

Effects of Harvester Ant (*Pogonomyrmex rugosus*) Nests on Soils and a Spring Annual,
Erodium texanum

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New colonies had a higher death rate than established ones. The cohort present at the beginning of the study had a net death rate of 0.02/year. The death rate for 29 colonies recruited since 1977 was 0.027, implying a life span of 36.3 years. This figure was calculated omitting several colonies from the margins of the population which were clearly long-established when found, although first marked after 1977. Survivorship curves of both groups are presented in Fig. 1.

While there are substantial differences between the estimates, it is clear that most established colonies of western harvester ants live several decades. The data further suggest that assumptions of equilibrium are in fact flawed, since the population grew 27% during the study period. This growth is not easily explained by climate, since, in the last decade, as many years have had below average rainfall as above (United States Department of Commerce, 1976-1986) and the grazing regime has not changed substantially (K. H. Keeler, pers. obser.; B. L. Gainsforth, pers. comm.).

Estimates of survivorship based on death rates may be more reliable than those derived from recruitment; if I missed a new colony for 2 years, it introduced a substantial error, since there are only 10 years of observations. Such errors are difficult to eliminate, whereas the death of marked ant colonies is unambiguous.

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EFFECTS OF HARVESTER ANT (*POGONOMYRMEX RUGOSUS*) NESTS ON SOILS AND A SPRING ANNUAL, *ERODIUM TEXANUM*

In the Chihuahuan desert, large expanses of perennial burro grass (*Seleropogon brevifolia*) occur essentially as monocultures on clay loam soils near the base of watersheds. In spring 1986, I noted bright green patches scattered within the uniform yellowish *S. brevifolia*. The bright green patches were the spring annual *Erodium texanum* in rings around the nest discs of the harvester ant *Pogonomyrmex rugosus* and on three kangaroo rat nests. There were no distinctive rings of spring annuals around the nest discs of *P. rugosus* in other habitats in the area and *E. texanum* essentially was restricted to the *S. brevifolia* habitat. Ants have been found to affect distributions of plant species on and around their nests (Beattie and Culver 1977; Hobbs, 1985) and to affect the biomass or plant size of plants associated with their nests (Gentry and Stiritz, 1972; Briese, 1982; Culver and Beattie, 1983). The differences in vegetation around ant nests have been attributed to differential seed selection by ants and elevated soil nutrients.

Based on the observations of *E. texanum* and the literature, I hypothesized that the density and biomass of *E. texanum* would be higher around the nest discs of *P. rugosus* because of higher soil nutrient levels. Elevated soil nutrients at the edges of mounds of seed harvesting ants have been described in other areas (Gentry and Stiritz, 1972; Briese, 1982; Culver and Beattie, 1983).

Plants and soil were sampled in paired locations at the edge of 12 nest discs of *P. rugosus* and at a distance of 3 m from the center of the nest disc. Two points on the circumference of the nest disc and a point on a circle with a diameter of 3 m centered on the ant nest were selected at random for the placement of quadrat frames 40 by 40 cm. All annual plants within the quadrat frame were counted and harvested. Two quadrats were sampled on the disturbed soil of the three

TABLE 1—Comparisons of density, biomass, and plant nitrogen of *Erodium texanum* around harvester ant (*Pogonomyrmex rugosus*) nests, kangaroo rat (*Dipodomys* sp.) dens, and adjacent areas. Data are means \pm 1 SD for 12 ant nest discs, 12 adjacent areas, and 3 rat dens. Numbers in a row followed by a different letter are significantly different at $P < 0.05$.

Plant character	Ant nest disc	Rat den	Adjacent area
Density (no./m ²)	82.8 \pm 26.2	110.6 \pm 31.3	89.4 \pm 53.1
Biomass (g/m ²)	301.5 \pm 127.3 a	335.0 \pm 131.2 a	41.9 \pm 38.7 b
Average mass/plant	4.0 \pm 2.0 a	3.3 \pm 1.4 a	0.5 \pm 0.4 b
Plant N (mg/g)	18.0 \pm 1.1 a	11.1 \pm 0.2 b	15.4 \pm 0.6 a

rodent dens in the area. The harvested plants were dried for 72 h at 60°C, weighed and ground in a Wiley Mill for nitrogen analysis.

Soil cores (2.5 cm in diameter, 15 cm in depth) were collected from the harvested plots on a subset of five nest discs and paired adjacent areas. Soil cores were also obtained from the disturbed soils of the rodent dens. Soils were analyzed for gravimetric moisture content, electrical conductivity, organic carbon, total phosphorus, ammonium, nitrate, and total nitrogen. Inorganic N (NH₄ and NO₂ + NO₃) was measured in 2.0 M KCl extracts with a 10:1 ratio of soil to KCl (Keeney and Nelson, 1982). NH₄-nitrogen was measured in the extracts by an automated salicylate procedure (Wall and Gehrhe, 1975; Nelson, 1983), and NO₂ + NO₃ nitrogen was measured by an automated cadmium reduction procedure (Henricksen and Selmer-Olsen, 1970). Soil for total nitrogen analysis by micro-kjeldahl digestion in an aluminum block digester was first ground in a motorized mortar and pestle to a mesh size of 0.15 mm (Nelson and Sommers, 1980). Ground plant tissues were subjected to micro-kjeldahl digestion and analyzed for total nitrogen (Nelson and Sommers, 1980). All automated procedures were performed with a Scientific Instruments Continuous Flow Analyzer. Analyses of electrical conductivity, organic carbon, and phosphorus were made at the New Mexico Soil and Water Testing Laboratory using standard techniques (Page et al., 1982).

There were no differences among annual densities on nests of *P. rugosus*, dens of *Dipodomys* sp., and surrounding undisturbed soil (Table 1). Standing crop biomass and plant size were significantly higher on the edge of the ant nest discs and rat dens than on surrounding undisturbed soils. However, nitrogen concentration in plant tissues was significantly lower in plants from rat dens than in plants from ant nest discs and surrounding undisturbed soil (Table 1). Soil organic matter was highest in soils from the edge of ant nests and lowest in soils from rat dens. Soil moisture was higher at ant nests and rat dens than in surrounding undisturbed soils (Table 2). There were no significant differences in NO₃-N, NH₃-N, and organic P in these soils, but total N was highest in soils from the edge of ant nests (Table 2).

Data indicate that the larger plants of *E. texanum* on the animal-modified soils was probably due to greater water availability and not to higher nutrient availability. It is likely that the rate of

TABLE 2—Properties of soils from the edge of nest discs of the harvester ant (*Pogonomyrmex rugosus*), kangaroo rat (*Dipodomys* sp.) dens, and adjacent areas. Data reported are means \pm 1 SD for 12 ant nest discs, 12 adjacent areas, and 3 rat dens. Numbers in a row followed by a different letter are significantly different at $P < 0.05$ unless otherwise indicated. ND indicates no data collected for that site.

Soil property	Ant nest disc	Rat den	Adjacent area
Electrical conductivity (ds/m) ¹	0.90 \pm 0.20 a	ND	0.70 \pm 0.30 a
Organic carbon (%)	0.50 \pm 0.10 a	0.30 \pm 1.00 b	0.35 \pm 0.10 v
P (ppm)	7.90 \pm 5.90	ND	8.00 \pm 1.50
NO ₃ -N (mg/kg soil)	1.40 \pm 0.50 a	1.70 \pm 0.30 a	1.60 \pm 0.50 a
NO ₄ -N (mg/kg soil)	4.50 \pm 1.90 a	3.90 \pm 1.90 a	3.60 \pm 1.40 a
Total N (mg/kg soil) ²	672.00 \pm 140.00 a	494.00 \pm 18.00 c	530.00 \pm 79.00 b
Moisture %	3.00 \pm 0.90 a	2.68 a	2.10 \pm 0.60 b
Organic matter (%)	1.10 \pm 0.10 a	0.80 \pm 0.10 c	0.90 \pm 0.10 b

¹ds/m is approximately equal to mg l liter sal concentration (Page et al., 1982).

²Significantly different at $P < 0.10$ but not at $P < 0.05$.

nitrogen mineralization was somewhat higher in soils of ant nests than in adjacent soils but not sufficiently different to result in differences in tissue N concentration. Soils of rat dens were undoubtedly of lower bulk density than surrounding soils because the den soil consisted of loose piles of excavated material. The lower bulk density would enhance infiltration and aeration which would stimulate microbial activity. This would result in low organic C and low organic matter content compared with undisturbed soils. Thus, the larger number of plants with low N content on the rat dens is probably due to increased water availability.

These data suggest that an important effect of seed harvesting ants is the modification of the soils around the cleared nest disc. In numerous excavations of ant colonies, we have found decomposing plant materials in shallow nest chambers that have apparently have been abandoned or closed off by natural processes. These abandoned chambers which extend beyond the cleared nest disc were probably the initial source of organic matter that increased the organic carbon fraction of soil influenced by nests of *P. rugosus*. Other soil parameters that were higher in nest-influenced soils (water content, nitrogen, and slightly elevated ions) would be expected to increase in soil with higher organic matter. The galleries and tunnels produced by ants provide channels that allow bulk flow of water into the soil. Levieux (1976) found that ant nests affected the macroporosity of savannah soils. Briese (1982) suggested that ant nests in heavy clay soils provide avenues for water infiltration. The high biomass and low N content of the *E. texanum* from the rodent-disturbed soils suggest that biomass production of *E. texanum* were probably the result of soil water status and not the nitrogen availability of the soil. Both nutrients and water were higher on ant nest discs than surrounding soils, but only soil moisture was elevated on disturbed soils of rodent mounds (Table 2). The higher biomass and greater mass per plant on the ant nests and rodent dens are, therefore, probably the result of higher soil moisture and not nutrients. *Erodium texanum* can apparently grow rapidly with sufficient moisture by sacrificing nutrient content of the tissues since N content of *E. texanum* from rodent-den soils was lower than that of plants on undisturbed soils and plants from the perimeter of ant nests (Table 1). Thus, the higher biomass of *E. texanum* on disturbed soils is probably the result of increased infiltration and water storage in comparison to undisturbed soils.

Most studies of vegetation on and around ant mounds or nests have attributed vegetational differences to soil chemistry (Gentry and Stiritz, 1972; Culver and Beattie, 1983). In mesic areas, soil moisture is undoubtedly not as important a factor affecting productivity as nutrients. However, in arid and semi-arid regions, water and nutrients, especially nitrogen, may limit productivity and affect species composition (Parker et al., 1982; Gutierrez and Whitford, 1986). In arid and semi-arid regions, soil disturbances by animals such as ants can have important effects on productivity and plant species composition. Data from the present study demonstrate that the effects of ant nests on soils and subsequently on vegetation is not simply the result of concentration of nutrients in mounds. The construction of mounds by rodents and nests by ants apparently affects infiltration and water storage. The interactions between available soil moisture and nitrogen availability in soil disturbed by animals in arid and semi-arid ecosystems is deserving of attention.

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PUPATION SITE AND PUPAL MORTALITY OF THE PREDACEOUS DIVING BEETLE *DYTISCUS DAURICUS*

Although a large volume of the ecological literature has been devoted to factors that influence population dynamics, processes regulating many populations in nature are poorly understood. Predaceous diving beetles of the genus *Dytiscus* are top predators in many fishless, lentic freshwater communities in North America (Arnett, 1963; James, 1969; Holomuzki, 1986; Holomuzki and Collins, 1987) and, consequently, strongly influence the dynamics of these communities. Quantitative life history data and information on factors which regulate their populations, however, are scarce. I reported information on location of pupation site and pupal duration and survivorship of a population of *Dytiscus dauricus* in the White Mountains of east-central Arizona (Holomuzki, 1985). In that paper, I also speculated that predation from ants and spiders was an important source of pupal mortality. Here, I present two additional years of data on the previous life history characters on the same population and provide evidence that trampling by cattle rather than predation from terrestrial invertebrates is a major source of pupal mortality.

My study population was at Big Meadows Tank (BMT) 1, a permanent pond 1.0 km NNW of Sunrise Lake, Apache Co. (elev. 2,774 m). Dominant littoral macrophytes in BMT 1 were *Sparganium emersum* and *Glyceria borealis*. Pond surface area and maximum depth were 0.17 ha and 3.0 m, respectively. The pond was an artificially deepened section of natural marsh in a subalpine grassland and was used to water cattle from late July to early fall.

In 1983, larval *D. dauricus* at BMT 1 began constructing pupal cells in late June and early July (Holomuzki, 1985). Pupal sites averaged 2.05 m from the pond's edge, and no pupae or enclosed adults were found in pupal cells after mid-September. Length of pupation was about 23 days, and 52% of larvae that constructed pupal cells successfully reached adulthood.

Data on location of pupal site, duration of pupation, and pupal survivorship for this study were collected at BMT 1 during summer in 1984 and 1985. Pupaion sites were found by overturning stones along the northern shore from the water's edge to 7 m inland on a weekly basis. Care was taken to return overturned stones to original positions to minimize habitat disturbance. Developmental stages of beetles were recorded, and stones over pupal cells were uniquely marked. Distance of cell from water and size of stone were measured. Lengths of major and minor axes of the roughly ellipsoid stones were used to compute surface areas. Duration of pupation was determined by emergence of adults from puparia of known age. Survivorship of pupae was assessed directly.