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THE ECOLOGICAL EFFECTS OF THE WESTERN HARVESTER ANT (*Pogonomyrmex occidentalis*) IN THE SHORTGRASS PLAINS ECOSYSTEM

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ABSTRACT

Ecological effects of the western harvester ant, *Pogonomyrmex occidentalis* (Cresson), were studied on the U.S. IBP Grassland Biome Intensive Site located in northeastern Colorado. Energy values were determined for populations in differentially grazed pastures by estimating the energy required for ant production and respiratory heat loss.

Colony density was measured in four differentially grazed areas: ungrazed, lightly grazed, moderately grazed, and heavily grazed. Densities ranged from 31 colonies/ha under moderate grazing pressure to 3 colonies/ha with heavy grazing. There are an estimated 2032 worker ants produced per colony each year based on counts from colony excavations. This estimate plus the production of 315 winged reproductives per colony result in an estimated 48.64 kcal/colony required for secondary production, a range of .01 to .15 kcal/m^2/year across study areas.

Energy for heat production was estimated by measuring CO_2 production of laboratory colonies at representative field temperatures. CO_2 production was monitored with a Beckman infrared gas analyzer. Calculations of respiratory energy loss were made separately for (i) foraging ants inside the nest at night, (ii) foraging ants outside the nest during the day, (iii) worker ants inside all season, and (iv) total colony population inside during the the winter. An estimate of 418.42 kcal/colony was made for respiratory heat loss. The respiratory energy requirements of the populations in the differentially grazed pastures ranged from .13 to 1.30 kcal/m^2/year.

Energy flow (heat production plus tissue production) ranged from .14 to 1.45 kcal/m^2/year in the study pastures, considerably less than for the

southern harvester ant, *Pogonomyrmex badius* (Latreille). The major area of difference occurs in estimates made of energy required for heat production.

The plant clearing habits of these ants were found to exert only a minor influence at the Pawnee Site, clearing a maximum of .28% of the total area. A compensating increase in vegetation standing crop values around the cleared disc (border effect) was also found which partially compensates for the clearings.

Ohter findings indicate that the ants move a large amount of soil during colony excavations (2.8 kg/colony) and modify certain soil characteristics. Bulk density was lower beneath the mound, and percent sand content of the colony area was higher than in the vegetated area. Nitrate and phosphorous content were higher in the vicinity of the mound.

The activity times of the ants were found to vary with soil surface temperatures. The relationship between surface temperatures and the number of foraging ants leaving the colony per minute is described by a polynomial equation.

Some 39% of forage particles brought into the colony were seeds, and 24% were litter. The remainder consisted of dead insect material, insect prey, fecal matter, and rocks being brought in for mound construction. Studies conducted on the populations in the light and heavily grazed pastures showed no significant differences in the rate of forage extraction, foraging distance, time per foraging trip, or in the availability of seeds. There was, however, a significant difference in the number of colonies in these two study areas.

INTRODUCTION

This study was designed to ascertain the effects of the western harvester ants in the shortgrass plains ecosystem. Of particular interest are the effects of the ants on the environment, the response of the ants to various environmental phenomena, their foraging activities, and their bioenergetic relationships.

One of the environmental effects of these ants is quite well known, i.e., their habit of clearing vegetation from around their colonies. This prompts the question of how much they clear and if the cleared areas represent a significant loss of vegetation. Other concerns are possible environmental responses to these cleared areas, i.e., soil water and vegetation responses.

Investigations of the western harvester ants' response to environmental factors establishes their operating parameters and determines their periods of daily and seasonal activity.

The granivorous foraging habits of these ants have been known for some time (McCook, 1882), but little is known concerning the rate of forage extraction or preferential foraging habits of the ants. The particular foraging activities of interest concern the types of forage materials selected, the rate of forage extraction in differentially grazed pastures, and utilization of the available seed supply.

The flow of energy through the system should be evaluated in terms of both energy stored as production and the energy required for respiration (Odum, Connell, and Davenport, 1962) since they both influence the energy requirements of the population. Golley and Gentry (1964) were the first to recognize the significance of harvester ant energetics from their study of the southern harvester ant, *Pogonomyrmex badius* (Latreille). Wiegert and Evans (1967) pointed out that the metabolic rates reported for the southern harvester ants were 5 to 10 times higher than those for other insects of comparable size and suggested additional studies to determine if this characteristic was common for ant populations. This suggestion served as the impetus for the bioenergetics portion of the present study.

REVIEW OF THE LITERATURE

Taxonomic Position

The western harvester ant was originally described by Cresson in 1865 as *Myrmica occidentalis*. The genus *Pogonomyrmex* was established in 1868 by Mayr; Cresson placed *occidentalis* in the genus in 1879 (Cole, 1968). The genus *Pogonomyrmex* Mayr belongs to the Myrmicinae which is the largest subfamily of the Formicidae (Borror and DeLong, 1964).

There has been some confusion in the literature as to the actual taxonomic status of western harvester ants. Cole described *Pogonomyrmex owyheei* Cole as a subspecies of *Pogonomyrmex occidentalis* (Cresson) in 1938. Creighton then elevated *P. owyheei* to full species status in 1950 after Mayr (1949) pointed out that *P. owyheei*'s distribution necessitated its being considered as a sibling species of *P. occidentalis*. Colley (1962) separated *P. occidentalis* and *P. owyheei* on the basis of the basal mandibular tooth and concluded that "two different but very closely related species populations are involved both of which have previously been considered as being of a single species."

Lavigne (1969) pointed out that many of the papers written prior to Cole's (1966) revision of the *P. occidentalis* complex really deal with *P. owyheei*, and the distribution of the species must be considered when referring to earlier papers.

Description of the Species

The western harvester ant worker has an overall length of 6½ to 8 mm (Wheeler and Wheeler, 1963), and the body is of a light medium ferrugineous red color (Cole, 1968). There has never been a definitive description of any caste system within the species (Cole, 1968).

The female has most of the characteristics of the worker (Cole, 1968), but is larger with a length of 11 mm (Wheeler and Wheeler, 1963).

The male is about the same size as the worker with a length of 8 mm (Wheeler and Wheeler, 1963). The head and thorax of the male are reddish to blackish brown. The gaster has a lighter color than the head and thorax (Cole, 1968).

Life Cycle

The following is a generalized life cycle for *P. occidentalis* in Wyoming according to Lavigne (1969), Lavigne and Fisser (1966), and Stevens (1965). During the winter months the colony consists of a mature queen and worker ants which overwinter in chambers located in the depths of the earth. The worker ants first appear in the mounds from late March to mid-April and are consistently foraging from mid-June through the middle of October, depending on weather conditions.

The queen starts laying eggs in May and larvae appear the first of June. Reproductive pupae are present from the end of June to mid-August, and worker pupae are present from late July to early October. It is assumed from these observations that the first larval brood develops into winged reproductives.

The adult reproductives first appear in mid-July and swarming takes place from late July to mid-August. During swarming, many winged reproductives emerge from different colonies and swarm at the same time. They fly to the highest point in the area where mating takes place. Following mating, the fertilized queen flies to a "suitable" location, bites off her wings, tunnels into the soil, and lays her first eggs.

The queen feeds the first brood from her own body reserves. This first brood develops into undersized workers that forage, take over colony maintenance, and feed larvae so that the queen may "devote" herself to reproduction.

Larvae are found in the nest until early October or about a month before the queen moves to the overwintering chambers. Most of the ants remain in a semicomatose condition during the winter. There is apparently little movement or feeding until spring when higher soil temperatures trigger movement to the upper levels of the nest.

Distribution of the Species

Western harvester ants are common inhabitants of the plains. They are characteristic of short- and tallgrass prairies and semidesert areas (Cole, 1934*a*).

Colorado is a type of locality with the center of species occurrence in the upper Sonoran zone. The altitudinal distribution of the ants in Colorado ranges from 3500 to 9000 ft (Gregg, 1963).

Pogonomyrmex occidentalis colonies are widely distributed and occur in Kansas, Arkansas, Texas, Oklahoma, North Dakota, western South Dakota, Nebraska, Wyoming (except northwestern part), Colorado, southeastern Idaho, central and northern New Mexico, Utah, Arizona, Nevada, and east-central California (Cole, 1968).

Mound Characteristics

Mound construction. Early observers reported that western harvester ants constructed their mounds from materials brought up from below as well as from materials found in the surrounding area (Todd, 1885; Headlee and Dean, 1908). Mound construction involves three stages; the first stage is indicated by the presence of a small pile of soil excavated by the queen during the establishment of the colony, the next stage consists of a crater-like mound typical of second year colonies, and the last stage consists of the typical cone-shaped pebble mound of mature colonies (Cole, 1932*b*).

Mound size. Wheeler and Wheeler (1963) measured 76 mounds in North Dakota and found that they varied from 12 to 53 inches in diameter and from 2 to 10 inches in height. Measurement of 20 colonies near Casper, Wyoming (Lavigne, 1969), showed the mound height vary from 0 to 10½ inches and mound diameter to vary from 0 to 44 inches. Comparison of mound sizes in other parts of Wyoming (Lavigne, 1966) showed that 220 colonies near Dwyer averaged 24 inches in diameter. Measurement of the same number of mounds near Riverton, Wyoming, averaged 30 inches in diameter.

It is possible for a mound to have a diameter of 4 to 5 ft and a height of 2 to 2½ ft (Lavigne and Fisser, 1966). Cole (1934*b*) measured an exceptional colony near Seligman, Arizona. It had a mound 3 ft high and 16 ft in diameter.

Purpose of the mound. Wheeler (1910) thought that the mound served primarily as an incubator for the young. This contention is supported by Cole's (1933) observation that the mound attains a higher temperature than the adjacent soil surface. This may be of benefit during the early spring months when the workers move the brood to those chambers having optimal temperature and humidity conditions (Stevens, 1965).

The purpose of the surface covering of the mound is probably to prevent erosion from strong winds and rains (Wheeler and Wheeler, 1963). The mounds are also resistant to the weight of small animals as well as being nearly impervious to water (Costello, 1947).

Disc Characteristics

Purpose of the disc. Nearly every publication concerning western harvester ants mentions their habit of clearing the vegetation from the area surrounding the mound. The reasons for this habit have remained obscure, although several suggestions have been made concerning possible advantages of the cleared disc. The denuded area may serve as a fire line in case of range fires (Cole, 1932*c*; Costello, 1947). The clearing of plants may also prevent water from entering the colony through decayed root passageways (Headlee and Dean, 1908; Costello, 1947) or the cleared area may promote the accumulation of heat in the soil and aid in drying the surface after a rain (Costello, 1947).

Headlee and Dean (1908) suggested that the presence of vegetation surrounding the mound might be an obstacle to the foraging ants, that it could provide concealment for their enemies, and that it would retain soil water after a rain which would favor the growth of fungi. Wight and Nichols (1966) speculated that denudation serves to increase the soil water in the area around the mounds by the removal of the transpiring plants.

Costello (1947) suggested that a healthy active colony would keep the disc free from all plants. Others have reported that at least some plants may be tolerated on the denuded area (Cole, 1932*c*; King, 1962).

Disc size. The actual size of the denuded area is rather variable. Cole (1932*c*) reported that the size and rate of denudation was proportional to the size and strength of the colony. Lavigne and Fisser (1966) found that the size of the cleared area was inversely proportional to the density of vegetation. Headlee and Dean (1908) reported that the size of the clearing depends upon colony age, size, and nature of the surroundings.

Maximum disc diameters were 14 ft in Kansas (Fritz and Vickers, 1942), 0 to 10 ft in North Dakota (Wheeler and Wheeler, 1963), 7 to 10 ft in New Mexico (Race, 1966), and 10 to 43 ft in Utah (Knowlton and Nye, 1946). Measurements of 220 colonies near Dwyer, Wyoming, showed that discs averaged 5 ft in diameter with a range of 1½ to 12 ft. Disc diameters of 220 colonies near Riverton, Wyoming, averaged 10 ft with a range from 3 to 17 ft (Lavigne, 1966).

The presence of the denuded area has resulted in the general belief that the western harvester ants destroy considerable amounts of pasture (Wheeler and Wheeler, 1963). However, Wight and Nichols (1966) found that the presence of denuded areas did not lower the production of a Nuttall saltbush community in Wyoming, since there was a compensating increase in plant producton around the perimeter of the denuded area. They also found that the soil water in the denuded area was appreciably higher than in the surrounding vegetated areas.

Density

Population estimates of social insects have proven to be difficult to make with accuracy. The best approach to estimating ant populations is to first determine the number of colonies per unit area and then multiply this figure by the average number of ants per colony.

Western harvester ant colony densities were reported to range up to 40 colonies per acre in the Raft River Valley of Idaho (Sharp and Barr, 1960). Subsequent knowledge concerning the distribution of the western harvester ants (Cole, 1968) leads to the conclusion that this study refers to *P. owyheei* rather than to the western ant, *P. occidentalis*.

Costello (1944) determined the number of colonies present in different stages of secondary succession on abandoned farmland in Colorado. He found from 0 to 4 colonies per acre in the Russian thistle stage, 3 to 11 colonies in the forb stage, 16 to 57 colonies in the *Aristida* stage, and 0 to 13 colonies in a shortgrass disclimax stage. He estimated that an average colony population for that area might be 10,000 ants per colony.

Fautin (1946), while studying the northern desert shrub biome in western Utah, found western harvester ant colonies present in shad scale, horsebrush, greasewood, and sagebrush communities. The greatest colony density (4 to 8 colonies per acre) occurred in the sagebrush communities. Similar findings were reported from Cole's (1932*a*) studies of harvester ant densities in the Tooele Valley of Utah and in the craters of the Moon National Monument in Idaho.

Melendez (1963) observed a greater density of *P. occidentalis* colonies in heavily grazed areas of central New Mexico than in areas of light grazing. Wheeler and Wheeler (1963) reported that greater colony densities occurred in overgrazed pastures in North Dakota, and as the pastures recovered the number of colonies and clearings decreased. Kirkham and Fisser (1972) used aerial photos to determine colony numbers for *P. owyheei* and reported that grazing intensities over a 10-year period did not influence ant abundance in Wyoming.

A measurement of western harvester ant numbers per colony was made by Lavigne (1969) who excavated 33 colonies in Wyoming and found the number to vary from 412 to 8796 ants per colony. Chew (1960) excavated a single colony with 8700 ants of *P. occidentalis* in Arizona and thought this average for a colony in that area based on the size of the mounds.

Foraging Activities

Effects of environmental factors. The nest protects the ants from adverse weather conditions, and the foragers venture out when conditions are most favorable. Stevens (1965) reported that the morning activities of *P. occidentalis* commenced when the mound surface temperature reached 24.4°C. The most active foraging took place at about 34.4°C and activity ceased when the mound surface temperature approached 47°C or the air temperature was near 33°C. This agrees with an observation by Fautin (1946) that the western harvester ants in western Utah were inactive when the air temperature exceeded 32°C.

Cole (1934*c*) reported, for what was probably *P. owyheei*, that harvesting activity occurred from daylight to dark, except for a period of inactivity that occurred when the temperature of the soil surface reached about 48°C. Willard and Crowell (1965) found that *P. owyheei* was greatly affected by daily temperatures in central Oregon. The ants became active when the mound surface temperature reached 16°C. From 16° to 20°C there was sluggish movement on the mound and from 20° to 23°C the ants began to forage away from the mound. Aestivation occurred if the soil surface temperature reached 50° to 54°C. Activity ceased for the night at a soil surface temperature of 20° to 22°C.

King (1962) reported that wind velocities had an important effect on harvester ants in the Big Horn Basin of Wyoming. Most foraging activity ceased when the wind velocity exceeded 25 to 30 mph.

Foraging. The seed harvesting activities of *P. occidentalis* were first reported by McCook in 1882. Western harvester ants feed primarily on seeds, but other food materials are acceptable as well (Wheeler and Wheeler, 1963).

The harvesting habits of the western harvester ants have been studied extensively, but little is known concerning the amount of material actually foraged. Lavigne and Fisser (1966) reported that a density of 10 colonies per acre in southeastern Wyoming could remove 5 lb. of grass seed and more than 10 lb. of forb seed, each year. Willard and Crowell (1965) experimented with the foraging habits of *P. owyheei* and found that workers of a single colony were capable of foraging 1/5 quart of cracked grain from around the mound in a 24-hr period.

Seed dispersal. Cole (1932*c*) mentioned that ants returning to the colony often temporarily lost their loads of seed. Such a loss could serve as a method of seed distribution if the ants occasionally fail to relocate the lost seeds. Wheeler (1910) points out that seed distribution can also occur as a result of seeds sprouting in the mound and being discarded by the harvester ants. He goes on to say that "one can imagine cases in which the ants during the lapse of long periods of time might pass the seeds of plants from colony to colony, until after a journey of many stages, the descendants of the antborne seedlings might find themselves transported to places far removed from the original home of their immediate ancestors."

Many of the earlier workers recognized that harvester ants were able to prevent seed germination in the mound and thought the ants bit off the radicle (Wheeler, 1910). West German scientists have recently shed new light on the mechanism harvester ants use to prevent seed germination. They isolated and identified a "herbicide" secreted by the harvester ants that serves to prevent seed germination (Anonymous, 1971). The observed germination of seeds in the nest probably occurs as a result of inattention by the ants or due to excessive soil water conditions.

Soil Relationships

Ant distribution, in general, does not show a close correlation with the nature of substratum. Climate and vegetation seems to be far more important in limiting the distribution of ant species (Gregg, 1963).

There is some evidence, however, that soil conditions may affect harvester ant colony density. Soil texture was the most important factor influencing the abundance of *P. owyheei* in Wyoming where the ants were more abundant in sandy areas than on heavier textured soils (Kirkham and Fisser, 1972). King (1962) studied what he thought to be western harvester ants in the Big Horn Basin of Wyoming and found the greatest ant concentrations occurring in the gray desert soil regions. The ants apparently preferred soils that provided desert pavement conditions and scattered gravels thoughout the profile. These ants were undoubtedly *P. owyheei* rather than the western harvester ant, *P. occidentalis*.

Melendez (1963) found that *P. occidentalis* colony density was twice as great in a pinyon-juniper area of New Mexico having gravelly soils than in grassland soils having a sandy-clay mixture.

Many soil animals play an important role in soil formation. The activity of these animals results in the pulverization, granulation, and transfer of large amounts of soil (Buckman and Brady, 1969). Jacot (1936) reported that ants and earthworms are the most important groups of invertebrate animals that move soil vertically. Earthworms, however, are not generally numerous in arid grasslands due to the dry conditions (Kendeigh, 1961).

Ants aid in soil formation by moving mineral particles from one horizon to another. They also provide channels for water penetration after the nests are abandoned and they transfer organic matter (food) into the nest where some of it is incorporated into the soil (Thorp, 1949).

The large mounds characteristic of western harvester ants are partially formed from soil excavated during nest construction. Thorp (1949) estimated that "a large red ant" in the west may pile up about 3400 lb. of earth per acre. He thought that most of this material was brought up from below ground. The clearings made by the ants expose the soil to wind and water erosion, and this may aid in the truncation and rejuvenation of the soils (Thorp, 1949).

Lyford (1963) studied the importance of ants in soil genesis in New England and estimated that 50 g/yd^2 was brought to the surface each year.

Lasius niger neoniger Emery brought 85.5 g/m^2 of soil to the surface in an oil field in Michigan (Talbot, 1953).

Bioenergetics

Lindeman (1942) first formulated the concept of trophic dynamics and generated a great deal of interest in the study of energy transfer through ecosystems. Energy flow studies may be conducted with reference to individuals, populations, or other components of interest. The measurement of energy flow provides a better method of determining the role of a population within its community than the measure of either biomass or numbers (Odum, 1959).

Energy flow measurements are based on a precise physical definition of the calorie and provide a particularly powerful tool in the analysis of ecosystem functioning in that they provide a comparison of the energy requirements of populations, permitting the assessment of relative importance of competing species (Macfadyen, 1967). Social insects are only beginning to be studied as components of the ecosystem. Ants may prove most useful in these studies as they form vast and continuous populations in favorable areas (Brian, 1967).

Wiegert and Evans (1967) defined energy flow as the caloric equivalent of the retained food materials. Energy flow includes the amount of energy required for respiration plus the energy required for tissue production. This may be shown as

$$A = R + P_s$$

where A equals the assimilated energy, R equals the amount of respiratory energy loss (heat loss) per unit of time, and P_s equals the caloric equivalent of new tissue produced per unit of time.

That insects may be important components in the transfer of energy through the ecosystem was shown by Odum et al. (1962) who measured the energy flow of three primary consumers in an old field ecosystem at the AEC Savannah River Plant in South Carolina. They found average energy flow figures of 3.6 kcal/m^2/year for sparrows, 6.7 kcal/m^2/year for mice, and 25.6 kcal/m^2/year for Orthoptera. They also reported that measurement of assimilation as intake minus excretion provided a better basis for estimating energy requirements for respiration than the measurement of oxygen consumption.

The community with the highest primary productivity is the community with the capability for the greatest secondary productivity. Each succeeding trophic level is dependent on the preceding level for its source of energy (Lindeman, 1942; Wiegert and Evans, 1967). It should not be surprising, therefore, to find that energy flow values vary considerably for insect populations in different communities.

Wiegert (1964) compared the population energetics of meadow spittlebugs in two different habitats in southeastern Michigan. The energy requirements of the spittlebug populations were 38.6 kcal/m^2/year on the alfalfa field, .6 kcal/m^2/year on an old field the first year, and 1.2 kcal/m^2/year on the same old field the following year.

Wiegert (1965) reported energy flow values for grasshoppers in Michigan. Grasshoppers in an alfalfa field assimilated 13.25 kcal/m^2/year and grasshoppers in an old field assimilated an average 1.36 kcal/m^2/year over a 2-year period.

Although there have not been any comparative energetic studies of ants occupying different habitats, it would appear reasonable to expect the energy flow values to vary in proportion to the available energy supply.

Golley and Gentry (1964) conducted a study into the bioenergetics of the southern harvester ant, *Pogonomyrmex badius* (Latreille). They determined the energy flow of the ant population by estimating the energy expended in heat and the energy stored in tissue production.

The heat energy requirement was determined by measuring oxygen consumption at different temperatures and converting the liters of oxygen consumed to kilocalories, using the appropriate caloric equivalent for a liter of oxygen. Maximum and minimum levels of heat production were calculated for environmental temperatures corresponding to the different seasons of the year and were related to periods of ant activity.

Ant tissue production was determined from adult ant density per colony, larval density per colony, and from changes in hill density. The energy required for secondary production equaled the number of ants produced per year times the average ant biomass times the caloric equivalent of a gram of ant tissue (2.5 kcal/g live wt). The energy stored as tissue production amounted to about .09 kcal/m^2/year.

The total energy flow for the population of southern harvester ants ranged from 14 to 48 kcal/m^2/year. This is equal to a range of 3.6 to 12% of the net primary production which Golley and Gentry (1964) estimated for the study area.

The above energy flow values indicate that *P. badius* has a high respiration/production ratio which may prove to be characteristic of social insects in general.

Study Area Description

Location. This study was conducted on the IBP Grassland Biome Intensive Site, the Pawnee Site, located on the Central Plains Experimental Range and operated by the U.S. Department of Agriculture.

The Central Plains Experimental Range is located on the western portion of the Pawnee National Grasslands and is approximately 12 miles northeast of Nunn, Colorado, and 25 miles southeast of Cheyenne, Wyoming (Klipple and Costello, 1960).

All of the 15,000-acre Central Plains Experimental Range is available for IBP investigations, but some of the area is primarily reserved for studies conducted by the Agricultural Research Service. The 105,000-acre Pawnee National Grasslands is available for studies requiring larger land areas (Jameson, 1969).

Sampling for this study was conducted on typical upland light, medium, and heavily grazed pastures in sections 15, 22, and 23 of Township 10N, Range 66W. Colony excavations were made in sections 22 and 26.

History. The following discussion concerning the history of the study area was drawn from Costello (1944) and Klipple and Costello (1960).

Most of the Central Great Plains was first used for livestock grazing, following the extirpation of the American bison. More than 90% of the land was eventually brought under management as a result of homesteading and the purchase or lease of land grant railroad sections and state school lands.

The eastern farming methods of the early settlers resulted in the plowing and subsequent erosion of millions of rangeland acres. Much of this early farmland was abandoned and now forms the Pawnee National Grasslands under management of the U.S. Forest Service.

Management. There are 12 half-section pastures of the Central Plains Experiment Range reserved for long-term experimentation which have been exposed to certain grazing treatments since 1939. The grazing treatments associated with this study are defined as (i) heavy use, where the aboveground biomass is not reduced below 341 kg/ha (300 lb./acre) by the end of a 6-month grazing season, (ii) moderate use, where approximately 455 kg/ha (400 lb./acre) is left, and (iii) light use where approximately 568 kg/ha (500 lb./acre) remains at the end of the season (Dr. Donald A. Jameson, personal communication). Livestock exclosures (1 or 2 acres) were established in each of the 12 pastures in 1939 and have remained ungrazed ever since (Klipple and Costello, 1960).

Abiotic factors. Precipitation is one of the most important factors affecting the area (Costello, 1944). The average annual precipitation ranges from 10 to 15 inches. About 72% of the annual precipitation occurred during the growing season from 1939 to 1953 (Klipple and Costello, 1960). Precipitation at the Central Plains Experiment Range headquarters during 1970 measured 9.54 inches, which was 2.76 inches below the average for the last 32 years (Bement, Houston, and Hyder, 1970).

Wind velocity may exceed 35 mph during the summer season and is an important factor in soil drying, seed distribution, soil erosion, and snow accumulation (Costello, 1944).

Daily temperatures averaged 26.7°C, with a high of 40.0°C and a low of -23.3°C during the growing season, from 1939 to 1958. Temperature extremes varied from 36.1°C in August to -24.4°C in January during 1970 with a frost-free period from June 6 to September 9 (Bement et al., 1970).

The soils of the area are representative of the dark brown and brown soils of the semiarid grasslands, where about 85% are loams ranging from clay to sandy loams (Klipple and Costello, 1960). Klipple and Retzer (1959) described soils occurring in one pasture as belonging to the Ascalon series, although they were not typical of that series. The soils on the intensive study portion of the Pawnee Site have been described as belonging to the Ascalon, Vona, Renohill, and Shingle series (Jameson, 1969).

Biotic factors. The climax community is composed of a buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.) and blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) association. Midgrasses such as western wheatgrass (*Agropyron smithii* Rydb.) and needle and thread (*Stipa comata* Trin. and Rupr.) may be locally abundant (Klipple and Costello, 1960).

Perennial forbs such as scarlet globe mallow (*Sphaeralcea coccinea* (Pursh) Rydb.), slimflower scurf pea (*Psoralea tenuiflora* Pursh), slenderbush eriogonum (*Eriogonum microthecum* Nutt.), scarlet gaura (*Gaura coccinea* Pursh), and prickle poppy (*Argemone intermedia* Sweet) are also found in the study area. Locally abundant annual forbs include Russian thistle (*Salsola kali tenuifolia* Tausch), *Crypthantha* sp. Lehm., stickseed (*Lappula* sp. Moench.), pale evening primrose (*Oenothera albicaulis* Pursh), lamb's-quarter (*Chenopodium* sp.), and prairie pepperweed (*Lepidium densiflorum* Schrader). Four-wing saltbush (*Atriplex canescens* (Pursh) Nutt.), winter fat (*Eurotia lanata* (Pursh) Moq.), rubber rabbit brush (*Chrysothamnus nauseosus* (Pall.) Britt.), broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt. & Rusby), and fringed sagewort (*Artemisia frigida* Willd.) are fairly common shrubs. Plains prickly pear (*Opuntia polyacantha* Haw.) is widely distributed, but supplies little forage (Klipple and Costello, 1960).

Costello (1944) found that several animal species were important in influencing secondary succession. Jackrabbits (*Lepus* sp.) clipped the stems of many grasses before the seeds had a chance to mature which resulted in retarding succession. Kangaroo rats (*Dipodomys ordii luteolus* (Goldman)) and white-footed mice (*Peromyscus* sp.) effectively eliminated *Agropyron smithii* from abandoned fields. Other native influents that he considered to be important were harvester ants (*P. occidentalis*), pronghorn antelope (*Antilocarpa americana* Ord), badgers, (*Taxidea taxus* (Schreber)), cottontails (*Sylvilagus* sp.), ground squirrels (*Spermophilus tridecemlineatus arenicola* (Howell)), and pocket mice (*Perognathus* sp.). Golden Eagles (*Aquila chrysaetos* (L.)) and coyotes (*Canis latrans* Say) also forage over the prairies and prey primarily on cottontails and jackrabbits (Engel and Vaughan, 1966).

METHODS

General

Data processing. Every effort was made to collect data in such a manner that it could be processed and stored in punch card form. Field data sheets were developed as an aid in data collection concerning the ants' forage selection, forage rate, foraging distance, and activity in response to environmental factors. These field data sheets were periodically forwarded to the biometrical service section of the Natural Resource Ecology Laboratory located at Colorado State University, Fort Collins, Colorado, for data summarization.

Colony characteristics. Nearly everyone who has worked or traveled in an area inhabited by harvester ants has been impressed with the ants' habits of building conical-shaped pebble mounds and clearing the vegetation from around the mounds. These are the most apparent effects that the western harvester ants have on their environment. Disc diameters, mound diameters, and mound heights were measured in each of the four study pastures to see if these characteristics varied as a result of differential grazing pressure. Disc diameter values were used to calculate the area cleared by the ants. Values pertaining to mound diameters and mound heights are included for future comparison with IBP studies in other areas.

General Ecological Effects

Soil water. Does the elimination of plants from the disc significantly alter the soil water relationships in the surrounding area? Soil samples were taken from beneath the disc and beneath an area of normal vegetation during ant colony excavations. Preliminary analysis indicated a higher percentage of soil water under the colony disc. An experiment was then designed to determine the level of significance of these moisture differences.

Six colonies of the approximate same size were selected from the population in the winter use pasture. All were located in the same vicinity, on the same soil type, and on approximately the same slope. Three of the colonies were in an area of typical vegetation and three of the colonies were located in a herbicide plot where all of the vegetation had been killed. Four 80-cm deep soil cores were taken from each colony. The first core was located 60 cm outside the disc area, the second 15 cm outside, the third 15 cm inside the disc edge, and the last soil core was taken 60 cm inside (approximately in the center) of the disc. The cores were immediately cut into 10-cm sections and placed in plastic bags. They were then taken to the laboratory, weighed, dried, and reweighed to determine percent soil water.

Vegetation relationships. Does the presence of western harvester ant colonies significantly affect standing crop values of vegetation in the area immediately surrounding the colony?

The presence of western harvester ants may affect vegetation standing crop values through the removal of vegetation from the area surrounding their mounds. The presence of the cleared discs may also affect soil water relationships, causing an increase in production of plants around the disc perimeter as reported by Wight and Nichols (1966) for colonies located in the Big Horn Basin of Wyoming.

An experiment was designed to determine if an increase in standing crop values occurs around harvester ant colonies at the IBP site. An initial inspection showed the ring of increased plant growth surrounding the colony to be no more than 15 cm wide. Some 50 colonies were then selected within the winter use pasture for more intensive study. Vegetation samples were oven-dried (65°C for 24 hr), and comparisons were made of the aboveground standing crop biomass at different distances from the colony.

The effect of vegetation clearing may be readily calculated by determining the average area cleared per colony and the number of colonies per hectare. This method was used to estimate the area cleared in the intensive study pastures.

Soil movement. How much soil do western harvester ants move to the surface per hectare? An estimate of the amount moved can be made from a summation of the volume of soil excavated during tunnel and chamber construction. Data for this summation were gathered during colony excavations. Measurements were made of the number of tunnels and chambers per colony, the diameter and depth of the tunnels, and diameter and height of the chambers. A summation of volume calculations from these data provides an estimate of the volume of soil removed to the surface. Soil samples were taken from the vicinity of the excavated colonies to determine average soil densities. Mass of soil excavated was then estimated by multiplying the volume of soil moved times average soil density.

Soil modification. Does the presence of western harvester ant colonies result in modification of soil properties?

The experimental design to answer this question consisted of selecting six colonies and taking three soil samples from each. One sample was taken directly beneath the mound, one from the disc, and the other from a vegetated area 3 m away from the colony. All samples were taken from 10 to 15 cm beneath the soil surface using a hand coring tool.

The soil samples were then analyzed for texture, bulk density, percent sand, percent silt, percent clay, and organic matter, and a routine analysis was made for phosphorous, potassium, nitrogen, iron, and zinc content.

Foraging Activities

Forage selection. What types of forage materials are selected by western harvester ants?

The type of forage selected by the ants was determined by collecting returning foragers for 5-min periods every hour during the day. The forage was grouped as plant vegetative parts (PLV), plant reproductive parts (PLR), seeds (PLS), animal prey (ANP), animal dead material (AND), animal feces (ANF), unknown animal substance (ANU), mineral (MIN), and unknown material (UNK). In addition, each of the types were classed as being part or whole pieces. Mineral particles (MIN) consist of small rocks and pebbles brought in by the foraging ants and placed on the mound. These materials are included in the sampling scheme even though they are not used for food.

A test was made using a sampling device that would automatically collect foraging ants returning over 5-min periods of each hour. The sampler consisted of a barricade with separate exit and entrance tubes, a 12-v releasing solenoid, and sliding tray containing collection vials. The barricade was erected on the edge of the disc so that the ants were forced to enter and leave the disc by way of the tubes (Fig. 1). The exit tube terminated with a short drop to the outside of the barricade, preventing reentry by this pathway. The entrance tube terminated with a short drop to a board that allowed the ants to continue on to the nest. The timer (Fig. 2) emitted an impulse at hourly intervals that engaged a solenoid, moving the sliding tray forward so that a vial came to rest under the entrance tube. The returning ants then came down the tube and dropped into the vial. Then 5 min later, the sliding tray would again move forward so that the ants once again dropped on the board and returned to the nest.

The device was installed and operated on a colony in the heavy use pasture. The ants learned to enter and leave the barricade in about 2 days. The device did not appear to be impeding their foraging activities after that time, but before data could be gathered to test this hypotesis the ants abandoned the colony and started a new one about 4 m away.

Foragers were subsequently collected by placing a small vial over each worker ant that returned to the disc with forage. The ant generally responded by attempting to climb up the side of the glass vial. The vial was then quickly inverted, entrapping the ant in the vial with the forage it had collected. All of the forage for the 5-min period was combined in one vial and labeled

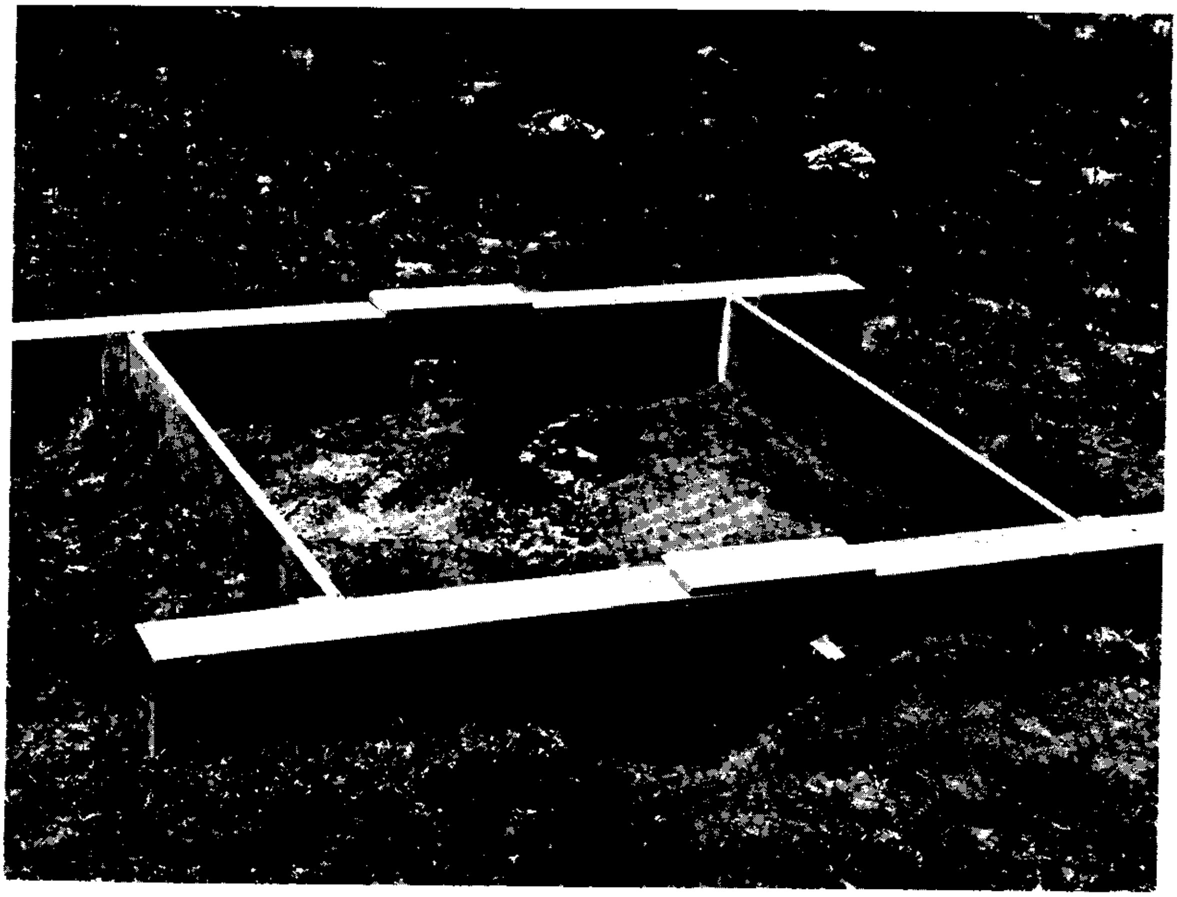

Fig. 1. Automatic ant sampler.

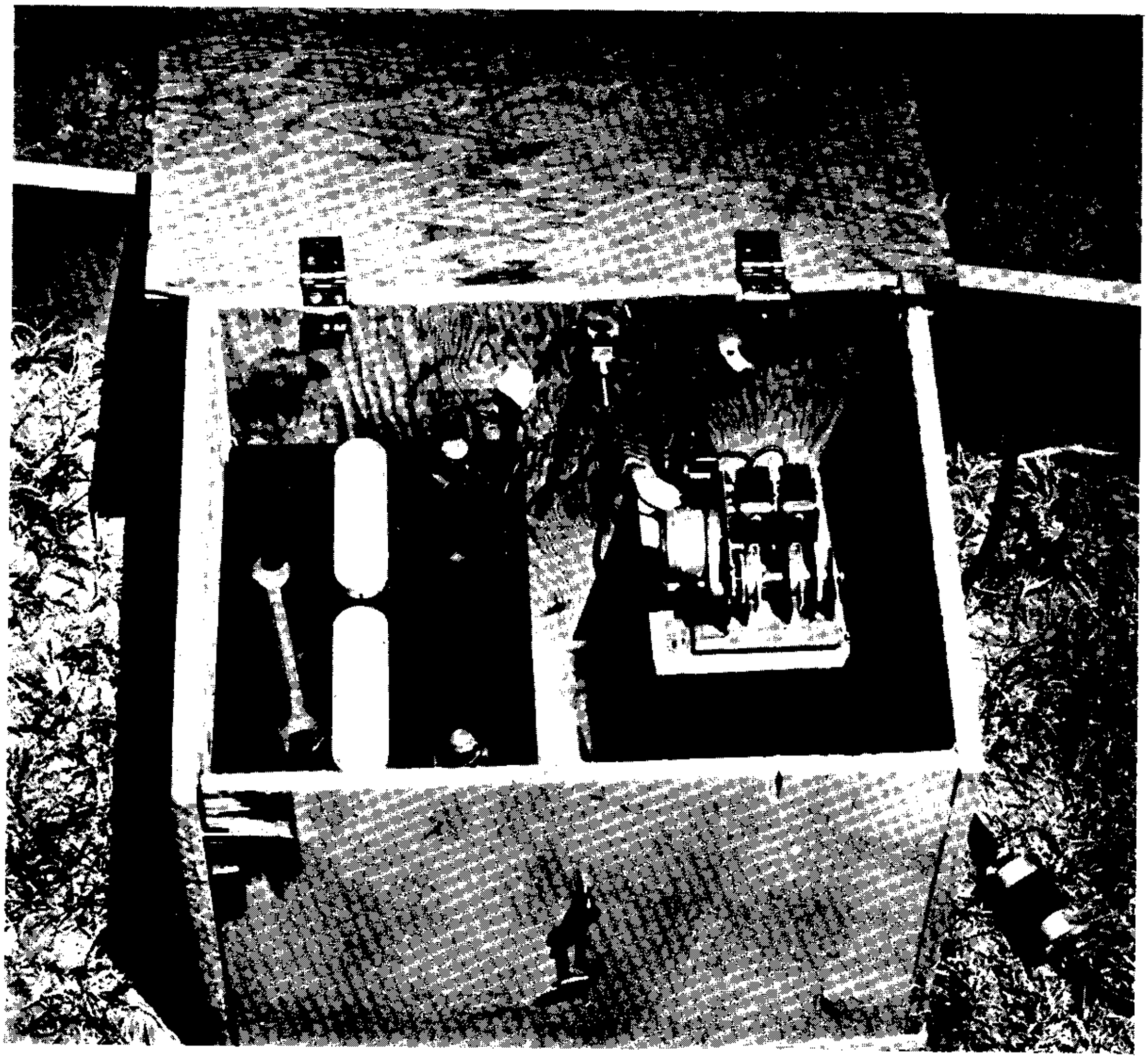

Fig. 2. Timer mechanism of automatic ant sampler.

with the collection date, time, pasture, and the number of foragers that had returned during that period. The forage material was then identified, oven-dried (65°C for 24 hr), weighed, and posted to the field data sheet (Fig. 3). Computer processing provided monthly summaries, grazing treatment summaries, and a total season summary, showing the number and weights of each forage type utilized.

The insects serving as prey (ANP) and scavenger material (AND) were usually rather severely damaged by the ants. For this reason, most identifications are limited to the order or family level. Seed identifications (PLS) were made by the State Seed Laboratory at the University of Wyoming, Laramie, Wyoming. A few seeds were also identified by the State Seed Laboratory at Colorado State University, Fort Collins, Colorado.

Influence of environmental factors. What are the effects of environmental factors on activities of the western harvester ants?

Specific types of activity under investigation were time of mound opening, initiation of foraging, cessation of foraging at night, initiation of mound closure, mound closure, and rate of departure of foragers throughout the day. Data for these activities were gathered by arriving at randomly selected colonies prior to the time of mound opening and making periodic observations concerning the behavior of the ants throughout the day. These observations were made weekly from mid-June through mid-September of 1970 on a total of 25 colonies. The time, activity code, surface temperature, and the number of foragers leaving per minute were recorded on the field data sheet shown in Fig. 4. Surface temperatures were taken by placing a 6-inch mercury thermometer on the surface of the soil. The bulb was covered with a thin layer of soil so that it was not exposed to the direct rays of the sun.

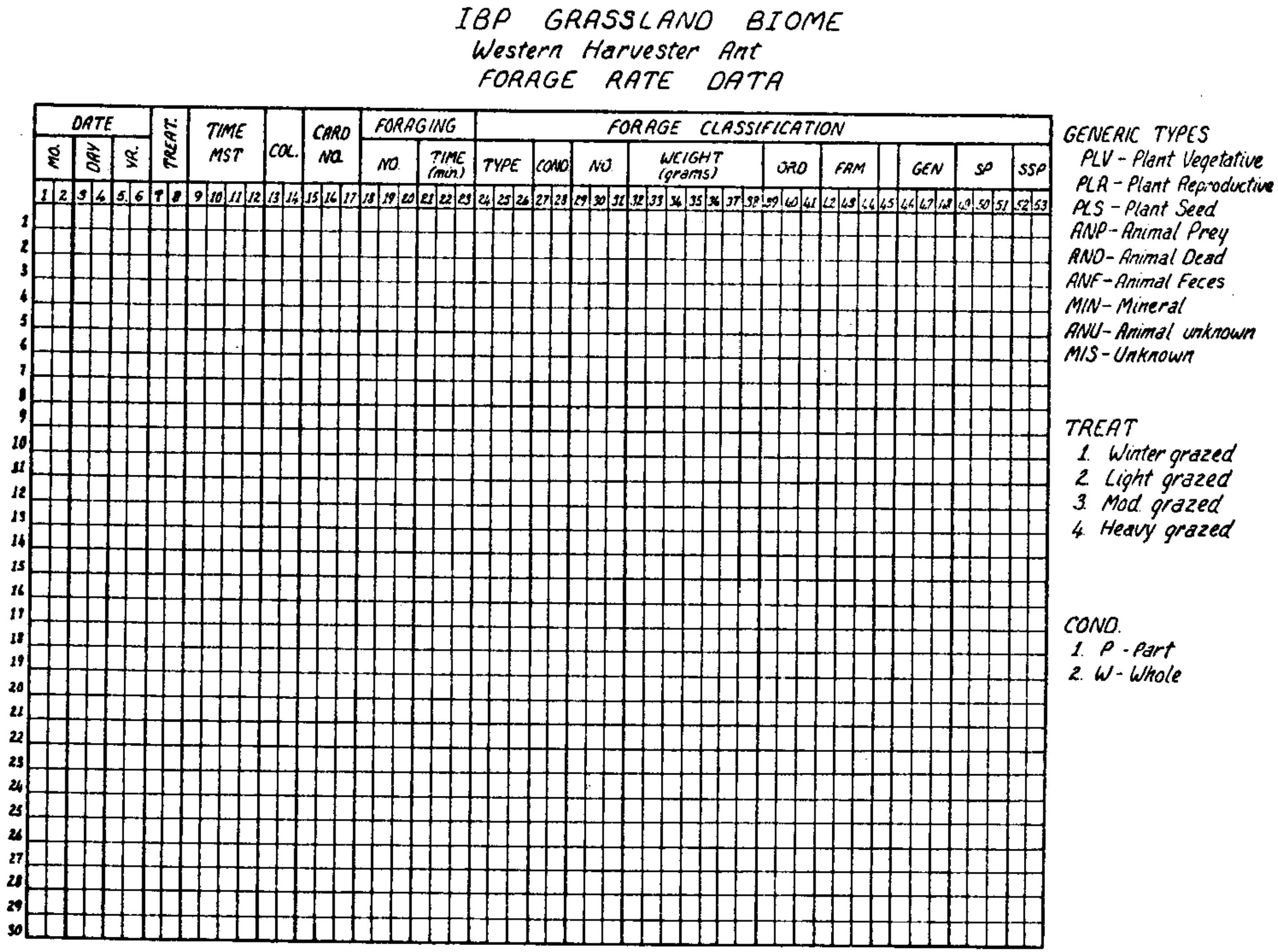

Fig. 3. Western harvester ant forage rate field data sheet.

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Western Harvester Ant Activity

Data Type	Site	Initials	Date			Treatment	Time	Colony Number	Activity Code	Surface Temperature (°F)	Number of foragers Leaving/minute	Notes
			DAY	MO	YR							
1-2	3-4	5-7	8-9	10-11	12-13	14	20-23	24-26	27-28	29-31	32-34	

DATA TYPE
11-Invertebrate

SITE
11 Pawnee

TREATMENT
1 Ungrazed
2 Lightly grazed
3 Moderately grazed
4 Heavily grazed

ACTIVITY CODES
0 Not foraging - morning
1 Mound opened
2 Foraging
3 Not foraging - midday
4 Not foraging - evening
5 Start of mound closure
6 Mound closed

Fig. 4. Western harvester ant activity field data sheet.

Correlations were made between activities of the western harvester ants and soil surface temperatures but not to other meteorological factors due to malfunctioning of the meteorological data acquisition system and resultant lack of meteorological data for the summer of 1970. In July of 1971 a colony was selected near the meteorological data acquisition system sensors for intensive study. This colony was observed continuously for 3 days from prior to the time of mound opening in the morning until time of mound closure at night. The purpose of these continuous observations were to obtain data relating foraging to various meteorological factors.

Forage rate. Is the rate of forage extraction per colony affected by cattle grazing intensities?

Data pertaining to the rate of forage extraction in light and heavily grazed pastures were gathered simultaneously with forage selection data. The number of ants returning with forage per unit of time were recorded on the field data sheet shown in Fig. 3. A computer program was designed to provide average weights and numbers per minute for each of the eight forage types utilized by the ants. This information was summarized by grazing treatment, month, and total for the season with overall means and standard deviations calculated for biomass and number data.

Foraging distance and time. Do the western harvester ants in the light and heavy use pastures travel the same distance and spend the same amount of time per forage trip?

The distance that a foraging ant traveled from the colony was determined by following individual ants from randomly selected colonies and marking their path with numbered markers. These data were recorded on the data sheet shown in Fig. 5. This method of study permitted the measurement of the total distance traveled by the ants as well as timing the foraging excursion.

Seed availability. How much seed is available to western harvester ant populations in the light and heavy use pastures?

The forage rate data provide information concerning the rate of forage extraction from the environment, but did not provide data concerning the availability of forage. Since seeds are a major part of the western harvester ants' diet, it was thought essential to obtain some measurement of the availability of seeds.

An estimate of seed availability based on direct counts of numbers per unit area would be a laborious and possibly inaccurate method. An estimate of plant density and associated seed production per plant would be more manageable, but seed production and seed availability to the ants are probably not the same thing. Lacking any information concerning seed production on the Pawnee Site, an estimate of the seeds available to the ants could be made by marking a known number of seeds and then sampling the ratio of marked to total seeds in the sample population. This is generally known as the Lincoln index method of estimating population size (Cox, 1968).

A known number of bluegrass seeds (*Poa pratensis* L.) were spread evenly around three colonies in both the light and heavily grazed pastures at approximately 10-day intervals. The even spreading of seeds was aided by the use of a Whirly-bird® seed spreader. Seeds were generally spread in the early morning when wind velocities were at a minimum. Pit traps (2 × 3 inch glass jars) were than placed at the edge of the disc to trap seed carrying ants as they returned from foraging. The collected sample provided an estimate of the

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Field Data Sheet

Western Harvester Ant Range Determination

Date	TRTM	Col. No.	Dist. from west boundary	Dist. from south boundary	Temp.	Time	Marker	Dist. from colony	Activity

Fig. 5. Western harvester ant foraging distance and time field data sheet.

ratio of marked to unmarked seeds serving as forage and permitted calculation of the number of seeds available to the ant population.

Density and Biomass

Density and biomass per colony. What is the ant density and biomass per western harvester ant colony?

Population densities and biomass per colony data were obtained by excavating colonies. Colony excavations were limited to the eastern edge of section 26 due to the destructive nature of the sampling technique.

A backhoe was used to dig down next to the edge of the disc area (Fig. 6). The entire mound of the colony was then removed and placed in a container. This usually removed most of the ants that were near the entrance of the mound. Ants that came to the surface in response to this disturbance were picked up with an aspirator and placed in a container. The remaining ants in the colony were uncovered by digging into the colony from the side as described by Lavigne (1969). As the ants were uncovered, they were placed in a container and marked according to their depth in the colony. As a routine practice, the colony was dug a foot deeper than the location of the last ant found in the colony. After excavating, the ants were taken to the laboratory, counted, and dried at 65°C for 24 hr. They were then weighed and their dry weights recorded.

Colony density. What is the density of western harvester ant colonies in the intensive study pastures?

The method used to determine colony density during the summers of 1969 and 1970 consisted of counting all colonies in a 36-ha area. Colonies were counted by walking back and forth across the sample areas in the light, heavy,

Fig. 6. Backhoe excavating alongside a western harvester ant colony.

moderate, and winter grazed pastures. Each colony counted was marked by spraying a spot of paint near the mound. This method permitted verification that all colonies had been counted.

Unfortunately, this method does not permit a measure of variation occurring within any one sample area. This reason plus the possibility that the sample plot in the heavy use pasture might be located in an area of unusually high colony density led to the adoption of a different sampling method the following year.

The sampling scheme for 1971 consisted of randomly selecting ten 2-acre plots in each of the study pastures. The winter use pasture was dropped from the sampling scheme and replaced with 10 replicates from the 2-acre livestock exclosures. The exclosures had been ungrazed since 1939 and are probably more representative of the ungrazed condition than the winter use pasture.

Bioenergetics

General. One of the primary aims of a model of the grassland ecosystem is to predict the flow of energy through the system. Since the western harvester ants were particularly abundant, it was considered essential to ascertain energy values for this species as part of the overall model.

Energy flow is here defined as the caloric equivalent of the retained food materials as previously discussed in the literature review section. The requisite information needed to calculate the energy required for respiration and secondary production of the western harvester ant population are (i) colony density per unit area, (ii) ant density per colony, (iii) average biomass per ant, (iv) number of ants produced per colony each year, (v) caloric equivalent per gram of ant tissue, (vi) caloric equivalent per liter of CO_2, and (vii) carbon dioxide production over the range of temperatures occurring in the western harvester ants' environment. The amount of respiratory energy loss may be calculated with indirect calorimetry methods using either O_2 consumption or CO_2 production, since both are closely correlated with heat production (Brody, 1945).

Caloric equivalents. What is the caloric value of western harvester ant tissue?

Ant tissue samples were dried at 65°C for 24 hr and burned in a Model 1241 adiabatic calorimeter manufactured by Parr Instrument Company. The ants were obtained from colony excavations at various times of the year. The caloric equivalent for a liter of CO_2 was taken from a table of thermal equivalents (Brody, 1945) at a respiratory quotient (RQ) of .81 (approximately 5.94 kcal/liter).

Measurements of secondary production. How much energy is required for tissue production?

Production of new ant tissue was estimated from counts of immature workers and adult winged reproductives found in the excavated colonies.

Cole (1934*c*) reported that western harvester ants require 30 days for worker brood development. An estimate of total number of individuals produced can then be made by multiplying the average number of worker larvae per colony times the number of 30-day developmental periods during the year (Golley and Gentry, 1964). The number of ants produced per colony can then be multiplied times the average biomass per ant. This value times the caloric value per gram of ant tissue provides an estimate of the energy required for secondary production. This method does not account for immature mortality or the energy of the cast skins, and for this reason must be considered as a minimal value.

Measurements of respiration. How much energy is required for respiratory heat loss?

Ascertainment of energy required for respiration consisted of identifying the daily activity periods and related temperatures of the ants in the field and determining the rate of carbon dioxide production (CO_2/ant/hr) over the range of field temperatures.

Field data were gathered by arriving at randomly selected colonies prior to the time of mound opening and making periodic observations concerning the foraging behavior of the ants in relation to temperature, throughout the day. These observations were made once each week from mid-June through mid-September of 1970. Temperature data pertaining to ants located in underground chambers were taken during colony excavations and from the meteorological data acquisition system located on the Intensive Site.

The relationship between temperature and carbon dioxide production per ant was measured in the laboratory. Two colonies were excavated and transferred, complete with queen, to gallon jars three-fourths full of sterilized sand. The colonies were stored at 15.6°C for 2 months while they established hills simulating natural conditions (Fig. 7). The ants were fed Friskies dried cat food and sterilized bluegrass seed during this time. The colonies were kept in Percival Pt-80 controlled environmental chambers under a 24-hr dark regime and maintained at ±.5°C of the desired temperature and between 40 to 60% relative humidity.

Carbon dioxide production was continuously monitored with a Beckman 315A infrared gas analyzer (Fig. 8) adapted to measure 0 to 600 ppm. Flow rates

(1.25 liters/min) were monitored with a Brooks Model 1357 flow meter and total gas volume was measured with a dry test meter (American Instrument Co.).

The number of ants per colony were counted when the colonies were established and at the end of the experiment. Dead ants were removed and counted before and after each experimental test period. There were 11 runs made on one colony and 9 on the other at temperatures ranging from 6.7° to 40°C. The test periods were scheduled for 24 hr each, but averaged closer to 17 hr. There were no apparent differences in CO_2 production per ant as a result of variations in run time. Each colony was allowed to equilibrate at a given temperature for a minimum of 24 hr before CO_2 production was measured.

RESULTS AND DISCUSSION

General

Colony characteristics. Disc diameter, mound diameter, and mound height measurements of colonies located in the differentially grazed pastures are shown in Tables 1 through 3, respectively. Disc diameter was greatest in the ungrazed treatment and least for colonies located in the moderately grazed pasture.

Average disc diameter measurements will be used in a later section to calculate the amount of area cleared in the intensive study pastures. Data pertaining to mound heights and diameters in the differentially grazed pastures will not be interpreted at this time, but are provided for later comparison with data taken from other IBP study sites.

Fig. 7. Laboratory colony of western harvester ants.

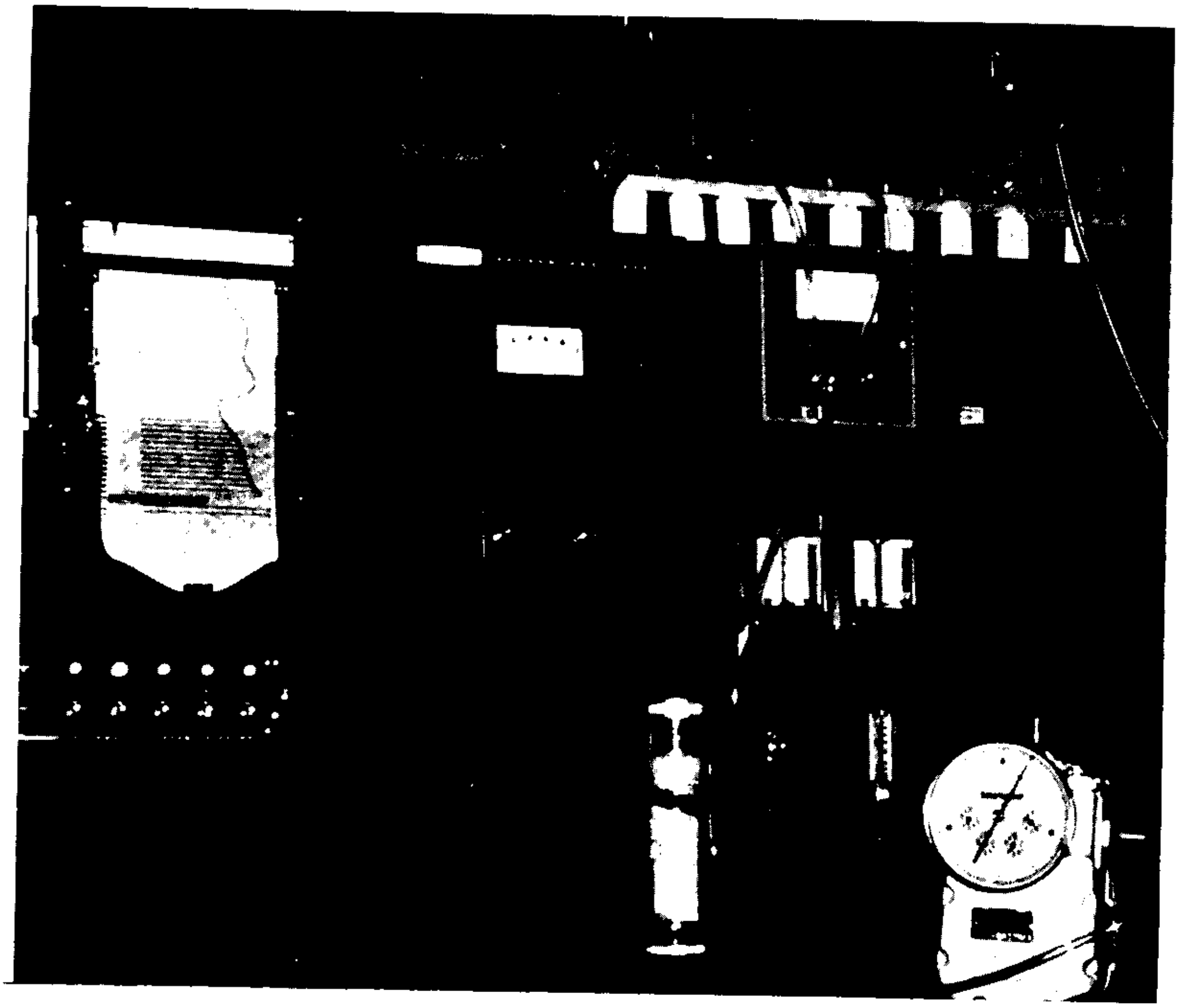

Fig. 8. Beckman infrared gas analyzer.

Table 1. Average disc diameters of western harvester ant colonies located on the IBP Intensive Site.

Grazing Treatment	Average	Range	Standard Deviation
	--------------------meters--------------------		
Ungrazed	1.23	.2 to 1.9	.99
Light	.92	.3 to 1.7	.31
Heavy	.90	.4 to 1.7	.29
Moderate	.71	.3 to 1.9	.24

Table 2. Average mound diameters of western harvester ant colonies located on the IBP Intensive Site.

Grazing Treatment	Average	Range	Standard Deviation
	------------------	centimeters	------------------
Heavy	31.6	0 to 73.7	9.6
Ungrazed	29.4	0 to 63.5	9.4
Light	25.4	10.2 to 53.3	8.3
Moderate	23.6	0 to 55.9	7.2

Table 3. Average mound heights of western harvester ant colonies located on the IBP Intensive Site.

Grazing Treatment	Average	Range	Standard Deviation
	centimeters		
Heavy	7.2	0 to 15.2	3.1
Ungrazed	6.0	0 to 17.8	2.8
Light	5.4	.6 to 15.2	2.7
Moderate	4.8	0 to 14.0	2.3

General Ecological Effects

Soil water. The hypothesis tested of no significant differences in the average percent water content of soil cores taken across the colony is described in the methods section. Soil water percentages were calculated on the basis of water content of dry soil, which is the usual method of expressing the amount of water present in the soil (Buckman and Brady, 1969).

Soil samples were taken from six colonies located in the winter use pasture. Three of the colonies were located in an area of live vegetation and three in an area where all the vegetation had been killed.

Results of the soil water determinations from colonies located in an area of live vegetation are shown in Table 4. The data show the average percent soil water to be greatest near the disc center (i.e., 60 cm inside the disc), slightly lower in the area just inside the disc edge (15 cm inside), lowest just outside the disc (15 cm outside), and slightly increased in percent soil water in the vegetated area (60 cm beyond the disc edge). An analysis of variance test shows these values to be significantly different at the .05 level (Table 5). Analysis of differences in means using Duncan's new multiple range test (Steel and Torrie, 1960) shows the average soil water content for the sample points located inside the disc to be significantly different from each other as well as from the sample points located beyond the disc (Table 6). No significant differences were detected between the two sample points located beyond the disc.

If the increased soil water content under the disc is due to the elimination of the transpiring plants, we should expect to find the same level of soil water in an area where the plants have been artificially killed. Results of soil water determinations from soil cores taken across colonies located in

Table 4. Average soil water content from western harvester ant colonies located in an area of live vegetation.[a/]

Depth	Outside Disc		Inside Disc	
	60 cm	15 cm	15 cm	60cm
10 cm	1.5	1.8	1.6	1.6
20 cm	2.2	1.9	2.4	3.6
30 cm	3.0	2.8	3.9	4.9
40 cm	4.0	3.6	4.3	5.0
50 cm	4.0	3.9	4.3	4.8
60 cm	3.8	3.5	4.6	4.8
70 cm	3.5	3.5	4.1	4.4
80 cm	3.5	3.0	3.3	4.5
AVERAGE	3.2	3.0	3.6	4.2

[a/] Each value is the average soil water percentage based on dry soil from three samples.

Table 5. Analysis of variance test of the soil water content of western harvester ant colonies located in an area of live vegetation.

Source	SS	df	MS	F
Block effect	24.7	7	3.53	32.1*
Treatment effect	6.7	3	2.24	22.4*
Error	2.3	21	.11	
TOTAL	33.7	31		

* Significant at the .05 level.

Table 6. Analysis of differences in soil water means from western harvester ant colonies located in an area of live vegetation. Data with the same letter are not significantly different at the .05 level.

Location of Sample	Average Soil Water (%)
60 cm outside disc	3.2a
15 cm outside disc	3.0a
15 cm inside disc	3.6b
60 cm inside disc	4.2c

an herbicide plot are shown in Table 7. An analysis of variance test showed that the water content of these soil core samples were not significantly different from each other (Table 8). This suggests that when the plants surrounding a colony are killed, the soil water of the vegetated area increases to the same level as that found on the bare disc.

The conclusions are that the presence of the cleared disc is associated with an increase in soil water around the mound. The elimination of transpiring plants is probably the mechanism creating the increase in soil water, as originally suggested by Wight and Nichols (1966).

Vegetation relationships. Western harvester ants are noted for their habit of clearing vegetation from around the colonies. These cleared areas represent a potential loss of grazing capacity to the herbivores present in the area.

Calculations of the area cleared were made using the disc diameters shown in Table 1 and colony densities per hectare data shown in Table 33. These estimates, of area cleared per hectare, are presented in Table 9. The values range from a high of 28.3 m^2/ha in the ungrazed area to 2.7 m^2/ha with heavy grazing pressure. This represents a range of .28% to .03% of the respective areas and suggests that the western harvester ants do not clear a substantial amount of vegetation at the Pawnee Site. Additionally there may be a compensating increase in plant production around harvester ant colonies (Wight and Nichols, 1966) which would further reduce the significance of the cleared areas.

Plant clippings were taken from the area surrounding the colony as described in the methods section. Statistical analysis tests the hypothesis

Table 7. Average soil water content from western harvester ant colonies located in an area of dead vegetation.[a/]

Depth	Outside Disc		Inside Disc	
	60 cm	15 cm	15 cm	60 cm
10 cm	1.9	1.7	2.5	3.2
20 cm	5.8	4.4	5.6	6.8
30 cm	8.5	7.1	6.3	7.1
40 cm	8.3	6.9	5.7	6.1
50 cm	7.5	6.1	5.6	5.2
60 cm	7.1	6.4	5.1	5.6
70 cm	6.1	6.5	5.1	5.4
80 cm	6.2	6.0	7.4	6.4
AVERAGE	6.4	5.6	5.4	5.7

[a/] Each value is the average percent soil water of three samples.

Table 8. Analysis of variance test of the soil water content of a western harvester ant colony located in an area of dead vegetation.

Source	SS	df	MS	F
Block effect	63.0	7	9.00	13.6*
Treatment effect	4.6	3	1.53	2.3
Error	13.8	21	.66	
TOTAL	81.4	31		

* Significant at the .05 level.

Table 9. Estimates of area cleared by western harvester ants at the IBP Intensive Site.

Grazing Treatment	Area Cleared (m^2/ha)	Percent Cleared
Ungrazed	28.3	.28
Light	25.8	.26
Moderate	22.0	.22
Heavy	2.7	.03

of no significant differences in standing crop values at the disc edge and 50 and 100 cm away from the disc edge (Table 10). Conclusions resulting from this test are that the standing crop values of the sample points are significantly different. Analysis of average standing crop values using Duncan's new multiple range test shows the standing crop at the disc edge to be significantly higher than for the other two sample points and that there are no significant differences between values at the 50-and 100-cm points (Table 11).

This increase in standing crop around the colony means that there is at least a partial compensation for the loss of plants on the disc. Calculations were made to determine the magnitude of this compensation. Table 12 shows a comparison of standing crop values in the area of colony influence with a typical vegetated area of equivalent size. The total standing crop in the area of colony influence was calculated to be 80 g compared to 127 g of dry plant material in the typical vegetated area. This means that instead of a 100% loss of plant vegetation on the colony disc, there is only an effective 37% net decrease in standing crop values associated with the presence of a western harvester ant colony.

Soil movement. Data from colony excavations were used to estimate the total volume of soil that western harvester ants move to the surface. The colony excavations showed that there were an average of five tunnels per colony .6-cm diameter each, with an average tunnel depth of 142 cm. There were also an average of 141 seed and brood chambers per colony, each with an average volume of 12.3 cm^3. Summation of the volume calculations provides an estimate of the total volume of soil excavated. Multiplication of the total volume excavated by the average density of soil from around the colony (1.4 g/cm^3)

Table 10. Analysis of variance test of standing crop values surrounding western harvester ant colonies.

Source	SS	df	MS	F
Amoung groups	75.1	2	37.6	19.8*
Within groups	284.1	147	1.9	
TOTAL	359.2	149		

* Significant at the .05 level.

Table 11. Analysis of differences in mean vegetation standing crop values (g dry wt) surrounding western harvester ant colonies at the IBP Intensive Site. Data with the same letter are not significantly different at the .05 level.

Location of Sample	Average Values	
	Per Grid	Per m^2
Disc edge	3.6a	160.2
50 cm from disc edge	2.2b	97.9
100 cm from disc edge	2.1b	93.5

Table 12. Comparison of standing crop values in the area of colony influence with a typical vegetated area of equivalent size.

Area Sampled	Zone	Area (m^2)	Standing Crop (g/m^2)	Total Standing Crop in Area of Colony Influence (g)
Ant colony	Disc	.76	0.0	0.0
	Border	.54	160.2	80.0
	Total	1.30	--	80.0
Typical vegetated area of equivalent size		1.30	97.9	127.0

results in a value of 2.8 kg of soil excavated per colony. This value was then extrapolated to the study pastures to show the amount of soil brought to the surface per hectare (Table 13). These values range from 87 kg/ha in the moderate use pasture down to 8 kg/ha in the heavy use pasture. It should be noted that these values were calculated from data gathered from average size colonies and represent the average amount of soil excavated over the life of the sampled colonies and are not annual values.

Soil modification. Soil samples were extracted from beneath the mound, disc, and beyond the colony in an attempt to determine what influence the western harvester ants might have on soil characteristics.

Results of sample analysis are shown in Table 14. Percent sand, nitrate content, phosphorous content, and bulk density all show significant variation between the mound, disc, and vegetated areas. Further analysis of bulk density (Table 15) shows that the soil samples taken from underneath the mound have a significantly lower density than those taken from either the disc or vegetated areas. This is probably due to the tunneling and excavating habits of ants which would tend to loosen and aerate the soil.

Analysis of phosphorous content (Table 16) shows significantly higher concentration in the mound areas but no significant differences in disc and vegetated area concentrations. This may be associated with the ants' habits of storing some organic waste materials (i.e., seed coats, litter, insect parts, etc.) in underground storage chambers.

Nitrate content was significantly higher in the area beneath the mound, with no significant differences in concentrations between the disc and vegetated areas (Table 17). This higher nitrate concentration may be due to

Table 13. Amount of soil moved to the surface per hectare by western harvester ants on various grazing treatments.

Grazing Treatment	Amount[1/] (kg/ha)
Moderate	87
Light	78
Ungrazed	64
Heavy	8

[1/] Amount expressed over the life of the sampled colonies.

Table 14. Analysis of soil samples associated with western harvester ant colonies.

Soil Characteristics	Mound Area	Disc Area	Vegetated Area	Result
Sand (%)	72.5	73.5	76.6	*
Silt (%)	16.0	14.9	12.7	
Clay (%)	11.5	11.6	10.7	
Zinc (ppm)	.2	.2	.2	
Iron (ppm)	18.5	16.2	14.7	
Nitrate (ppm)	4.0	1.3	.7	*
Potassium (ppm)	180.4	182.8	208.8	
Phosphorous (ppm)	21.3	11.2	8.7	*
Bulk density (g/cm^3)	1.47	1.54	1.54	*
Organic matter (%)	.8	.8	.8	
Texture	Sandy loam	Sandy loam	Sandy loam	

* Significant at the .05 level.

Table 15. Analysis of bulk density associated with western harvester ant colonies. Data with the same letter are not significantly different at the .05 level.

Sample Location	Average Values (g/cm^3)
Mound area	1.47*a*
Disc area	1.54*b*
Vegetated area	1.54*b*

Table 16. Analysis of phosphorous content associated with western harvester ant colonies. Data with the same letter are not significantly different at the .05 level.

Sample Location	Average Values (ppm)
Mound area	21.3*a*
Disc area	11.2*b*
Vegetated area	8.7*b*

Table 17. Analysis of nitrate content associated with western harvester ant colonies. Data with the same letter are not significantly different at the .05 level.

Sample Location	Average Values (ppm)
Mound area	4.0*a*
Disc area	1.3*b*
Vegetated area	.7*b*

excreta deposited by the ants within the nest. Percent sand was higher in the vegetated area with no appreciable difference between the mound and disc areas (Table 18), indicating that the ants may select areas of lower sand content or, more likely, that their tunneling activities combined with resulting wind erosion decrease sand content in the nest area.

Foraging Activities

Forage selection. Forage material selected by the western harvester ants was determined by sampling 23 colonies as described in the methods section. It was not surprising to see that the most frequently selected type of forage (Table 19) was seeds (39%), since these ants are reported to be granivores. It was surprising, however, to note that litter comprised 24% of the forage particles, since they are not known to utilize this type of forage as food. Insect prey, dead insect material, and plant reproductive parts (other than seeds) each comprised about 10% of the total number of forage particles. Much lower percentages of fecal matter and mineral substances were foraged.

There were 39 species of seeds, representing 32 genera, foraged by western harvester ants as shown in Table 20. *Eriogonum effusum* Nutt. is primarily foraged in early September and represented 27% of the total number of seeds foraged. *Lepidium densiflorum* Schrader accounted for 12% of total seeds foraged and was primarily selected during July. *Bahia oppositifolia* (Nutt.) DC. represented 11% of the total and served as principal forage during August. These three species of plant seeds comprised 50% of the total number of seeds foraged.

A total of 22 plant species served as litter forage for the western harvester ants (Table 21). Two grasses, *Sporobolus cryptandrus* (Torr.)

Table 18. Analysis of percent sand associated with western harvester ant colonies. Data with the same letter are not significantly different at the .05 level.

Sample Location	Average Values (%)
Mound area	72.5*a*
Disc area	73.5*a*
Vegetated area	76.6*b*

Table 19. Types of forage material selected by western harvester ants at the IBP Intensive Site.

Data Code	Material	Total Number (%)
PLS	Seeds	39
PLV	Litter	24
PLR	Plant reproductive	10
ANP	Prey (insects)	10
AND	Dead animal matter	10
ANF	Feces	3
MIN	Rocks	3
MIS	Unknown material	1
ANU	Unknown animal substance	0

Table 20. Seeds foraged by western harvester ants at the IBP Intensive Site.

No.	Scientific Name	Common Name
1.	*Allium* sp.	Onion
2.	*Amaranthus retroflexus*	Red-root amaranth
3.	*Aristida longiseta*	Red three-awn
4.	*Aristida oligantha*	Prairie three-awn
5.	*Aster tanacetifolius*	Tansy-leaf aster
6.	*Astragalus* sp.	Milk vetch
7.	*Bahia oppositifolia*	Plains bahia
8.	*Bouteloua gracilis*	Blue grama
9.	*Buchloe dactyloides*	Buffalo grass
10.	*Carex* sp.	Sedge
11.	*Chenopodium* sp.	Goosefoot
12.	*Chenopodium leptophyllum*	Slimleaf goosefoot
13.	*Corispermum* sp.	Tickseed
14.	*Cryptantha minima*	Cryptantha
15.	*Cymopterus acauli*	Stemless cymopterus
16.	*Dactylis glomerata*	Orchard grass
17.	*Elymus canadensis*	Canada wild rye
18.	*Elymus glaucus*	Blue wild rye
19.	*Elymus junceus*	Russian wild rye
20.	*Eriogonum effusum*	Spreading wild buckwheat
21.	*Festuca octoflora*	Six-weeks fescue
22.	*Gaura coccinea*	Scarlet gaura
23.	*Hackelia* sp.	Tickweed
24.	*Heterotheca villosa*	Hairy golden star
25.	*Lappula* sp.	Stickseed
26.	*Lappula occidentalis*	Stickseed
27.	*Lepidium densiflorum*	Prairie pepperweed
28.	*Mirabilis linearis*	Four o'clock
29.	*Mirabilis nyctagenea*	Heartleaf four o'clock
30.	*Musineon divaricatum*	Leafy musineon
31.	*Oenothera albicaulis*	Pale evening primrose
32.	*Opuntia polyacantha*	Prickly pear
33.	*Oxytropis sericea*	Silky crazyweed
34.	*Polygonum aviculare*	Prostrate knotweed
35.	*Schedonnardus paniculatus*	Tumblegrass
36.	*Stipa comata*	Needle and thread
37.	*Stipa viridula*	Green needlegrass
38.	*Thelesperma* sp.	Greenthread
39.	*Tragopogon pratensis*	Meadow salsify

Table 21. Litter foraged by western harvester ants at the IBP Intensive Site.

No.	Scientific Name	Common Name
1.	*Agropyron smithii*	Western wheatgrass
2.	*Aristida longiseta*	Red three-awn
3.	*Artemisia frigida*	Fringed sagewort
4.	*Atriplex canescens*	Four-wing saltbush
5.	*Bahia oppositifolia*	Plains bahia
6.	*Bouteloua gracilis*	Blue grama
7.	*Carex heliophila*	Sun sedge
8.	*Cirsium undulatum*	Wavy-leaf thistle
9.	*Eriogonum effusum*	Spreading wild buckwheat
10.	*Gaura coccinea*	Scarlet gaura
11.	*Gutierrezia sarothrae*	Broom snakeweed
12.	*Lepidium densiflorum*	Prairie pepperweed
13.	*Lithospermum incisum*	Gromwell
14.	*Mirabilis linearis*	Four o'clock
15.	*Oenothera coronopifolia*	Crown evening primrose
16.	*Opuntia polyacantha*	Plains prickly pear
17.	*Parmelia chlorochroa*	Lichen
18.	*Psoralea tenuiflora*	Slimflower scurf pea
19.	*Sphaeralcea coccinea*	Scarlet globe mallow
20.	*Sporobolus cryptandrus*	Sand dropseed
21.	*Thelesperma trifidum*	Three-cleft greenthread
22.	*Verbena bracteata*	Big bract verbena

A. Gray and *Bouteloua gracilis*, each account for 24% and a lichen, *Parmelia chlorochroa* Tuck, accounts for 11% of the total number of pieces of litter foraged.

Insects serving as forage material are presented in Table 22. Some Lepidoptera (Pyralidae), Coleoptera (Scarabaeidae), and Isoptera were taken into the colony alive, indicating that these ants do prey on other insects. Other insects serving as forage were assumed to be scavenger material, although in some instances the prey may have been killed and partially dismembered by the ants prior to being transported to the colony.

Influence of environmental factors. Daily activity patterns of the western harvester ants varied through the season as shown in Table 23. The colony remains open for the longest period during the month of July, and as the season progresses, the mound is opened later and closes earlier. The monthly average of numbers of foragers leaving per minute at hourly intervals are shown in Fig. 9.

Activities of the western harvester ants are probably associated more closely with temperature than with time of day. Table 24 shows the relationship between activity and average surface temperatures. The ants open the mounds when the soil surface reaches 24°C, but little activity takes place until the temperature reaches approximately 27°C when the ants start foraging. Foraging activities continue at a brisk pace until the surface temperature reaches about 47°C, which precipitates a drastic reduction in the number of foragers leaving the colony. After the sun has passed its zenith and the soil temperatures have cooled, foraging will resume and continue until evening. The ants generally stop foraging when the surface temperature falls to 32°C.

Table 22. Insects serving as forage for western harvester ants at the IBP Intensive Site.

Order	Family	Common Name
Acarina		Mite
Coleoptera	Carabidae	Ground beetle
	Curculionidae	Weevil
	Histeridae	Hister beetle
	Scarabaeidae[a/]	June beetle
	Tenebrionidae	Darkling beetle
Diptera	Asilidae	Robber fly
	Chloropidae	Frit fly
Hemiptera	Lygaeidae	Chinch bug
	Nabidae	Damsel bug
	Scutelleridae	Shield-backed bug
Homoptera	Aphididae	Aphid
	Cicadellidae	Leafhopper
Hymenoptera	Chalcididae	Chalcid wasp
	Formicidae	Ants
Isoptera[a/]		Termite
Orthoptera	Acrididae	Grasshopper
Lepidoptera	Pyralidae[a/]	Pyralid moth

[a/] Some of these insects were taken into the colony alive.

Table 23. Activity times (MST) of the western harvester ant.

Activity	June	July	August	September
Mound opening	0712	0648	0723	0742
Start foraging	0824	0712	0748	0818
Stop foraging at night	1730	1830	1736	1648
Start of mound closure	1716	1748	1724	1654
Mound closed	1821	1842	1824	1742

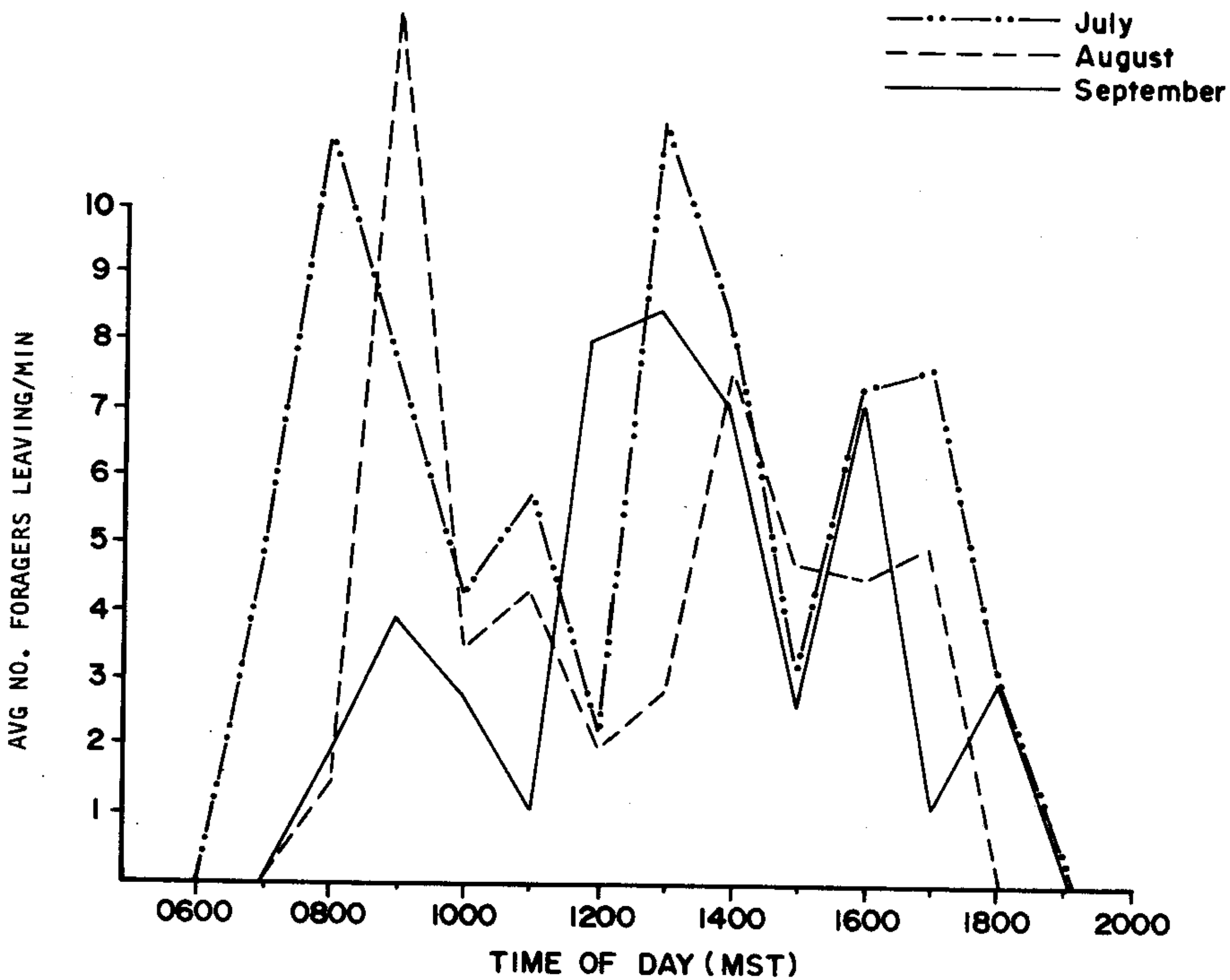

Fig. 9. Changes in daily activity patterns of western harvester ants through the summer of 1970.

Table 24. Temperatures associated with activities of the western harvester ant at the IBP Intensive Site.

Activity	Surface Temperature Average (°C)	Surface Temperature Range (°C)	SD
Mound opening	23.8	18.3 to 30.0	3.9
Start foraging	27.5	19.4 to 35.6	4.4
Stop foraging (midday)	47.0	37.2 to 54.5	4.9
Stop foraging (night)	32.1	25.6 to 43.4	5.3
Start of mound closure	29.1	18.9 to 43.4	6.8
Mound closed	25.2	17.8 to 30.6	4.6

They start to close the mound when it reaches 29°C, and the last ant will have retreated inside the colony for the night by the time the soil surface temperature has fallen to 25°C. These data correspond closely with previous findings as reported for *P. occidentalis* and *P. owyheei* (Cole, 1934*c*; Stevens, 1965; Willard and Crowell, 1965).

During the summer of 1971 a colony was selected near the meteorological data acquisition system sensors, during a period when the equipment was known to be functioning properly. Data were gathered pertaining to the number of ants leaving the colony per 5-min intervals in an attempt to find a more precise relation between their foraging activity and the meteorological data. The meteorological factors of interest were soil temperatures at 3 cm, surface temperatures, air temperatures at 50 cm, net incoming radiation, and total incoming radiation.

The best correlation was found between the number of ants leaving in 5-min increments and surface temperatures. It appears, therefore, that the temperature at the air-soil interface exerts the greatest influence on the foraging ants.

The relationship between foragers leaving and surface temperatures is shown in Fig. 10. Once the surface temperatures rise above about 27°C, the ants start foraging at a rapid rate. Foraging continues until the surface temperatures reach approximately 47°C at which time there is a rapid decline in the rate of departure from the colony. Foraging ceases altogether when surface temperatures reach about 50°C, and shortly thereafter all ants retreat into the colony. Later in the day the ants will emerge and commence foraging once again. This relationship is described by the formula

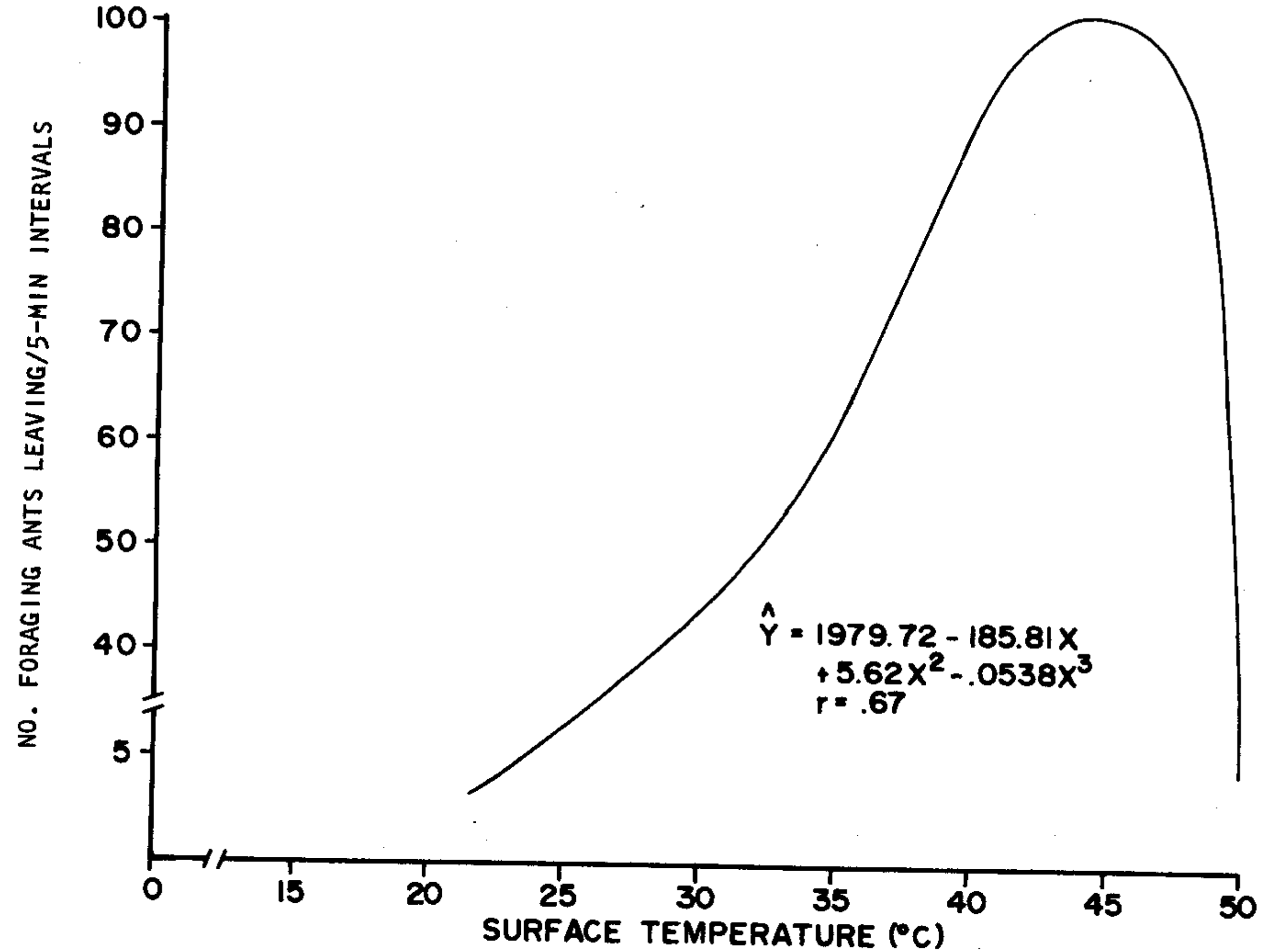

Fig. 10. Third degree polynomial showing the relationship between the number of foraging ants leaving the colony and surface temperatures.

$$\hat{Y} = 1979.72 - 185.81X + 5.62X^2 + .0538X^3$$

where Y equals the number of foragers leaving per 5-min intervals and X equals surface temperatures.

Forage rate. Analysis of the forage rate data tests the hypothesis that there are no significant differences in the rate of forage extraction in the light and heavy use pastures. The test of this hypothesis uses the weight of transported forage particles as the variable measured and the time interval of the observation as a covariate. The model is assumed to be partially crossed and partially nested with month, treatment, and type the crossed factors, and days within months the nested factor. The model for the test was

$$Y_{ijkl} = \mu + m_i + d(m)_{j(i)} + t_k + s_l + mt_{ik} +$$

$$ms_{il} + ts_{kl} + bX_{ijkl} + e_{ijkl}$$

where

Y_{ijkl} = the weight of the food particle foraged

m_i = month $i = 1,\ldots,4$ 1 = June

2 = July

3 = August

4 = September

$d(m)_{j(i)}$ = day(month) $j = 1,\ldots,23$

t_k = treatment $k = 1, 2$ 1 = light grazing
2 = heavy grazing

s_l = food type $l = 1,\ldots,5$ 1 = animal dead (AND)
2 = plant vegetative (PLV)
3 = animal feces (ANF)
4 = plant seed (PLS)
5 = mineral (MIN)

X_{ijkl} = time interval of collection

Only five forage types are included in the analysis due to the limited amount of plant reproductive, animal prey, and unknown material utilized as forage.

Analysis of these data (Table 25) show that the rate of forage extraction is not significantly different in the light and heavy use pastures as indicated by the F value (.24) associated with the treatment effects. The significant type effects are due to the weight of foraged mineral particles. Exclusion of these mineral particles from analysis resulted in insignificant type effects and in detection of significant month-treatment interactions. The significant interaction effects are probably due to differences in forage availability, over time, between the two pastures.

Since there were no significant differences in the rate of forage extraction between the light and heavy use pastures, the data were combined and are shown in Table 26 as the rate of forage extraction for these two pastures.

Foraging distance and time. Distances foraged by western harvester ants in the light and heavy use pastures are shown in Table 27. The maximum distance foraged was 14.3 m in the light use pasture and 11.0 m in the heavy use

Table 25. Analysis of the rate of forage extraction from the light and heavy use pastures.

Source	df	SS	MS	F
Month	3	.00160	.00053	2.52
Treatment	1	.00002	.00002	.24
Type	4	.00516	.00129	15.79*
Month × treatment	3	.00040	.00013	1.62
Days (month × treatment)	15	.00308	.00021	2.57*
Month × type	12	.00425	.00035	4.27*
Treatment × type	4	.00028	.00007	.82
Covariate = time	1	.00002	.00002	.23
Error	534	.04368	.00008	
Pooled error	538	.04396	.00008	
TOTAL	577	.05849		

* Significant at the .05 level.

Table 26. Estimates of the rate (mg/min/colony) of forage extraction from the light and heavy use pastures.

Type	June	July	August	September
Seeds (PLS)	.4	1.0	.4	1.1
Litter (PLV)	.9	.6	.9	.2
Plant reproductive (PLR)	.0	.1	.0	.1
Prey (insects) (ANP)	.0	.1	.1	.0
Dead animal matter (AND)	.2	.1	.5	.1
Feces (ANF)	.2	.6	.6	.1
Rocks (MIN)	1.5	2.0	.2	1.6
Unknown material (MIS)	.0	.0	.1	.0
Unknown animal substance (ANU)	.0	.0	.0	.0
TOTAL	3.2	4.5	2.8	3.2
Mean ± SD	.4 ± .5	.6 ± .7	.4 ± .3	.4 ± .6

Table 27. A comparison of the maximum distances (m) foraged by western harvester ants in the light and heavy use pastures.

Observation No.	Foraging Distances	
	Light Use	Heavy Use
1	4.0	9.5
2	9.4	4.6
3	6.7	3.1
4	1.2	1.2
5	14.3	8.5
6	2.7	5.5
7	6.7	1.2
8	4.9	.9
9	11.9	6.7
10	3.7	3.7
11	7.3	1.8
12	5.2	2.4
13	4.0	11.0
14	1.5	1.5
15	1.2	9.4
16	9.4	1.8
17	7.9	2.4
18	7.6	1.2
19	3.1	1.8
20	5.8	1.8
21	10.1	2.4
22	2.4	4.6
23	.7	4.6
TOTAL	131.7	91.6
Mean ± SD	5.7 ± 3.7	4.0 ± 3.1

pasture. The average distances foraged were 5.7 ± 3.7 m and 4.0 ± 3.1 m in the respective pastures.

The time per foraging trip, in minutes, is shown in Table 28. The average foraging time per trip in the light use area was 22.7 ± 16.3 min, and the average for the heavy use area was 22.5 ± 18.3 min. It is interesting to note that while the ants ranged further in the light use pasture, the average time per forage trip was very nearly identical in the two areas. A t-test was used to test the hypothesis that there were no significant differences in the foraging distance or time per forage trip in the light and heavy use pastures. These tests found no differences at the .05 level of significance.

Seed availability. The size of the seed population (N) available to the western harvester ants was estimated using a Lincoln index method. Calculations were based on the number of seeds spread (S), the total seeds in the pit trap sample (T), and the number of marked seeds recovered in the pit trap sample (R), according to the formula

$$N = \frac{ST}{R}$$

The available natural seed population (A) may be calculated

$$A = N - S$$

Applying an average weight per seed permits expression of the seed population in terms of biomass rather than numbers per unit area.

Table 28. A comparison of time (min) per foraging trip by western harvester ants in the light and heavy use pastures.

Observation No.	Time	
	Light Use	Heavy Use
1	28	67
2	34	37
3	57	44
4	12	4
5	65	47
6	5	59
7	26	8
8	19	22
9	14	15
10	25	20
11	24	18
12	34	25
13	19	33
14	40	15
15	4	50
16	36	11
17	12	4
18	6	5
19	20	15
20	23	9
21	9	12
22	6	35
23	3	3
TOTAL	521	518
Mean ± SD	22.7 ± 16.3	22.5 ± 18.3

Estimates of the available seed biomass are shown in Table 29. An analysis of variance test of these estimates revealed no significant differences between them at the .05 level. The high estimate for July 3 in the light use area was primarily due to the large amount of prairie pepperweed *Lepidium densiflorum* Schrader) being foraged which apparently was not available to the ants in the heavy use pasture. On August 23, the ants in the heavy use pasture were bringing in mostly six-weeks fescue (*Festuca octoflora* Walt.) and some *Eriogonum effusum* Nutt. seed. Very little six-weeks fescue, and no *Eriogonum effusum* seed were picked up by the ants in the light use pasture at this time. The high available seed estimates made for September1 were due to harvesting of *Eriogonum effusum* seed in both pastures.

These data seem to support the forage rate data presented earlier. There were no significant differences in the rate of forage extracted in the light and heavy use pastures, and now we see that there are no significant differences in the amount of seed available to the ant populations in these two areas.

Seed utilization. The measurement of seed availability around the ant colonies and estimation of the rate of forage extraction from the area around the colony permit an evaluation of the utilization of the available seed supply. This can only be an approximation of true seed utilization since the measurement of seed availability is not a measure of seed production and the amount of seed foraged does not represent the actual amount of seed consumed. The apparent utilization of available seeds is still of interest as a measurement of the impact of the harvester ant population on the seed population.

Table 29. Amount of seed available (g/m^2) to western harvester ants in the light and heavy use pastures.

Date	Amount of Seed	
	Light Use	Heavy Use
June 19	3.1	3.2
July 3	6.4	.6
July 13	1.7	.2
July 23	1.0	.3
August 2	.8	1.3
August 12	.6	.2
August 23	.8	2.7
September 1	3.2	4.0
September 11	1.3	.6

An estimate of the utilization of seeds by the western harvester ant population is presented in Table 30. Data were combined for the light and heavy use pastures since no significant differences were found in the rate of forage extraction, seed availability, foraging distance, or time per foraging trip. The utilization values range from 1 to 5% with the low occurring in June and the highest rate of utilization occurring during the month of July.

Density and Biomass

Density and biomass per colony. A total of 11 colonies were excavated at different times of the year. The number of worker ants in the 11 excavated colonies varied from 1548 to 4443 with an average of 2676 worker ants per colony (Table 31), which is probably representative of colonies in this area. This compares with an average of 1759 overwintering worker ants per colony from 20 excavated colonies, in a similar habitat, near Casper, Wyoming (Lavigne, 1969). There were an average of 91 alate female reproductives and 224 alate male reproductives per colony. Larvae and pupae were present from June through September with an average of 547 larvae and 585 pupae per colony during the season.

The average dry weight biomass of adult worker ants was determined to be 8.06 g per colony (Table 31). The dry weight per ant was 3.0 mg for workers, 11.6 mg for female reproductives, and 5.4 mg for male reproductives.

Colony excavations were not permitted within the differentially grazed pasture boundaries which forced a supposition that all colonies contained the same number of ants irrespective of grazing treatment. This presumption is not entirely without support as an analysis of the rate of forage extraction showed no significant differences between colonies in the light and heavily

Table 30. Apparent seed utilization by western harvester ants at the IBP Intensive Site.

Seed	June	July	August	September
Seed availability (g/m^2)	3.2	1.7	1.1	2.3
Amount foraged (g/m^2)	.03	.08	.03	.08
Apparent utilization (%)	1	5	3	4

Table 31. Number and dry weight (g) of western harvester ants per colony.

Colony	Month	Adult Workers		Alate Reproductives				Larvae[a/]		Pupae	
		No.	Weight	No.	Weight	No.	Weight	No.	Weight	No.	Weight
				Male		Female					
1.	April	4,443	14.04	0	0.00	0	0.00	0	0.00	0	0.00
2.	April	3,382	10.11	0	0.00	0	0.00	0	0.00	0	0.00
3.	June	1,577	6.90	0	0.00	0	0.00	295	0.66	0	0.00
4.	July	1,548	4.44	114	0.60	23	0.26	246	0.54	202	0.23
5.	July	3,309	9.20	229	1.54	165	1.93	761	1.67	599	0.65
6.	July	4,406	11.59	329	1.48	86	0.99	1,372	3.00	1,371	2.96
7.	August	1,626	3.57	0	0.00	0	0.00	349	0.74	298	0.75
8.	August	1,810	5.42	0	0.00	0	0.00	438	1.41	883	1.89
9.	August	1,650	4.62	0	0.00	0	0.00	418	1.26	362	0.91
10.	September	2,182	5.67	0	0.00	0	0.00	499	0.54	383	0.85
11.	October	3,506	13.12	0	0.00	0	0.00	0	0.00	0	0.00
TOTAL		29,439	88.68	672	3.62	274	3.18	4,378	9.82	4,098	8.24
Mean		2,676	8.06	224	1.21	91	1.06	547	1.23	585	1.18
± SD		±1,155	±3.72	±108	±0.52	±71	±0.84	±369	±0.83	±413	±0.93

[a/] Includes both reproductive and worker larvae.

grazed areas. This could be interpreted as meaning the colonies contain approximately the same number of foraging ants.

Another method was also employed to evaluate ant density per colony in the study pastures. This method was developed by Race (1964) for selecting colonies of western harvester ants having a similar population size and being in a similar stage of development. His method consisted of grinding ants in a blender and placing a drop of the liquid near the colony entrance and observing the immediate and frenzied response of the ants to the "ant juice."

A slight variation was introduced in this study. The "ant juice" was applied near the mound entrance (Fig. 11) and then a 35-mm color slide was taken of the disc area 1 min later. The camera was always held the same distance above the disc so that the resultant picture would always cover the same surface area. A count of ants responding to the "ant juice" was then taken from the slide. This method was used to compare the ant response in the intensive study pastures with the colonies in section 26 where colony excavations occurred. An analysis of variance test found no significant difference in the number of ants responding to the "ant juice" in the various study areas. This is taken as additional evidence that the western harvester ant colonies in the study areas all have approximately the same number of ants per colony.

Colony density. Colony density data were necessary to determine if grazing intensity affects the colony density of western harvester ants, to determine if there is a fluctuation of colony density in succeeding years, and to permit the calculation of energy requirements for the western harvester ant populations in the study pastures.

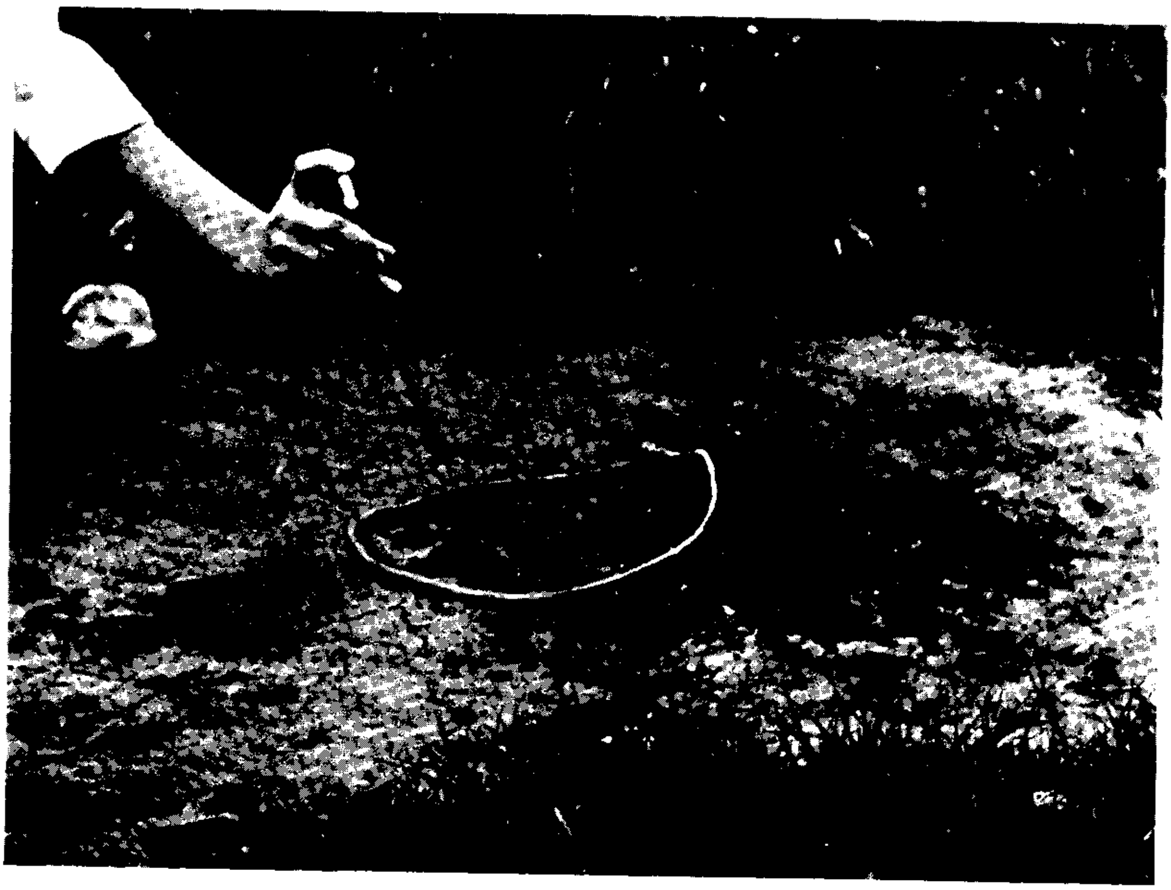

Fig. 11. Application of "ant juice" near entrance of western harvester ant mound.

Colony density was measured during the summer of 1969 by counting all colonies in a 36-ha area. Highest density occurred in the winter use pasture with 798 colonies located in the sample area, as compared to 597 in the light use pasture, 600 in the moderate use area, and only 245 colonies in the heavily grazed pasture sample area. A comparison of colony density in the light and heavily grazed pastures in the summers of 1969 and 1970 showed no significant changes in hill densities between these years (Table 32).

In the summer of 1971, colony densities were estimated using a random sample technique. The highest colony density occurred in the moderately grazed study area with 31 colonies/ha; this compares with 28 colonies/ha under light grazing, 23 colonies/ha with ungrazed conditions, and 3 colonies/ha in the heavily grazed treatment (Table 33).

Bioenergetics

Caloric equivalents. The caloric value of ant tissue was determined to be 6.5 kcal/g for alate female reproductives, 4.8 kcal/g for alate male reproductives, and an average of 5.6 ± .5 kcal/g for worker ant adults (Table 34).

Energy for secondary production. Production of new ant tissue was estimated separately for workers and winged reproductive ants. An estimate of the total number of worker ants produced was made by multiplying the average number of worker larvae per colony (508) times the number of 30-day developmental periods during the year (4), for an estimate of 2032 worker ants produced per year.

Table 32. A comparison of western harvester ant colony density in two different years on light and heavy use pastures.

Sample Area[a]	Density		Calculated Chi-square[b]	Conclusion
	1969	1970		
Light use	597	619	.36	Not significant
Heavy use	245	258	.29	Not significant
				$Chi\text{-}square_{95,1} = 3.84$

[a] Each sample area consists of 36 ha.

[b] Since there is only one degree of freedom, a correction for continuity was applied by reducing each (observed-expected) value by .5 before computing the Chi-square value.

Table 33. A comparison of western harvester ant colony density in differentially grazed study areas.

Grazing Intensity	Density (colony/ha)	SD
Moderate	31	9
Light	28	16
Ungrazed	23	16
Heavy	3	4

Table 34. Caloric values of western harvester ant tissue from the IBP Intensive Site.

Date	Number of Determinations	kcal/g	Standard Deviation
Male reproductives			
July	1	4.8	--
Female reproductives			
July	1	6.5	--
Workers			
April	2	6.2	.2
July	2	5.5	.9
August	6	5.1	.3
September	3	5.5	.3
October	2	6.2	.6
Mean		5.6	.5

A comparison of ant density per colony failed to show an increase at the end of the season (Table 31) which is probably a result of the limited number of colony excavations permitted on the Pawnee Site. A comparison of three Wyoming colonies excavated in November and December showed an increase of approximately 2600 ants per colony over three spring excavations (Lavigne, 1969). The estimate of 2032 worker ants produced per colony also compares favorably with Golley and Gentry's (1964) estimate of 2000 ants produced per colony for the southern harvester ants.

Energy required for worker ant production was determined by multiplying the number of worker ants produced per colony each year (2032) times the average worker biomass (3.0 mg) times the caloric value of worker ant tissue (5.6 kcal/g dry wt). Similar computations were made for the winged reproductives, estimating 224 male ants times 5.4 mg/male times 4.8 kcal/g dry wt and estimating 91 female reporductives per colony times 11.6 mg/female times 6.5 kcal/g dry wt. The summation of these computations yields a value of 48.64 kcal for production of ant tissue per colony. Table 35 shows the extrapolation of energy values per colony to the intensive study pastures on a seasonal basis. The highest values occur in the summer when most ant tissue is produced. There is some carry-over in production to fall as reflected by the reduced energy values required for production during this seasonal period.

Energy for respiration. The results of the measurement of CO_2 production in relation to temperature are shown in Fig. 12. Analysis showed no significant differences in CO_2 production or in slope of regression lines for the individual colonies. Data points from both colonies were therefore combined for calculation of a single regression line.

Table 35. Seasonal energy requirements for production of western harvester ant tissue.

Season[a/]	Ungrazed	Light	Moderate	Heavy
Fall	.03	.03	.04	.00
Summer	.08	.10	.11	.01
TOTAL[b/]	.11	.13	.15	.01

a/ Energy values expressed as kcal/m^2/season (fall = 91 days, summer = 92 days).

b/ Energy values expressed as kcal/m^2/year.

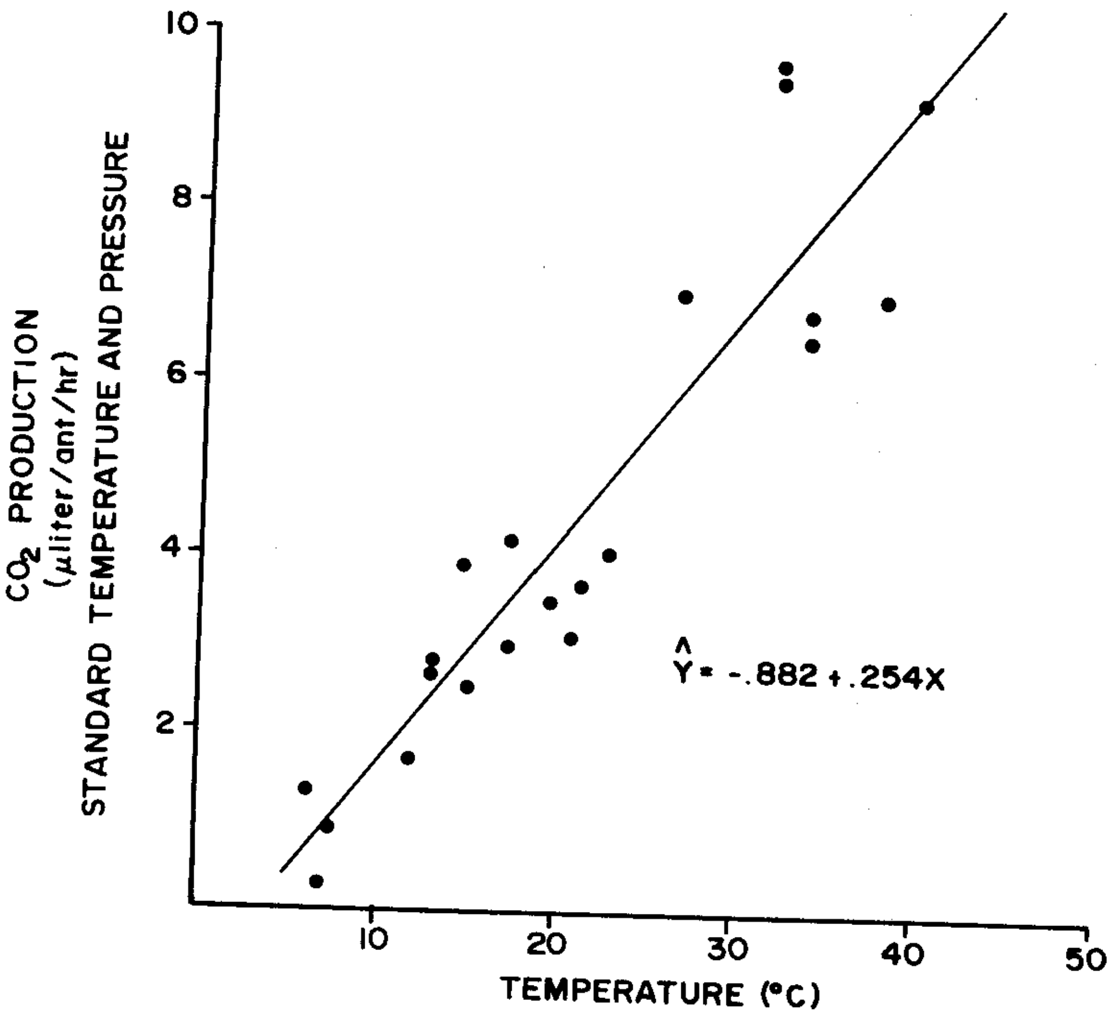

Fig. 12. CO_2 production of western harvester ant workers over the temperature range found in their habitat.

In order to convert CO_2 production to its caloric equivalent, it is necessary to know the ratio between the volume of CO_2 evolved and O_2 consumed (CO_2/O_2). This ratio is known as the respiratory quotient (RQ value) and approximates .81 for mixed protein oxidation. The caloric equivalent for a liter of CO_2 was taken from a table of thermal equivalents (Brody, 1945) and is 5.94 kcal/liter of CO_2.

The amount of energy expended in heat production was calculated separately for (i) the time the foragers were outside the nest during the day, (ii) the time the foragers were inside the nest at night, (iii) the workers that remain inside all season, and (iv) the total colony population during the winter. This type of computation was used because of the seasonal variation of temperature and because ants who venture outside are exposed to higher temperatures than those remaining inside the colony. These computations are based on data (Lavigne, unpublished) which indicate that only one-tenth of the members of a western harvester ant colony are active foragers.

Respiratory energy loss per colony for foragers outside in summer was calculated by multiplying the amount of time the foragers were outside per day (8.5 hr) times the number of foraging days (92) times the number of foragers active during the day (268) times the CO_2 production rate (Fig. 12) at 40°C (9.3 μliter/ant/hr). This value was then multiplied by the caloric equivalent for a liter of CO_2 (5.94 kcal) for a value of 11.58 kcal/colony.

Energy required for respiration of foragers inside at night was determined in a similar manner. The only difference was the use of 24°C for 15.5 hr/day. The estimated values for non-foragers remaining inside all summer were derived by using 2408 ants at a temperature of 24°C for 92 days. Respiration values for the winged reproductives were calculated using 315 ants for 60 days at

24°C. Similar computations were made for the other seasons and for the ants in the other grazing treatments. A summation of the calculations of energy required for respiration results in an annual estimate of 418.42 kcal/colony. Table 36 shows the seasonal energy requirements for respiration by the western harvester ant populations in the differentially grazed pastures. These values range from a high of 1.30 kcal/m^2/year in the moderate use pasture down to .13 kcal/m^2/year in the heavy use pasture.

Energy flow. Seasonal summations of energy required for tissue production and respiration per colony were extrapolated to colony densities found in the differentially grazed pastures. These values are shown in Table 37 as the amount of energy flowing through the western harvester ant population. The annual values range from 1.45 kcal/m^2/year in the moderately grazed pasture to .14 kcal/m^2/year in the heavily grazed pasture.

An examination of Golley and Gentry's (1964) data concerning the southern harvester ant shows that values for both studies are independently equivalent, except for average ant density per colony and respiration values. A comparison was made of the energy requirements of these two congeneric species at 30°C using CO_2 production for the western harvester ant (6.8 μliter CO_2/ant/hr) as taken from Fig. 12 times 5.94 kcal/liter, and O_2 consumption for the southern harvester ant (.09 ml O_2/ant/hr) as taken from Fig. 1 (Golley and Gentry, 1964) times 4.8 kcal/liter O_2. These calculations result in energy values about 10 times greater for the southern harvester ant and are the major reason for the difference in population energy flow values. Additional studies are needed to verify this range of energy flow values for ant populations.

Energy utilization. Aboveground net primary production values for the moderate and ungrazed pastures were 476 and 568 kcal/m^2year, respectively, for 1970 (Sims and Singh, 1971).

Table 36. Seasonal energy requirements for western harvester ant respiratory heat loss.

Season[a/]	Ungrazed	Light	Moderate	Heavy
Winter	.09	.12	.13	.01
Spring	.18	.22	.24	.03
Summer	.47	.57	.63	.06
Fall	.22	.27	.30	.03
TOTAL[b/]	.96	1.18	1.30	.13

a/ Energy values expressed as kcal/m^2/season (winter = 90 days, spring = 92 days, summer = 92 days, fall = 91 days).

b/ Energy values expressed as kcal/m^2/year.

Table 37. Seasonal energy flow through the western harvester ant population at the IBP Intensive Site.

Season[a/]	Ungrazed	Light	Moderate	Heavy
Winter	0.09	0.12	0.13	0.01
Spring	0.18	0.22	0.24	0.03
Summer	0.55	0.67	0.74	0.07
Fall	0.25	0.30	0.34	0.03
Annual[b/]	1.07	1.31	1.45	0.14

a/ Energy values expressed as kcal/m^2/season (winter = 90 days, spring = 92 days, summer = 92 days, fall = 91 days).

b/ Energy values expressed as kcal/m^2/year.

The amount of energy flowing through the western harvester ant population was calculated to be 1.45 kcal/m^2/year for the ants in the moderate use pasture and 1.07 kcal/m^2/year for the population in the ungrazed area. These values represent .3 and .2% utilization of the aboveground net primary production values in the respective pastures (Table 38). This is certainly not a significant portion of the total available energy, but comparisons will have to be made against other animal populations at the Pawnee Site before the true significance of these values can be adjudged.

SUMMARY AND CONCLUSIONS

This study was conducted on the IBP Intensive Site located near Nunn, Colorado, and was designed to determine the effects of the western harvester ants in the shortgrass plains ecosystem.

One of the most easily observed effects of the harvester ants is their habit of clearing the vegetation from around the colony. Calculations of the total area cleared were made from measurements of colony disc diameters in the differentially grazed pastures. The maximum area cleared (28.3 m^2/ha) occurred in the ungrazed treatment. This represents .28% of the total area. In addition, standing crop values measured in the area immediately surrounding the cleared disc were larger than those of surrounding rangeland vegetation. This border effect is undoubtedly due to the presence of increased soil water concentration under the disc. The increase in crop values around the colony result in a partial compensation for the cleared area. Instead of a 100% vegetation loss due to the cleared disc, there is a net 37% decrease for the area under the influence of the colony. Apparently, then, the plant clearing

Table 38. Utilization of aboveground net primary production by western harvester ants in the ungrazed and moderately grazed pastures.

Category[a/]	Grazing Intensity	
	Moderate	Ungrazed
Aboveground net primary production	476	568
Energy flowing through the western harvester ant populations	1.45	1.07
Percent utilization	.3	.2

[a/] Aboveground net primary production and energy values are expressed as kcal/m^2/year.

activities of the western harvester ants exert only a minor influence at the Pawnee Site.

Western harvester ants were also found to move substantial amounts of soil. Measurements of the volume of soil excavated showed 2.8 kg of soil translocated per colony or from 87 kg/ha moved by the ant population located in the moderate use pasture to 8 kg/ha for the population in the heavy use pasture.

Not only do these ants move a substantial amount of soil but they also apparently influence soil characteristics. Bulk density measurements of soil samples from beneath the mound were lower and percent sand content of the colony area were higher than out in the vegetated area; nitrate and phosphorous content were higher in the mound area. These differences are probably attributable to the ants tunneling habits, their bringing organic matter into the colony, and to the excreta deposited in the vicinity of the mound.

Some 39% of the forage particles brought into the colony consisted of seeds. There were 38 species of seeds harvested, but 3 species (*Eriogonum effusum*, *Lepidium densiflorum*, and *Bahia oppositifolia*) comprised 50% of the total number of seeds foraged. Of the forage particles 24% were litter, 10% dead insect material, 10% insect prey, 3% fecal material, 3% rocks, and 1% unidentifiable material.

The activity times of the ants were shown to vary with soil temperatures. The rates at which foraging ants left the colony correlated closely with soil surface temperatures and are predicted with a third-order polynomial equation. The temperature at the soil-surface interface appears to be the environmental factor exerting the greatest influence on foraging activities of the western harvester ants.

The most significant effect of differential grazing treatments was the reduction in western harvester ant colony density associated with heavy grazing pressures. Highest densities occurred in the moderately grazed pasture with 31 colonies/ha. This compares with 28 colonies/ha in the lightly grazed area, 23 colonies/ha with ungrazed conditions, and only 3 colonies/ha in the heavily grazed treatment. No significant changes were detected between years.

The rate of forage extraction, expressed in milligrams per minute per colony, were measured in the light and heavy use pastures. There was no significant differences in the rate of forage extraction in these two pastures. Nor were there any differences in the foraging distance or time per foraging trip for ant populations in these two areas. Investigation of the amount of seed available to the ants also showed no significant difference between the two study areas.

The utilization of seeds ranged from 1 to 5% of the seeds available to the harvester ant population. The major difference between the western harvester ant populations in the light and heavy use pastures was that significantly fewer colonies were located in the latter. This leads to the conclusion that the colonies that become established and are able to maintain themselves in both light and heavily grazed pastures are located in areas of similar seed production.

Colony density in the heavily grazed pasture may be associated with the grazing behavior of cattle. Highest colony densities occurred in those parts of the pasture grazed late in the season, possibly allowing near normal seed production and a resultant high colony density in the area.

Excavation of colonies revealed that worker ant numbers ranged from 1548 to 4443, with an average of 2676 per colony. There was an average of 91 female alate reproductives and 224 alate male reproductives per colony during the month of July. Larvae and pupae were present from June through September, with an average of 547 larvae and 585 pupae per colony.

The amount of energy flowing through the western harvester ant population was determined by measuring the energy required for respiratory heat loss and the energy required for the production of ant tissue.

Energy required for production was determined by converting the number of ants produced per year to an annual biomass figure and multiplying this times the caloric value per gram of ant tissue. The caloric value of ant tissue was determined to be 6.5 kcal/g for alate female reproductives, 4.8 kcal/g for alate male reproductives, and 5.6 kcal/g for the worker ants. A summation of production calculations yields a value of 48.64 kcal required for annual production of ant tissue per colony. Extrapolation of these values to the intensive study pastures shows that from .01 to .15 kcal/m^2/year are required for production of ant tissue.

Energy required for respiratory heat loss was determined by measuring CO_2 production over the range of environmental temperatures applicable to the western harvester ant population. The CO_2 data were then converted to energy values using the caloric value per liter of CO_2. A summation of the calculation for the energy required for respiratory heat loss in the different seasons resulted in an annual estimate of 418.42 kcal per colony. The energy requirements of the population in the differentially grazed pastures ranged from 1.30 kcal/m^2/year in the moderate use pasture to .13 kcal/m^2/year in the heavy use pasture.

Seasonal summation of the energy requirements for tissue production and respiration resulted in a value of annual energy flow values ranging from 1.45 kcal/m^2/year in the moderate use pasture to .14 kcal/m^2/year in the heavy use pasture.

The energy flowing through the western harvester ant population represents .2% of the aboveground net primary production in the ungrazed treatment and .3% in the moderately grazed pasture. Calculations were not possible for the other grazing treatments due to the absence of aboveground net primary production values.

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APPENDIX I

FIELD DATA

Western Harvester Ant Forage Rate Data

Western harvester ant forage rate data is Grassland Biome data set A2U306B. Data were collected on the data form shown as Fig. 3. A listing of sample data appears on pages 63 through 76 of Technical Report No. 107 (Lavigne, Rogers, and Chu, 1971).

Western Harvester Ant Activity Data

Western harvester ant activity data is Grassland Biome data set A2U305B. Data were collected on the data form shown as Fig. 4. A listing of the data appears on pages 77 through 84 of Technical Report No. 107 (Lavigne et al., 1971).