates field observations.

difference between observed nearest neighbor type frequency and chance between 1973 cultural sites and ant mounds (Figure 3.6 and Figure 3.7) regardless of iteration count, cutoff distance, or simulation method. In Figure 3.6, the field observation of 17 mounds with chipped stone occurring nearest to cultural sites occurred in 10 percent of the simulations. In Figure 3.7, the field observation of 7 mounds with chipped stone occurring nearest to cultural sites occurred in 15percent of the simulations. In both cases, chance alone could explain the apparent proximity of the mounds with chipped stone to cultural sites. Failure to find strong correlation between cultural sites and chipped stone is likely due to several factors: the relative age of the survey (30 years) in comparison to the life span of an ant colony (20 years), the highly eroding nature of the surveyed area (drainages) and the possible disappearance of sites, the accuracy of the compass bearing/aerial photograph cross-mapping technique used to provide coordinates for the cultural sites, and the unknown contents of the sites themselves - many may not have originally contained materials that ants could harvest.

Conclusion

Unlike prior reports, *P. occidentalis* colonies at Hudson-Meng are aggregated at all spatial scales regardless of assessment method. The average nearest neighbor distance of 37.7 m is considerably larger than that reported by earlier studies. Colonies, do however, locate themselves on areas of disturbance such as arroyo edges and roadsides, much as has been documented by others. The combination of aggregation and situation along discontinuities may suggest that the Hudson-Meng area is marginal for *P. occidentalis.* Colonies show a clear avoidance of grassy areas and active drainages leaving the only potential nest sites along arroyo edges or other disturbed areas such as roadways or construction areas. The large separation distance may also be a result of the limited spatial width available along these edge habitats. More research is needed to understand why the pattern of the colonies at Hudson-Meng seems to deviate from that reported by other researchers.

If, however, the pattern seen at Hudson-Meng is typical of at least some *P. occidentalis* communities, then the potential for using them for productive survey is high. The mounds are prolific, on average they are closer together than twice their foraging distance, and their spacing is such that a typical 15-m survey transect would detect most mounds. Further, the preference for disturbed locations is also of benefit to archaeologists. Since the mounds tend to locate along arroyo edges and other disturbed areas, the ants will often be foraging in newly exposed areas both vertically and horizontally. Systematic inspection of mounds located along eroding edges has the potential to provide an indication of when an anthropogenic deposit has been exposed on an arroyo side wall well before erosional processes can remove the surface completely.

This study also highlights one of the major limitations of using ant mound survey - it is only of use where mounds are present and visible. At Hudson-Meng, significant areas of the landscape are not within 20 m of a harvester ant colony. However, the aggregation of mounds in areas where they occur and the virtual absence of mounds elsewhere suggests that stratified sampling designs can be productively used to improve survey efficiency (sensu Orton 2000:15).

Although not specifically addressed in this study, mound location changes may have the potential to indicate changes in land use. At Hudson-Meng, mounds almost never appeared in interior grassy areas. The appearance of mounds in these areas would suggest a general reduction in covering vegetation that would allow queens to successfully establish nests.

Chapter 4. Remote Sensing Application

Chapters 2 and 3 examined the patterns of *Pogonomyrmex occidentalis* (western harvester ant colonies) at both a local and landscape scale. It was shown that harvester ants routinely forage for nest building and maintenance materials from up to 12 and occasionally as far as 20 m or further from their nests and that colonies are dispersed in an aggregate fashion with an average nearest neighbor distance of about 40 m. This suggests that foraging areas overlap and that colony densities are sufficiently high to make mound examination a feasible survey technique. Survey effectiveness could potentially be improved if colony locations could be identified prior to sending a survey team into the field. Unique stratified sampling schemes could then be developed for areas with and without ant colonies. In areas with identifiable colonies, locations could be determined using computer-aided identification techniques and the locations of the colonies to be sampled downloaded into handheld GPS units (global positioning system). Rather than use field survey to find colonies, the field team would use the GPS coordinates to walk directly to them. Remote sensing techniques such as aerial photography and satellite imagery may offer a way to do this. This chapter reviews prior use of remotely sensed data for ant mound detection and examines the feasibility of remote detection of colonies in satellite imagery based on a study site in north eastern Colorado.

Remote Sensing of Harvester Ant Colonies

Relatively few remote sensing studies have investigated the detection of *Pogonomyrmex* harvester ant mounds. Crist and Wiens (1996:302) demonstrated the successful use of color aerial photography (altitude 300 m, 23 x 23 cm negatives) with an estimated scale of 1:2000. Although ant mound densities determined by ground truth verification were not significantly different, inactive or young mounds with small discs were difficult to detect in the photos as was distinguishing active and inactive nests with large discs. Similar results were obtained using stereographic techniques by Fisser and Kirkam (1970) who also noted that small colonies were difficult to detect. Everitt et al. (1996:423) demonstrated the use of an airborne (600 - 1800 m elevation) analog black and white video system with color encoder and digitizer. Ant mounds in Texas pasture were most visible in the September images when viewed in the narrow band red (0.623-0.635 µm) black and white image due to contrast of the cleared circular discs with the surrounding vegetation (Everitt et al. 1996:427). Ant mounds could not be detected in near IR imagery.

For archaeological survey, the issues encountered by these researchers may not be a problem. First the inability to detect small mounds may not be important since small colonies do relatively little foraging and will collect little material from the surrounding landscape. Second, the inability to separate living from dead colonies may also not matter since dead colonies at one point were actively foraging and it is likely the foraged material source is still present if the remnant mound is still visible.

There are, however, two drawbacks of these approaches from an archaeological standpoint: the need to manually identify and count mounds in the photo or video and the need for a contracted overflight to collect imagery. Computer-aided image classification of either photographic or digital imagery has the potential to overcome the first issue. The second issue can be avoided if the site of interest lies within a satellite overflight area and if satellite imagery has the resolution to distinguish features of the scale of harvester ant mounds. The current study (Chapter 4) investigated both of these aspects

Harvester ant colonies have several attributes which make them amenable to potential detection in satellite images. First, the roughly elliptical disks surrounding the mounds average about 1-m in maximum diameter (see data below; Schoville et al. 2002). Fine resolution satellite imagery such as that obtained from Quickbird2® has a spatial resolution of 0.60 m in the panchromatic band, so disks should be detectable if they provide a unique spectral signature (DigitalGlobe 2003). Second, although disks are almost always near other disks, they are seldom adjoined and their semi-elliptical shape makes them unique when compared to other bare soil areas such as rodent mounds or cow trails (see Chapter 3, above). Further, they are often regularly or over dispersed at small scales and aggregated at large scales (Crist and Wiens 1996; also Chapter 3 above). This suggests two benefits: that at a resolution of slightly better than 1-m individual disks will remain distinct and that any area that has disks will have many disks rather than a few making human and computer recognition less problematic. Third, mounds and disks are well maintained during the ants' active period (late spring through early fall) suggesting that disk spectral response should be relatively stable through this period.

The analysis presented in this chapter attempts to extract small bright areas from fine spatial resolution imagery using data pre-processing and classification approaches and to correlate the extracted areas with field data on known mounds. In the following sections, the materials and methods used for the analysis are explained in detail, results obtained from data pre-processing and classification are presented, and discussion and conclusions are offered.

Satellite Imagery Analysis

To evaluate the use of fine resolution satellite imagery and computer classification to locate harvester ant mounds, sample imagery was obtained, analyzed, and compared to field data from a small site in northeastern Colorado.

Study Site

The Central Plains Experimental Range (CPER), Weld County, Colorado (Figure 4.1), is part of the Pawnee National Grasslands administered by the United States Department of Agriculture and Colorado State University (CSU) and is a unit of the Long-Term Ecological Research (LTER) study funded by the National Science Foundation. The CPER was selected for this analysis due to its proximity to Fort Collins, Colorado, the availability of fine resolution satellite imagery of the area, and the on-going presence of western harvester ants (see for example Coffin and Lauenroth 1990; Crist and Wiens 1996; and Fontaine 2002). The CPER is located at an elevation of 1300 m with annual precipitation of 311 mm (Crist and Wiens 1996). The ecological setting is short grass steppe with perennial grasses and shrubs and has been subject to periodic cattle grazing since 1939.

Imagery and Other Data

Fine resolution imagery from the Quickbird2® satellite was obtained from DigitalGlobe® of Longmont, Colorado. The imagery was minimally processed with only

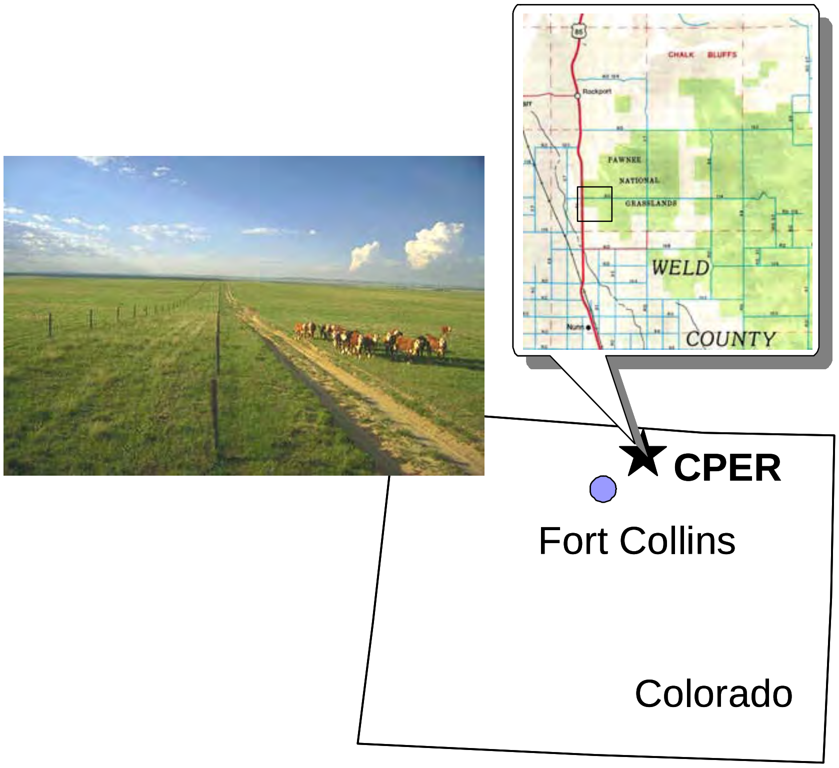


Figure 4.1. The study site location at the CPER in northern Colorado. (Photo from http://sgs.cnr. colostate.edu/About/PhotoGallery/grazing.htm)

radiometric and sensor correction, i.e., DigitalGlobe's "ortho-ready standard" product. Two 25 km^2 images were obtained that were bounded on the western edge by US Highway 85 and extended roughly 1.6 km north of the CPER access road and 3.4 km south and 5 km to the east of the highway. Both images were acquired on December 3, 2002 at 10:49 am local time (17:49 GMT) with 7° nadir offset and 0 percent cloud cover. The panchromatic (0.45-0.90 µm) image (Figure 4.2, left) had a 0.60-m pixel resolution and the multispectral (blue 0.45-0.52µm, green 0.52-0.60 µm, red 0.63-0.69 µm, and near infrared 0.76-0.90 µm) image had a 2.4-m pixel resolution (DigitalGlobe 2003). Images were obtained in 16-bit GeoTiff 1.0 format.

Ancillary data included the USGS (United States Geological Survey) topographic maps of the 1972 vintage Dover, Colorado and Eastman Creek South, Colorado quadrangles in DRG (digital raster graphic) format and 1993 vintage 10-m DEMs (digital elevation models) of these quads. NAPP (National Aerial Photography Program) black and white (6,000 m altitude, 1:42,000 scale, 1-m resolution) and color infrared (CIR, 1:62,000 scale) photos of the area taken in October 1999 and July 1995, respectively, obtained from the USGS EROS Data Center were also available. Additionally, a field survey of *P. occidentalis* harvester ant mounds in a 50-m x 770-m area was conducted in April 2003 (Figure 4.2, right). During the survey, mound location, maximum disk dimension (average 1.3 m, range 0.5 to 2.6 m), and status were recorded. Two reference points and 73 mound locations were collected using a Trimble GeoExplorer II® GPS unit with differential correction. A companion set of 75 random locations (known to be mound free) was generated from the 75 field points to use as a control. Except for the aerial photos, all imagery and ancillary data was in UTM Zone 13N projection with a NAD 1927 datum.

Analysis Framework

The objective of the analysis was to be able to extract digital signals from the relatively flat vegetation free disks surrounding the stone covered ant mounds (Figure 2.2, Chapter 2). It was hypothesized that the flat disks and reflective stone mounds would create a bright digital signal that, although small in spatial extent, would be distinguishable from surrounding vegetation and landforms. Other bright signals in the images would be from large reflective areas like gravel roads or aluminum roofed buildings. It was anticipated that these features could be removed by masking. Figure 4.3 illustrates the differing areas of brightness in the panchromatic image.

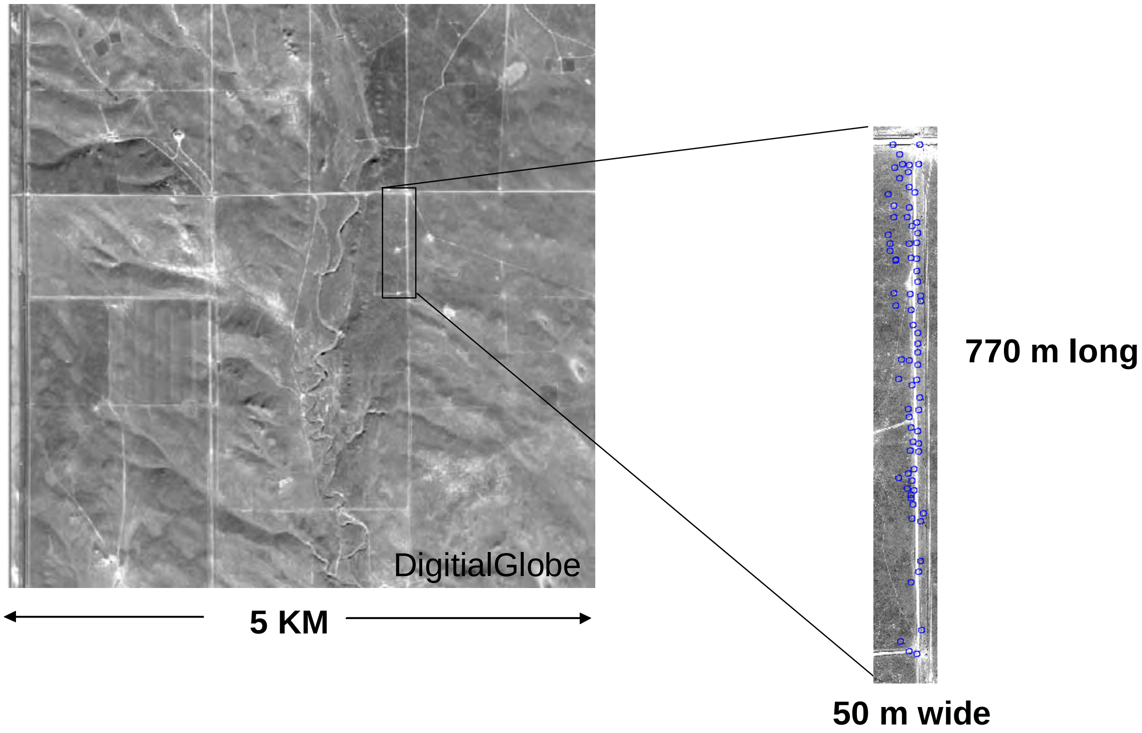


Figure 4.2. Panchromatic image (left) and subset area (right) with field surveyed ant mounds (blue circles). Uppermost circle at top right and lowermost circle at bottom right are control points (east side of access gate and west side of utility pole, respectively).

To identify a method of data pre-processing and classification that would best extract bright mound pixels, seven filters were tested (none, adaptive, low pass, medium pass, high pass, edge enhancement, and very high pass), two spectral sensitivities were used (panchromatic and multispectral), two pixel clumping tests were used (4 and 8), and two spectral class aggregation strategies were employed (panchromatic: brightest only or two brightest; multispectral: brightest or three brightest). Method success was assessed by comparing the number of small bright areas extracted by each method that coincided with the known mound and non-mound locations (controls) from the field data. To maintain a manageable file size, the original satellite images were subset to an area encompassing the field sample area (Figure 4.2, right).

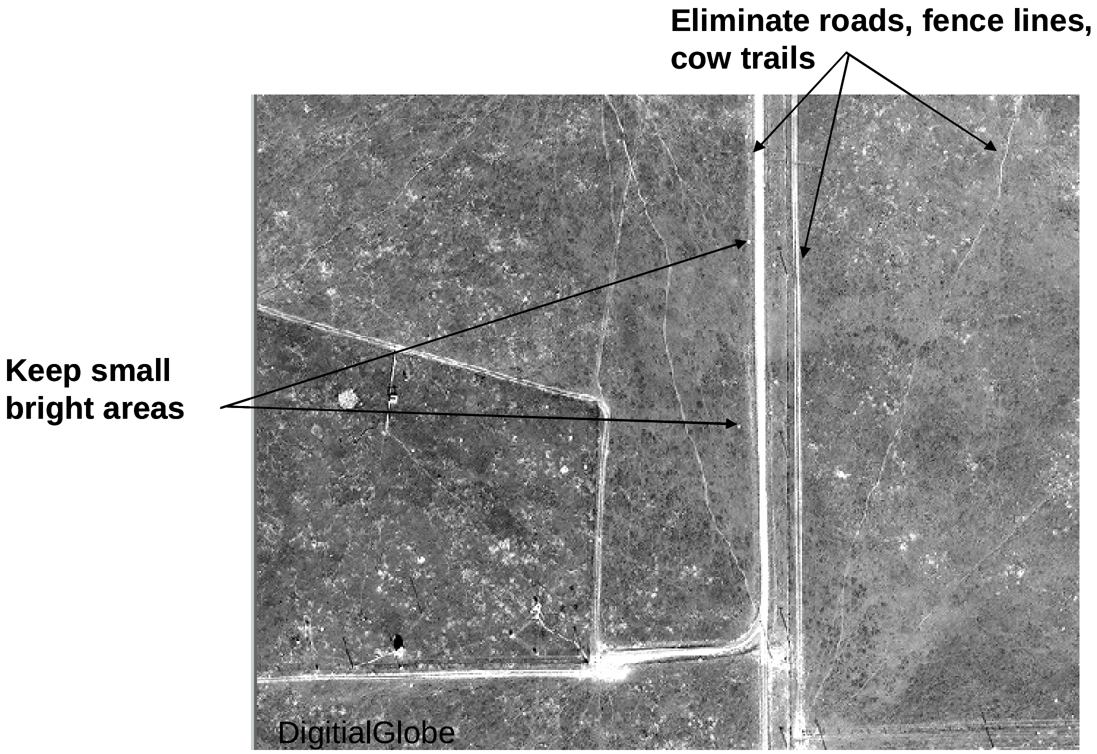


Figure 4.3. Detail view of panchromatic image showing small and large bright areas. Note length and orientation of utility pole shadows indicating a winter morning image collection period.

Processing

Processing consisted of two steps: preprocessing and classification. Each of these is described in detail below.

1. Preprocessing. Figure 4.4 depicts the process flow that was used to extract the small bright areas that were assumed to be mounds. Figure 4.5 illustrates the processing sequence for the results that are discussed below. All processing was conducted in ERDAS Imagine 8.5 on a Unix platform or ESRI ArcGIS 8.2 on a Windows XP, PC platform. Due to a difficulty opening the GeoTiff imagery files in ERDAS Imagine®, these files were converted to standard *.tif (Tagged Image File Format) files using Adobe Acrobat 7.0® with no compression and IBM format. To create preliminary registration

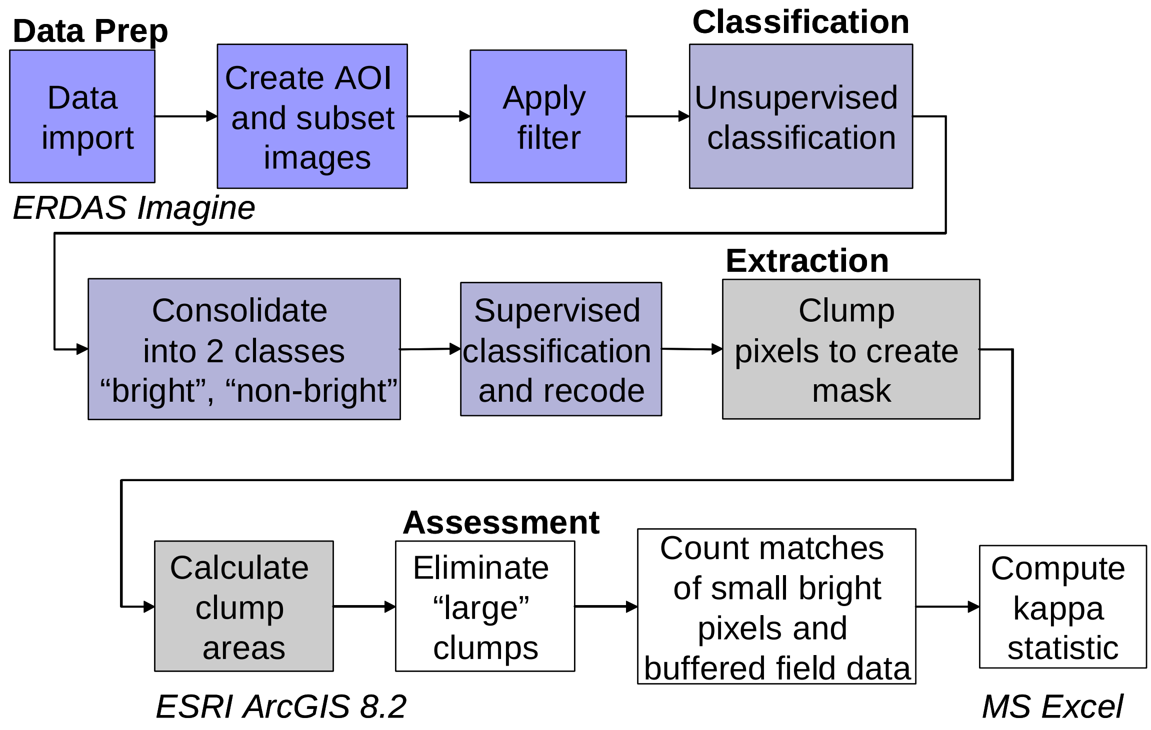


Figure 4.4. Process flow diagram.

these files were opened in ESRI ArcGIS®8.2 and visually aligned to the Dover DRG. The UTM coordinates of the upper left corner of the images were used to develop a world file (*.tfw). The resulting *.tif and *.tfw files were imported into Imagine with 16-bit signed data. After import, the images were superimposed and the upper left coordinates fine-tuned in the Image Info utility for optimal alignment of the subset images. Georeferencing of these images was deferred until processing was complete to avoid alteration of pixel values. The black and white aerial photo was scanned at 1600 dots per inch on an Epson flat-bed scanner and the image saved as a *.tif file then imported into Imagine. The Dover and Eastman Creek South DRG *.tif files were imported into Imagine, mosaicked, and then subset to a size comparable to the original satellite imagery (5-x-5-km) in preparation for final georeferencing.

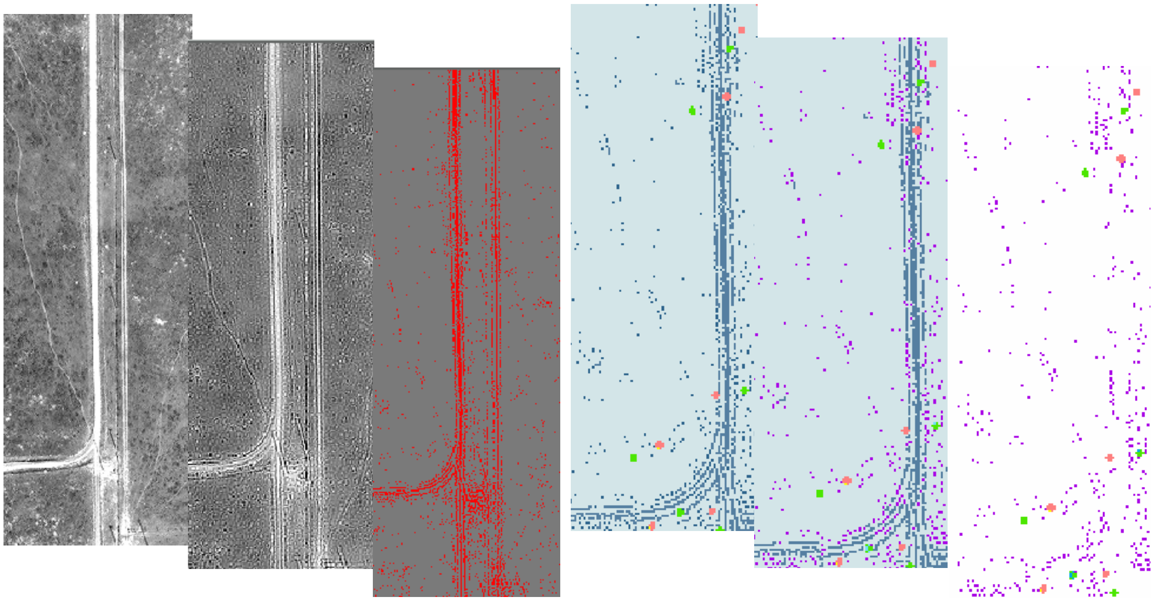


Figure 4.5. Image processing results for medium pass filter, 100 unsupervised classes with clump test level at 4 pixels. From left to right: Original image, after medium pass convolution filter, after classification into "bright" and "non-bright" classes, after clumping (display from ArcGIS), after partition of clumps into "large" (> 0.73 m^2, dark blue) and small (purple) and mapped against field mounds (green) and non-mounds (pink), after removal of large clumps and matching of small clumps to mounds (yellow) and non-mounds (teal).

Field data for mounds were loaded into a Microsoft Excel® spreadsheet, saved as an ASCII text file, and then imported into Imagine as a vector file. Since the images were not georeferenced and the subset area small, the field data were manually aligned to the subset images using control points located at the field gate and a utility pole base (Figure 4.2, right). After alignment of the mound field data, a second set of 75 random points was generated in Excel based on the mound locations using a random direction and a random distance between 5 and 10 m from each source mound. The two Excel files were saved as *.dbf (dBase 4.0 format) and imported into ArcGIS where mound and non-mound coverage layers were created. The Buffer wizard was used to create a 1-m buffer around each point in these layers. The buffer layers were then converted to raster layers with a pixel resolution identical to the imagery to be compared (0.60 for panchromatic and 2.4 for multispectral). These layers were then used for accuracy evaluation of the ability to extract correct "mound" pixels from the panchromatic and multispectral imagery.

Once imported and subset in Imagine, the images (both panchromatic and multispectral) were used to create fourteen variations of the image based on differing filtering methods: none, adaptive filter using a 3x3 pixel area, low pass filter (kernel: 1,1,1; 1,1,1; 1,1,1), medium pass filter (-1,-1,-1; -1, 6, -1; -1, -1, -1), high pass (same as medium pass kernel but with a center value of 9), edge enhancement filter (center value of 17), and very high pass (center value of 25). The low pass, high pass, and edge enhancement filters were from the Imagine default library while the medium and very high pass filters were modified from the default library. The use of high pass filtering was intended to increase the heterogeneity of the digital values in the image, so as to make the brightest and least bright pixels have more extreme values than in the original image. The variety of filtering kernels was intended to find that degree of digital number adjustment which would maintain the brightest pixels as a single class during classification but not make that class so small that the very brightest areas would not remain contiguous. The low pass filter was included to verify that smoothing was likely to create the opposite effect - a loss of extremely bright pixels from the image and a resulting inability to detect mounds. It was hoped that the adaptive filter would increase the digital value of relatively bright pixels within an area in the event that mound pixels were the brightest pixels in a local area but not necessarily the brightest pixels across the image.

2. Classification. An unsupervised classification was conducted on the fourteen filtered images using 25 classes, 15 iterations, and a 0.95 convergence level. To test the effect of spectral class size, the medium pass, panchromatic image was also classified using 100 classes. After unsupervised classification the resulting spectral classes were partitioned into two classes: bright and non-bright. For panchromatic images, spectral classes were partitioned by assigning either the single brightest spectral class to "bright" and all other classes to "non-bright" or assigning the two brightest classes to "bright" and the remainder to "non-bright" (recall the original hypothesis was that ant mounds would result in very bright isolated pixels, the goal of classification was to identify the bright pixel population). For multispectral images, either the brightest or the three brightest classes were assigned to "bright". The goal in these two assignments was to determine the effect of class aggregation on the ability to isolate small bright pixels. With too much aggregation, it was anticipated that few bright single pixels would remain to be extracted in subsequent steps (that is, the brightest pixels would become pooled with other slightly less bright adjacent pixels and create large bright areas that would later be discarded due to their size relative to the target ant mounds). The two-class images were reclassified using a supervised classification. The resulting images were then recoded with class values of "0" for non-bright pixels and "1" for bright pixels. The Imagine GIS Analysis function "clump" was then used on all images to create aggregations of pixels of the same class values. Two settings for adjacency were used: 4 or 8 nearest pixels. It was anticipated that testing with fewer pixels (4) would result in more small bright areas.

Small Area Extraction

The 42 image files created as a result of classification and clumping were opened in ArcGIS for clump area computation, large area removal, and comparison of remaining bright areas with mounds and non-mounds. Clump areas were computed using raster algebra with the expression clump_area = zonalarea (clumped.img). An assumption was made based on an average mound size of 1 m, that a mound would create one or at most two bright pixels in the imagery. Clump areas greater in extent than two pixels (0.73 m^2) for panchromatic images or one pixel (5.8 m^2) for multispectral images were eliminated using the raster algebra expression small_clumps = setnull (clump area > {0.73, 5.8}, 1). The remaining pixels were compared to both the buffered mound raster layer and the buffered non-mound raster layer for the respective image type (panchromatic or multispectral) using the raster algebra combinational operator "CAND": match = small_clumps CAND {raster buffer of mounds, raster buffer of non-mounds}. Curly brackets indicate that each computation was completed using one of the enclosed values. Figure 4.5 provides a visual display of the processing steps just described. Results were recorded for the count of pixels in the match computations and the count of small clumps in the small clump computations. Kappa hat, $\hat{\kappa}$, statistics (observed - expected / 1-expected) for each processing sequence were computed based on a comparison of the correct matches of small bright areas to mound/non-mound locations (total number of possible matches = 150; Campbell 2002:396-398).

All treatment combinations were carried through the process described above except the following multispectral treatments. The very high pass filter (center value of 25) failed in class merging after unsupervised classification so was dropped from further analysis. The multispectral treatment results were also not compared to non-mound field data since the mound data matches were so poor. Since there was no control data from non-mounds, kappa statistics were not computed for multispectral treatments.

Georeferencing

After completion of processing using the field subset, the original satellite images and black and white aerial photograph were georeferenced to the mosaicked and subset DRG map of the area. Due to the small size of the area (5-x-5-km) and the small variation in elevation (less than 150 m) across the area, a small number of ground control points was used and elevation correction was omitted. Due to slight errors in mosaicking the Dover and Eastman Creek South DRG's, ground control points were only selected from the Dover portion of the mosaicked DRG (which accounted for over 75 percent of the area). Seven ground control points were selected using primarily anthropogenic features such as road intersections and fence features. Root mean square error (RMSE) in pixel units for the georeferenced images were as follows: panchromatic image, 0.87 (max 1.639), multispectral 7.66 (max 11.628), and aerial photo 1.79 (3.61). The georeferenced aerial photograph image is shown in Figure 4.6. The poorer results of the multispectral georeferencing relative to the panchromatic image are likely due to the much higher resolution of the panchromatic and aerial images and underlying errors in the DRG data due to the age of the data set.

Results

The objective of the processing just described was to find the combination of pre-processing and classification parameters that would best match existing ant mounds

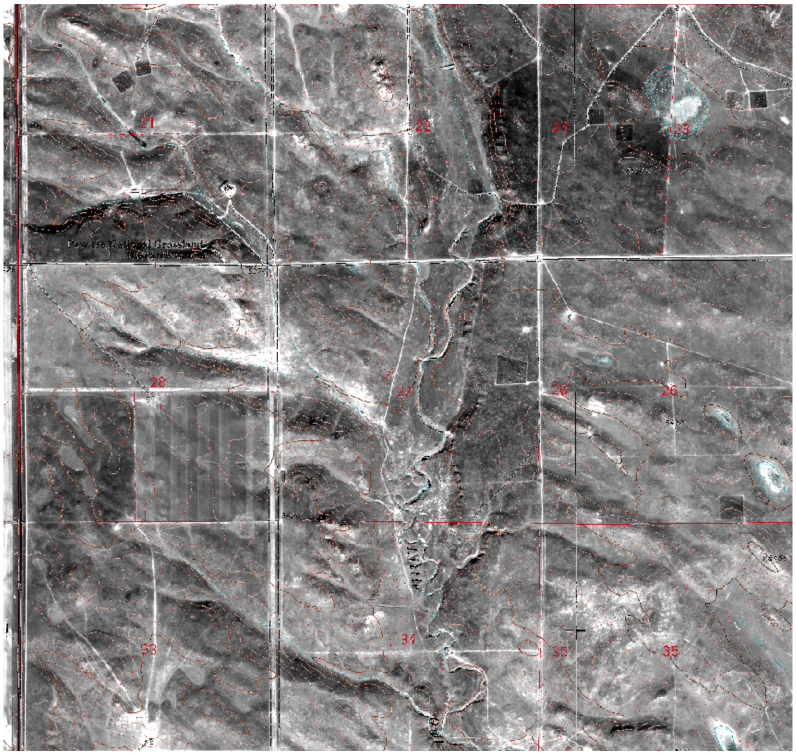
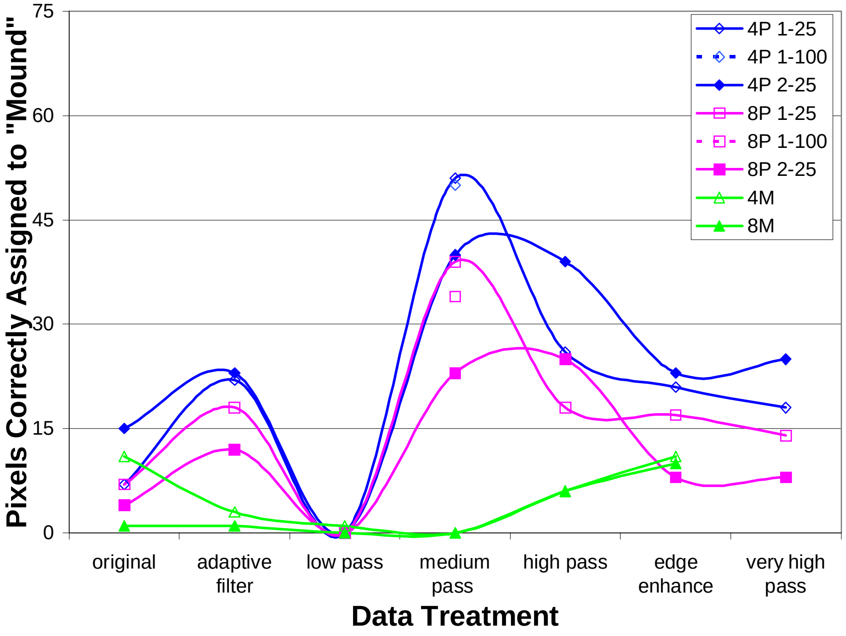


Figure 4.6. Georeferenced aerial photograph relative to Dover and Eastman Creek South mosaicked and subset DRG image.

identified in the field with bright pixels extracted during processing. A companion goal was to minimize the number of pixels extracted that did not match known mounds. Figure 4.7 compares the number of matches (pixels in the comparison phase) that matched either mounds or non-mounds (control locations) by pre-processing and classification treatments. Although it appears that the medium pass filter using a 4-pixel clump value provided the highest number of mound matches, it also provided the highest number of non-mound matches. Recall that the mounds represented actual field observations for 73 mounds and two reference points. A perfect technique for pixel extraction would achieve a match value of 73. In contrast, the non-mound points were known to not contain mounds and so should have had a match value of 0 in a perfect extraction technique. Clearly, all extraction techniques were equally poor at isolating



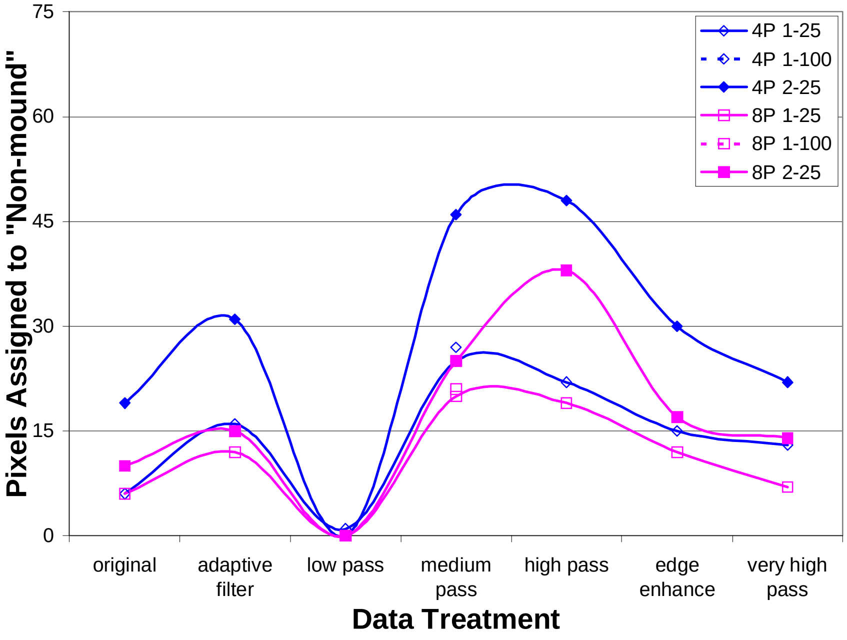


Figure 4.7. Number of pixels matching mounds (top) and non-mounds (i.e., controls, bottom) by treatment. 4/8 indicates clump test level, P/M indicates panchromatic or multispectral imagery, 1/2 indicates whether the brightest (1) or two brightest (2) spectral classes were assigned to the information class "bright", 25/100 indicates the number of unsupervised classes.

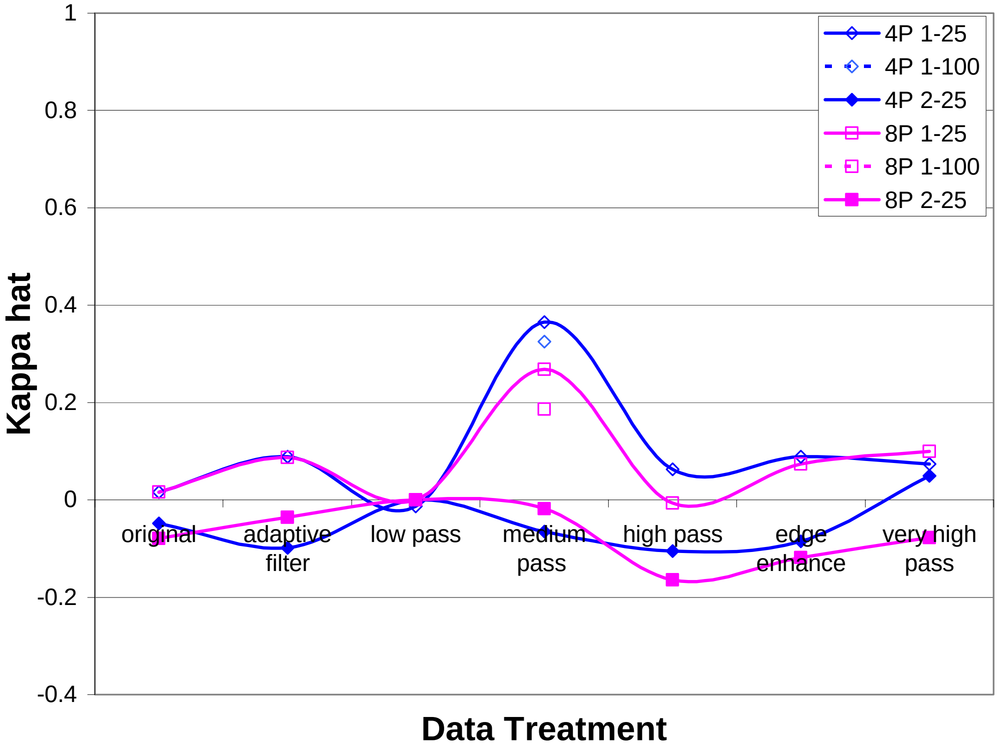


Figure 4.8. Kappa hat statistic by treatment and classification parameters for panchromatic imagery. Coding identical to Figure 4.7.

pixels containing mounds from those not containing mounds. Further confirmation of the poor performance of the evaluated methods is given by the kappa hat statistic shown in Figure 4.8. A kappa hat of 1.0 suggests perfect match of classification assignments to reference data (Campbell 2002:397). Low values of kappa hat indicate that matches are as likely due to chance as to method efficacy. The low values of Figure 4.8 indicate that chance was the driving mechanism for matches of extracted pixels to mounds and non-mounds (controls).

Figure 4.9 compares the total number of pixels extracted by each of the treatments and classification methods. Since only 73 single or double pixel clumps should have been extracted (since there were 73 mounds) and all the methods extracted many more

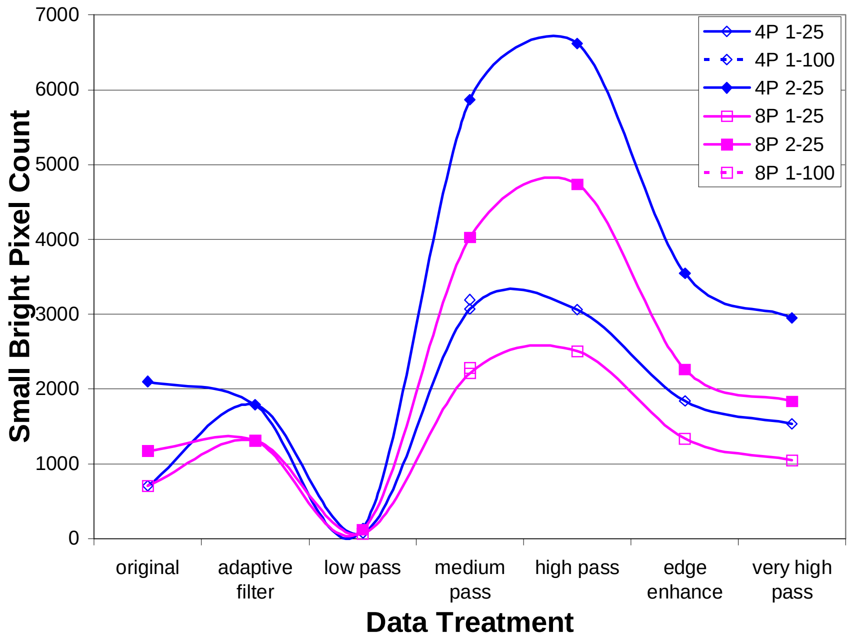


Figure 4.9. Extracted pixel count by treatment and classification parameters for panchromatic imagery. Coding identical to Figure 4.7.

pixels than this, the methodology used is obviously flawed. This is further confirmed in Figure 4.10 in which the number of pixels extracted is plotted against the number of matched mound pixels. There is a strong correspondence of increasing mound matches with increasing pixel counts.

Discussion

Data presented in the previous section indicate that the method used to extract small bright pixels failed to provide good correlation with known harvester ant mounds in the field. Several aspects of both the input data and method have contributed to this mismatch. Image seasonality, resolution levels, and the base hypothesis all contributed to the disappointing results. The winter season (early December) of the imagery may have had multiple impacts on the ability to detect mounds. Ants are inactive during the winter

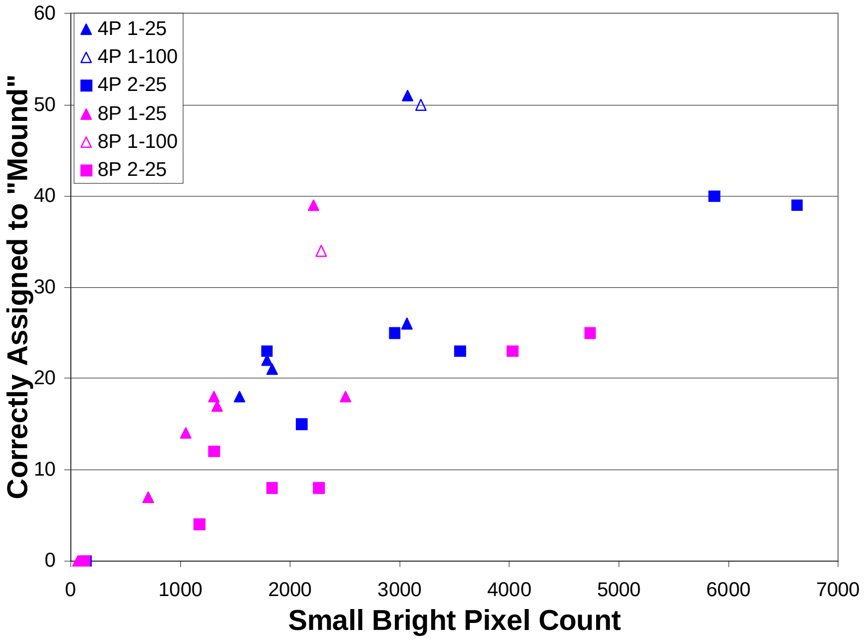


Figure 4.10. Number of correctly assigned pixels against total number of bright pixels by classification parameters for panchromatic imagery. Coding identical to Figure 4.7.

and do not maintain their gravel cones or remove vegetation and debris from the disks. When mounds were observed in April, most had completely degenerated cones with gravel washed away and considerable debris on the disks. It is likely this process was well under way in December. Deterioration of the mounds in conjunction with very low sun angles in December combined to make the original assumption of a bright reflective surface from mounds and disks invalid. Comparison of Figures 4.2 and 4.6 illustrates a second effect of seasonality. The aerial photograph in Figure 4.6 was taken in October and shows slightly darker vegetation patches in exclosure areas (note for example the small squared fenced areas in the northeastern corner of the image) than are apparent in Figure 4.2 taken two months later after a much drier year. The December image contains much less active vegetation (to be expected in a short-grass steppe area) than the October image and it is likely that many of the bright areas of the later image are simply bare soil without masking vegetation. Small bright soil patches were impossible to distinguish from potential mounds, particularly given compromised mound reflectance as previously discussed. Potentially, imagery collected during the growing season with high sun angle would eliminate these seasonality problems.

Less easily addressed is the problem of mixed pixels. Given that disks at the CPER were roughly 1-m in size, it is unlikely that all or even most disks were the sole brightness contributor to a single or even double pixel at the satellite sensor. If dried vegetation contributed to the signal, it is likely the sensor registered a lower overall brightness than from the disk alone and if bare soil surrounded the disk, the sensor might record a bright value but the number of contiguous bright pixels would be larger than expected for a mound alone. In combination with the image seasonality mentioned earlier, the mixed pixel problem suggests that few, if any, strong bright pixels could be reliably credited to mounds. More likely, brightness signatures from disks were far from "bright" and were easily diluted by adjacent ground signals. The methods tested had no way to extract "relatively" bright pixels in addition to absolutely bright pixels as the mixed pixel problem requires. The mixed pixel problem also explains why the performance of the multispectral imagery was so poor. Given that the largest disk in the field survey was 2.6-m across and the multispectral resolution was 2.4-m, almost all disks would have represented only a portion of the signal received at the sensor. In this case, even if disks were extremely bright, the signal detected at most sensor elements would have been confounded by other components such as dried vegetation or soil.

Finally, the original hypothesis that ant mounds would be one of the few bright sources on the landscape did not hold for this imagery. In retrospect, the hypothesis seems somewhat naive but examination of Figure 4.5 shows that the idea has merit if an appropriate methodology can be established to both identify appropriate pixels and remove undesirable ones. In Figure 4.5, the far left panel shows the original imagery; a cattle path (weaving diagonally from the left edge), two-track gravel road (running N-S in the center), and fence line (N-S on right side) are easily seen as bright areas. As processing proceeds across the figure, most but not all of the pixels of the cattle track, road, and fence are eliminated. Residual pixels of these features can still be observed in the right-most panel. Better understanding of why these pixels failed to be removed would go a long way to eliminating the extra pixels in the final comparison step. In addition, while it seems reasonable to expect to be able to eliminate bright pixels from roads or aluminum roofs, it is less clear how to eliminate bright pixels generated from ant mound-like areas such as the cleared areas produced by some rodent activity. This example also illustrates the difficulty in finding a balance between number of unsupervised classes, degree of class aggregation, clump parameter, and clump size cutoff. The parameters used to create Figure 4.5 obviously created an excessive number of small isolated bright areas.

Conclusion

The methods tested (pre-processing filtering and classification variations) were unsuccessful in detecting harvester ant mounds in fine spatial resolution imagery due to image seasonality and signal mixing. Given that an ability to remove many bright pixels from the images under test was demonstrated, the methods do have potential applicability with continued development. In particular, the methods could be applied to low or medium altitude aerial digital photographs collected during the growing season. Lower elevation imagery would have higher spatial resolution relative to feature size and would allow recognition of disk features such as the typical elliptical outline. Growing season imagery would both reduce bare soil signatures and allow masking of areas with high near-infrared signals (i.e., vegetation). Growing season imagery would also strengthen the signals from the mounds and disks since they would be optimally maintained and sun angles would be high providing maximum illumination. Alternatively, the methods could be re-evaluated using fine resolution satellite imagery from an area with higher normal levels of vegetation. Mixed grass prairie sites, for example, retain considerable vegetative cover throughout the year compared to the short-grass steppe. Seasonality issues might be less of a problem in this type of ecosystem.

Chapter 5. Conclusion

This thesis set out to address three questions with respect to the relationship of western harvester ants (*Pogonomyrmex occidentalis*) and archaeological inquiry:

1. Do individual western harvester ant colonies display patterns of collection of gravel-like materials that can be quantified and if so are these patterns useful on an archaeological scale?

2. Do colonies have an arrangement on the landscape and with each other that allows inference beyond the colony level?

3. Can satellite imagery be used to locate colonies to improve field survey efficiency?

This thesis has shown that *Pogonomyrmex occidentalis* (western harvester ants) are active taphonomic agents in a mixed grass prairie setting. While it raises many questions (which will be enumerated below) about ant foraging behavior, it has also established a baseline of mound material foraging behavior upon which subsequent research can be based. In particular, it has been shown that:

- 98 % of foraging occurs within 20 m of the nest
- 2.5 mm, 25 mg materials are preferred over smaller (1 mm, 10 mg) or larger (4 mm, 75 mg) materials at foraging distances beyond 4 m
- Foraging for "large" materials is not a rare event, 11 % of the materials moved represent a burden rate of 13 (75 mg load)

- Successful foraging occurs at densities as low as 50 items/m^2
- Foraging occurs in all directions from the nest
- Foragers find point deposits less reliably than uniform scatters
- Foraging is an on-going activity associated with nest maintenance
- Nests are close enough together that foraging areas often overlap
- Nests are located along disturbed areas and seldom in dense grass
- If a nest has anthropogenic materials, chances are good that its neighbor (within the foraging distance) will have material also
- Detection of colonies in satellite imagery was unsuccessful

These observations are by no means suggested as universals. In particular, the preference for medium beads over large may only indicate that the large beads were too large for these ants to successfully move long distances. The inability to find point deposits may be a function of vegetation density or colony vitality. And nest location may have more to do with general soil conditions than vegetation, per se.

For archaeologists, this research has shown that survey of harvester ant mounds has the potential to be an effective way to look for small items using reasonably spaced (15-m) transects. If colonies are actively foraging, they are very likely to reveal the presence of small anthropogenic material around their nests. Colonies are close enough together that their foraging areas overlap and neighboring mounds will often exhibit the same presence/absence of materials. Inability to find a surface material source within 20 m when materials are found on a nest should suggest the presence of material under the nest, although this has not been investigated here. Further, if no materials are found on a vigorous colony, it is likely there are no exposed materials within a radius of 20 m. In addition, if during an excavation, a semi-elliptical deposit of very small gravel is encountered, consideration should be given to it being a collapsed ant mound. This would be suggested by both deposit diameter and gravel size. Determination as to whether the deposit is a result of ant or human activity may be aided by a analysis of item size distribution against what would be expected in a human generated debris pile (see for example Toft 1991:61). Recognizing that ants preferentially forage for items weighing about 25 mg, a deposit enriched in this size material may be a remnant mound. Further exploration of this phenomena is warranted. Finally, presence of harvester ant mounds has specific indications for climatic inference - in particular, harvester ants require semi-arid to arid conditions, sandy soils, and relatively open vegetation. It is important to remember that materials found on or in an ant nest are removed from their primary context and as such provide only a pointer to the original deposit and provide little information about the source itself.

Given the conclusions just presented, the research has also generated a wealth of questions which require additional study in order to fully understand the role of harvester ants in material transport. Beyond testing the work done here with other ant species in other habitats, other investigative avenues are important. A key question, although difficult to explore experimentally, is the relative contribution to mound material from below ground sources (i.e., during nest excavation). The work presented here indicates that a significant amount of material is collected from the surface but clearly (see for example Bass and Johnson 2003:22) materials are also excavated. In a similar vein, can the material displacement patterns of other bioturbators (rodents, snakes, or beetles) and surface collectors (bower birds, for example) be better quantified as has been attempted here for harvester ants. If, for these bioturbators, patterns can be established, what do these patterns look like in the archaeological record. In particular, does the pattern of 25-mg mound material sustain through other formation processes.

Another investigative avenue is that of material selection. Although glass beads provide a poor surrogate for common anthropogenic debris like chipped stone debitage, the ability of ants to collect these experimental materials should spur additional research with more representative sample materials. The correspondence of the observed gravel collection range to that reported for seed foraging does imply that seed research can be used as a starting point for further gravel-like material collection studies.

In addition, this study failed to make a clear correlation between collection of experimental materials and the actual occurrence of archaeologically interesting material on mounds. At this point, it is speculation that mound materials can be profitably used to locate an anthropogenic deposit. Given harvester ants' ability to recover materials at fairly low densities on the landscape, material on mounds may just be an indication of a certain background level of debris. This in itself is worth study - that is, the ability to discriminate between background "noise" and a unique archaeological deposit. This may be an ideal application for exploring Ebert's (2001) "distributional archaeology" concepts.

A secondary outcome of the research presented here has been a type of "public archaeology". Although no true archaeology was conducted during this research, the experiments were open to the visitors to the Hudson-Meng Bison Bonebed who often became caught up in the idea of ants engaged in archaeology and then being able to observe archaeology (or at least archaeological research) in action. The follow-on questions posed above readily lend themselves to additional ways that the public, particularly middle school students, could contribute to this research. Beads are a standard material and are readily available, the other equipment required is cheap and easy to obtain, and harvester ants are prevalent across much of the western U.S. A middle school science class could easily set up experiments such as the distance one described above and monitor it on a weekly basis. As well as learning about archaeological processes, the students would be developing naturalist observation skills as well as learning the experimental method. If the school is partnered with another school in a different location, they could do a series of experiments to understand the different responses their particular ants display. The ideas could go on.

In conclusion, although this research was intended to expand the understanding of harvester ants as taphonomic agents, it has also contributed to a better understanding of ants within their ecological setting. The harvester ants in the study area clearly selected disturbed areas over grassy ones and were quick to respond to changes in disturbed area locations. The digitized roadway and buildings in Figure 3.1 were completed since 1997 and already display high concentrations of ant colonies. As well as responding rapidly to large scale landscape changes, this research showed that ants are quick to respond (within minutes) to the introduction of material within their foraging areas. It also demonstrated that ants behave as central-place foragers and maximize the return on their foraging trips. Finally, although not directly tested, the similarity of the results obtained in this research to those reported for seed foraging, suggests that western harvester ants have a single foraging behavior that is directed to retrieving both food items and non-food items.

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Appendix A. Glass Properties

Table A.1. Physical Properties of Glass, Quartz, and Stone

Property	Glass	Quartz	Sandstone
Density	2.6 g/cm^3	2.65	2.25
Specific heat	0.2 cal/g K	0.18 cal/g K	0.22

Note: From CRC 1976:177, 178, 187.

Appendix B. Field Data Details

Table B.1. Summary of Experimental Treatments and Deposited Bead Count Detail

							Quantity		
Experiment	Mound ID	Setup Date	Density[a]	Quadrant or Distance	Color(s)	Small	Medium	Large	Total
Qualification	AH 215	6/2/03	400	4 m	All 12	900	900	900	2700
	AH 219	6/2	400	4 m	All 12	900	900	900	2700
	AM 040	6/4	1500	1 m	10 (no pink, purple)	0	2400	0	2400
	LB 01	6/2	800	2 m	All 12	900	900	900	2700
Total beads									10500
Distance	AH 758	6/13	400	4 m	White	900	900	900	2700
			400	8 m	Light Blue	1800	1800	1800	5400
			400	8/12 m	Dark Blue	2700	2700	2700	8100
			400	20 m	Black	4500	4500	4500	13500
			400	32 m	Yellow	7200	7200	7200	21600
	AH 760	6/4	400	4 m	Light Green	900	900	900	2700
			400	8 m	Orange	1800	1800	1800	5400
			400	12 m	Light Blue	2700	2700	2700	8100
			400	20 m	Yellow	4500	4500	4500	13500
			400	32 m	Dark Green	7200	7200	7200	21600
			400	48 m	White	10800	10800	10800	32400
	AH 769	6/5	400	4 m	Orange	900	900	900	2700
			400	8 m	Dark Blue	1800	1800	1800	5400
			400	12 m	Red	2700	2700	2700	8100
			400	20 m	Dark Green	4500	4500	4500	13500
			400	32 m	Black	7200	7200	7200	21600
	AM 023	6/5	400	4 m	Black	900	900	900	2700
			400	8 m	Red	1800	1800	1800	5400
			400	12 m	Light Green	2700	2700	2700	8100
			400	20 m	Dark Blue	4500	4500	4500	13500
			400	32 m	Orange	7200	7200	7200	21600
	AM 031	7/4	400	4 m	Dark Green	900	900	900	2700
			400	8 m	Black	1800	1800	1800	5400
			400	12 m - Veg.	Yellow	1350	1350	1350	4050
			400	12 m - Road	Orange	1350	1350	1350	4050

Table B.1. Summary of Experimental Treatments and Deposited Bead Count Detail (continued)

							Quantity		
Experiment	Mound ID	Setup Date	Density[a]	Quadrant or Distance	Color(s)	Small	Medium	Large	Total
Distance	AM 031		400	20 m - Veg.	Red	2250	2250	2250	6750
			400	20 m - Road	White	2250	2250	2250	6750
			400	32 m - Veg.	Dark Blue	3600	3600	3600	10800
			400	32 m - Road	Light Blue	3600	3600	3600	10800
Total beads									288900
Direction	AM 004	6/4	400	Southeast / 8 m	Red	0	400	400	800
			400	Southwest / 8 m	Black	0	400	400	800
			400	Northwest / 8 m	Yellow	0	400	400	800
			400	Northeast / 8 m	Dark Green	0	400	400	800
	AM 022	6/3	400	East / 8 m	Dark Green	0	400	400	800
			400	South / 8 m	Orange	0	400	400	800
			400	West / 8 m	Dark Blue	0	400	400	800
			400	North / 8 m	White	0	400	400	800
Total beads									6400
Density	AH 781	6/4	200	8 m	Red	0	800	800	1600
	AM 002	6/4	100	8 m	Dark Blue	0	400	400	800
	AM 013	6/4	50	8 m	White	0	200	200	400
Total beads									2800
Distribution	AH 766	6/27	400 beads	20 cm pile / 8 m	Dark Green	0	200	200	400
	AH 772	6/13	400 beads	20 cm pile / 8 m	Yellow	0	200	200	400
	AM005	6/13	400 beads	20 cm pile / 8 m	Orange	0	200	200	400
	AM009	6/27	400 beads	20 cm pile / 8 m	Black	0	200	200	400
Total beads									1600
Grand Total									310200

Notes:

[a] Density in beads/m^2 unless otherwise noted.

Table B.2. Summary of Mound Status By Week and Bead Presence

Week	1	2	3	4	5	6	7	9	11	13
Date	6/6	6/13	6/20	6/27	7/4	7/11	7/18-7/19	8/1	8/18	8/29
Survey Window [a]	Morn	Mid	Mid	Mid	Mid	Mid	Eve/Mor	Mid	Mid	Mid
Mound ID										
AM 001	ND	ND	ND	I[b]	I	I	A	I	I	I
AM 002	I	**A**	**I**	A	I	**I**	**A(1)**	**I**	**I**	**A(2)**
AM 003	ND	ND	ND	A	I	A	A	A	A(1)	A(3)
AM 004	**A**	**A**	**A**	**A**	**A(1)**	**A**	**A**	**A**	**A**	**A**
AM 005	ND	ND	**A(1)**	A	I	**A**	**A**	**A**	**A(1)**	**A**
AM 006	ND	ND	I	A	I	**A**	I	**I**	**I**	**A(1)**
AM 007	ND	ND	I	A	I	A	A(1)	I	I	**A(1)**
AM 008	ND	ND	I	A	I	**A**	A	I	**I**	I
AM 009	ND	ND	I	A	I	A	A	**A**	**I**	**A**
AM 010	ND	ND	**A**	**A**	**I**	A	A	I	A(1)	A
AM 011	ND	A(1)	A	A	I	A	A	I	I	A
AM 012	ND	A(1)	A	A	I	A	A	A(1)	I	A
AM 013	I	**A**	**A(1)**	**A**	I	**I**	A	I	**I**	A
AM 014	ND	ND	A	A	I	CNL	I	I	CNL	CNL
AM 017	ND	ND	**A**	**A**	**I**	**I**	**A**	**I**	**I**	**A**
AM 018	ND	I	I	I	I	I	I	I	I	I
AM 019	ND	ND	**A**	**A**	**I**	**A**	**A**	**I**	**I**	**A(1)**
AM 020	ND	A(1)	ND	A	I	I	A	I	I	I
AM 022	**A**	**A**	**A**	**A**	**I**	**I**	**A**	**I**	**I**	A
AM 023	**A**	**A**	**A**	**A**	**I**	**A**	**A**	**I**	**I**	**A**
AM 030	ND	ND	**ND**	**A**	**I**	**ND**	**A**	**I**	**I**	**A(1)**
AM 031	ND	ND	ND	A	A	**A**	**A**	**A**	**I**	I
AM 032	ND	ND	ND	ND	I	A	I	I	I	I
AM 033	ND	ND	ND	A	A	A	A	A	I	**A**
AM 040	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**

Table B.2. Summary of Mound Status By Week and Bead Presence (continued)

Week	1	2	3	4	5	6	7	9	11	13
Date	6/6	6/13	6/20	6/27	7/4	7/11	7/18-7/19	8/1	8/18	8/29
Survey Window [a]	Morn	Mid	Mid	Mid	Mid	Mid	Eve/Mor	Mid	Mid	Mid
AH 215	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**
AH 218	**A**	A	A	A	A	A	A	A	A	A
AH 219	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**
AH 758	ND	ND	**A(2)**	**A**	**I**	**A**	**A**	**I**	**I**	**A**
AH 759	ND	ND	**ND**	**ND**	**I**	**I**	**A**	**I**	**I**	**A**
AH 760	**A**	**A**	**A**	**A**	**A(1)**	**A**	**A**	**I**	**I**	**A**
AH 766	ND	ND	I	A	I	A	A	I	I	I
AH 767	ND	ND	I	A	I	A	A	I	I	A(1)
AH 768	ND	ND	ND	I	I	A	**A**	A	**A**	**A(1)**
AH 769	ND	**A**	**A**	**A**	**A(1)**	**A**	**I**	**A**	**A(2)**	**A**
AH 770	ND	A(1)	ND	A	I	I	A	I	I	A
AH 771	ND	A(1)	ND	A	I	A	A	I	I	I
AH 772	ND	ND	A	A	I	I	I	I	I	A
AH 774	ND	A(1)	I	I	I	A	I	A	ND	I
AH 781	I	**A**	**I**	**A**	**I**	**A**	**A**	I	**A**	I
AH 864	ND	A(1)	ND	A	I	I	A	I	I	A
LB 01	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**	**A**

Notes:

[a] Survey Window: Morning = early in the day (before 10:00), Mid = midday period (between 10:00 and 13:00), Evening = later portion of the day (after 17:00).

[b] Key to Coding:

A: Mound was active (ants outside the door or visible immediately inside the entrance. If only a few ants were visible then the count is in parentheses

CNL: The mound could not be located	I: Mound was inactive, no ants were observed
ND: No status was recorded	**Bold**: Beads were present on the mound

Table B.3. Experimental Mound Categorization and Nearest Neighbor Relationships

Mound ID	Primary Assignment	Nearest Neighbor (NN)	Distance to NN, m
AM 002	Density	AH 781	32
AM 004	Direction	AH 769	19
AM 005	Distribution	AH 768	16
AM 009	Distribution	AM 008	18
AM 013	Density	AM 011	25
AM 023	Distance	AM 014	42
AM 031	Distance	AM 006	27
AM 040	Qualification	N.D.	-
AH 215	Qualification	N.D.	-
AH 219	Qualification	AH 218	9
AH 758	Distance	AM 016	36
AH 760	Distance	AM 018	13
AH 766	Distribution	AM 030	42
AH 769	Distance	AM 004	19
AH 772	Distribution	AH 770	30
AH 781	Density	AM 002	32
LB 01	Qualification	N.D.	

Notes:

N.D. - Not Determined.

Table B.4. Auxiliary Colony Summary and Relationships

Auxiliary Mound	Primary Assignment	Source Mound	Distance to beads, m	Nearest Neighbor	Distance to NN,m
AM 004	(Direction)	AH 769	**1, 7**, 11, 13,15	AH 769	19
AM 005	(Distribution)	AM 031	**8**, 20	AH 768	16
AM 006	Auxiliary	AM 031	**5, 7, 15**, 19, 23	AM 007	18
		AH 769	15		
AM 007	Auxiliary	AM 031	12	AM 007	18
		AH 769	**15**		
AM 008	Auxiliary	AM 031	**10**, 22	AM 009	18
AM 011	Auxiliary	AM 013	17	AM 012	12
AM 013	(Density)	AM 023	18	AM 011	25
AM 017	Auxiliary	AH 760	**3**, **13**, 23	AH 759	28
AM 018	Auxiliary	AH 760	1, 5, 7, ,9, 19	AH 760	13
AM 019	Auxiliary	AH 760	**2, 6, 10, 14,** 14	AH 760	18
AM 020	Auxiliary	AH 760	14	AH 760	62
AM 030	Auxiliary	AH 760	**7, 23**	AH 759	29
		AH 758	**19**		
AM 032	Auxiliary	AH 758	19	AH 767	26
AM 033	Auxiliary	AM 022	**13**	AM 022	21
AH 218	Auxiliary	AH 219	**9**	AH 219	9
AH 759	Auxiliary	AH 760	**7**, 23	AM 017	28
		AH 758	**14**		
AH 768	Auxiliary	AM 031	**4, 8, 16**, 20	AM 005	16
		AM 005	**8**		
		AH 769	19		
AH 769	(Distance)	AM 004	11	AM 004	19
AH 774	Auxiliary	AH 769	2, 14	AM004	27

Notes:

Bold indicates that beads were collected from that distance from the source mound. Auxiliary AM019 was 14 m away from two different bead bands around AH760 (the band at 4 m and the band at 32 m), so 14 appears twice in the distance column for this relationship.

Table B.5. Control Mound Summary

Mound ID	Primary Assignment	Nearest Neighbor (NN)	Distance to NN, m	Nearest Bead Source	Distance to Beads, m
AM 001	Control	AH 781	46	AH 781	38
AM 003	Control	AM 002	91	AM 002	83
AM 010	Control	AM 009	27	AM 009	33
AM 012	Control	AM 011	12	AM 013	24
AM 014	Control*	AM 024	39	-	-
AH 767	Control	AM 032	26	AH 758	24
AH 770	Control	AH 772	30	AH 772	30
AH 771	Control	AM 020	16	AH 772	65
AH 864	Control	AH 771	21	AM 022	58

Notes:
Two yellow beads were found on AM 010.
* - This mound could not be located after week six. It may have been initially misidentified as a mound or the colony may have died. This mound was excluded from the control group during analysis.

Table B.6. Experiment Mound Size Information

Mound ID	Disk Length	Disk Width	Mound Length	Mound Width	Disk Orientation	Door Orientation
AH215	1460	600	610	390	-	-
AH219	2860	2860	700	590	-	-
AH758	700	600	360	300	-	-
AH760	880	795	420	400	154	93
AH766	700	600	360	270	-	-
AH769	990	840	450	320	-	-
AH772	600	490	270	200	-	180
AH781	1000	935	287	225	214	274
AM002	830	610	230	210	168	184
AM004	1000	960	300	250	159	123
AM005	1000	600	430	300	-	140
AM009	670	500	170	160	-	240
AM013	915	655	310	290	52	193
AM022	519	441	400	330	181	102
AM023	-	-	-	-	-	-
AM031	850	490	350	250	-	-
LB01	730	530	730	530	-	-

Notes:
All length and width measurements are in mm. Orientations are in degrees, North = 0º.

Table B.7. Mound UTM Locations from Garmin 12XL (Zone 13N)

Mound ID	Alternate ID / Description	Easting, m	Northing, m
AM001		614729	4741873
AM002		614659	4741898
AM003		614569	4741885
AM004		614631	4741798
AM005		614578	4741760
AM006		614629	4741734
AM007		614647	4741734
AM008		614635	4741702
AM009		614646	4741688
AM010		614673	4741683
AM011		614687	4741654
AM012		614699	4741652
AM013		614672	4741634
AM014		614627	4741610
AM017		614814	4741668
AM018		614835	4741699
AM019		614866	4741700
AM020		614872	4741754
AM022		614961	4741760
AM023	AM024	614661	4741586
AM030		614796	4741716
AM031		614603	4741728
AM032	AM015	614703	4741720
AM033		614941	4741753
AH215		614392	4742836
AH218		614477	4742637
AH219		614483	4742622
AH758		614749	4741698
AH759	AM016	614794	4741688
AH760		614848	4741697
AH766		614787	4741758
AH767		614716	4741743
AH768		614593	4741755
AH769		614637	4741780
AH770		614876	4741809
AH771		614875	4741770
AH772		614896	4741832
AH774		614605	4741792
AH781		614683	4741877
AH864	AM021	614896	4741770
LB01		614416	4742873
Ref. Locations			
LB017*	Northeastern corner of FS918 and access road intersection	614609	4741571
LB04	Datum southeast of bonebed and west of stock pond.	614329	4742708
LB06	Northwestern corner of trailhead and access road west of restroom building	614446	4742628

Note:

UTM readings are in WGS84 (equivalent to NAD83).

LB017, LB04, and LB06 are included as reference locations to aid in locating the other coordinates in the future. LB017 and LB06 can be identified in aerial photos.

Appendix C. S-Plus Scripts for Nearest Neighbor Determination

1. Script to create a distance matrix containing distances between each point and all other points.

"nndata" is a 2 column x n row matrix where column 1 is an adjusted UTM Easting and column 2 is UTM Northing for each point in the data set of n points which has been read into S-Plus 6.0. Eastings and northings can be adjusted so the smallest values in each data set are 0 (subtract the minimum value from each set of values) to reduce computation time and memory requirements.

The script computes the distances between all points and all other points (including the reference point) and sets distances less than 1 and greater than 100 to NA. S-Plus ignores NA values during calculation. An n x n matrix of distances is returned.

```
neighdis <-function(nndata)
{
      norc <- nndata[, 2]
      easc <- nndata[, 1]
      len <- length(norc)
      dis <- matrix(0, len, len)
      nortm1 <- matrix(norc, len, len)
      nortm2 <- t(nortm1)
      ncombine <- nortm1 - nortm2
      ncombine <- ncombine * ncombine
      eastm1 <- matrix(easc, len, len)
      eastm2 <- t(eastm1)
      ecombine <- eastm1 - eastm2
      ecombine <- ecombine * ecombine
      dis <- (ncombine + ecombine)^0.5
      dis[dis < 1] <- NA
      dis[dis > 100] <- NA
      return(dis)
}
```

2. Script to determine the pairing relationship between all nearest neighbors.

"reps" is the number of replications to run. "cs" is the count of colonies with chipped stone. "dis" is the distance matrix computed with the neighdis function above.

The script randomly assigns each point in a vector of length n, to have chipped stone or not (ratio of cs/n). Status of pairs of points is computed as point 1 (row value) plus point 2 (column value) where the row and column value for no chipped stone is 0, the row value for chipped stone is 2, the column value for chipped stone is 1. So pairings are:

Row	Column	Status Code
No Chipped stone (0)	No chipped stone (0)	= 0 + 0 = 0
No chipped stone (0)	Chipped stone (1)	= 0 + 1 = 1
Chipped stone (2)	No chipped stone (0)	= 2 + 0 = 2
Chipped stone (2)	Chipped stone (1)	= 2 + 1 = 3

Counts of each pairing are tabulated by replication. A 4 column by "reps" row matrix is returned.

```
nearneigh <- function(cs,reps,dis)
   {
   len <- ncol(dis)
   place <- matrix(0, 1, len)
   test <- matrix(0, len, 1)
   flag <- matrix(0,len,len)
   fplace <- numeric()
   i <- numeric()
   iflag <- matrix(0, len, 1)
   newrow <- matrix(0, 4, 1)
   countmat <- matrix(0, reps, 4)
   for(n in 1:reps) {
      col <- matrix(runif(len), 1, len)
      row <- t(col)
      col[col >= (cs/len)] <- 1
      col[col < (cs/len)] <- 0
      row[row >= (cs/len)] <- 2
      row[row < (cs/len)] <- 0
      colm <- matrix(col, ncol = len, nrow = len, byrow = T)
      rowm <- matrix(row, ncol = len, nrow = len)
      flag <- numeric()
      flag <- colm + rowm
      for(i in 1:len) {
         test[i] <- min(dis[i,  ], na.rm = T)
         place <- (1:len)[dis[i,  ] == test[i]]
         fplace <- min(place[!is.na(place)])
         iflag[i,] <- flag[i,fplace]
         flagtable <- table(iflag)
      }
      newrow <- as.numeric(unlist(flagtable))
      countmat[n,  ] <- t(newrow)
   }
   countmat
}
```