Longevity of harvester ant colonies in southern Idaho

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Abstract

Harvester ant colonies (*Pogonomyrmex owyheei* Cole) in southern Idaho were monitored periodically for 9 years. Mortality rates indicate that established colonies live 14–30 years ($\bar{x}$ = 17). Mounds were commonly reactivated after the death of an old colony; consequently, some may be utilized for many decades. Clearings with active mounds showed almost no change after 9 years of observations while those without active mounds were rapidly filled by annual herbs and then gradually by perennial shrubs. Harvester ants are clearly a very persistent component of cold desert shrub communities.

Key Words: *Pogonomyrmex*, persistence, survivorship, mounds, clearings

Pogonomyrmex harvester ants are conspicuous features of rangelands throughout much of western North America. This is especially true of the northwest species, *Pogonomyrmex owyheei* Cole, which constructs distinctive gravel-covered mounds surrounded by large clearings. Harvester ants have been considered pests (Crowell 1963, List 1954) because they occasionally clear up to 10% of range area (Sharp and Barr 1960, Willard and Crowell 1965). Fortunately, the percentage of land cleared is generally much less (Sneva 1979, Rogers and Lavigne 1974) and the damage is largely compensated by increased vegetational production around clearing perimeters (Wight and Nichols 1966, Rogers and Lavigne 1974).

Colonies construct clearings by systematically clipping off plants emerging too near their mounds (Clark and Comanor 1975). This behavior exposes the mounds to direct sunlight earlier in the morning when it is most beneficial for thermoregulation (Seeley and Heinrich 1981). Clearings may also benefit the colony by speeding transit of foragers and eliminating hiding places for harvester ant predators (Clark and Comanor 1975).

Earlier observations indicated that harvester ant mounds and clearings changed little from year to year (Sharp and Barr 1960), and that the colonies themselves may be very long-lived (Michener 1942, Wildermuth and Davis 1931). In order to investigate the longevity of harvester ant colonies, we monitored approximately 120 mounds over a 9-year period, 1977–1986.

Methods

This study was undertaken in Raft River Valley, Ida., as part of a larger environmental monitoring program (Jorgensen 1979). All plots were located in mixed sagebrush *(Artemisia tridentata wyomingensis)* and greasewood *(Sarcobatus vermiculatus)* plant associations. These shrubs together with *Lepidium perfoliatum, Sitanion hystrix, Descurainia richardsonii, Bromus tectorum* and *Ceratoides lanata* accounted for >95% of the vegetation. Rainfall averaged about 24 cm (9.5 inches) in 1977 and 1978. Plots were located on the lower parts of alluvial gravel deposits interspersed with intermittent drainage streams. Livestock grazing was generally moderate from November to May, leaving range condition fair but needing improvement (Burley District, BLM).

We initially mapped *P. owyheei* mounds at 3 small plots (0.25 ha) and 1 large plot (2.72 ha, Fig. 1) in 1977. Mounds and clearings

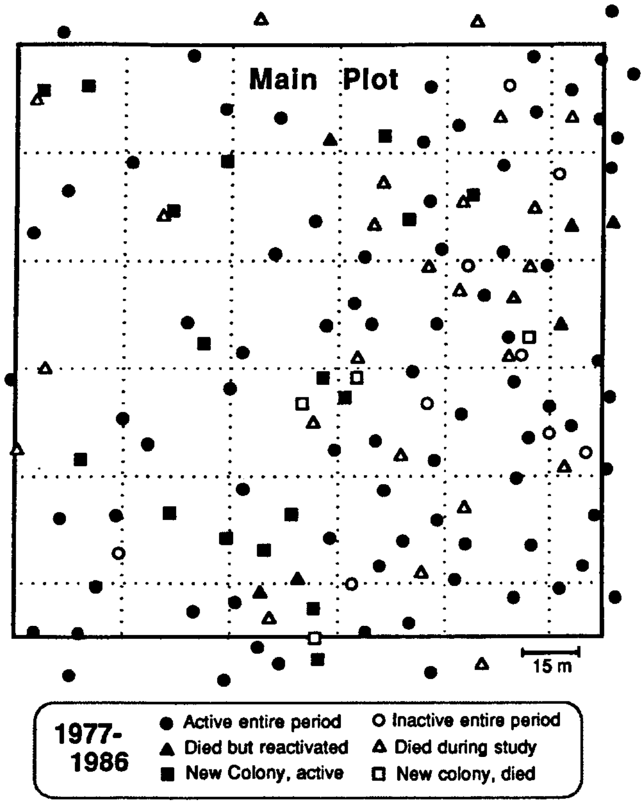

Fig. 1. *Distribution and activity of* Pogonomyrmex owyheei *mounds on the main plot from 1977–1986. Closed symbols indicate active mounds in 1986 and open symbols indicate the inactive ones.*

in 2 of the small plots (A and B) were measured and checked for activity several times a year during 1977–1980 and again in 1986. Colonies at the third small plot (removal) were poisoned with Diazinon (1977) to determine how rapidly an area was reinvaded after the inhabitants died. Mounds at the main plot (Fig. 1) were mapped and checked for activity in 1977, 1979, partially in 1980, and again in 1986. These mounds were assigned to size classes according to their diameters: small (<30 cm), medium (30–60 cm), and large (>60 cm). Mound activity was determined either by the presence of ants or fresh piles of chaff deposited near the mound. If a mound appeared to be inactive, we dug into the mound to confirm the absence of ants; this avoided the possibility that a mound would be declared inactive simply because the colony had not been foraging recently. Vegetational cover for the main plot and plots A and B was 18%, 31%, and 15%, respectively.

Results

Persistence of Mounds

Mound densities on our study plots averaged 40/ha with about 4% of the area included in clearings. The total number of active

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mounds remained relatively stable at 122, 128, and 119 mounds in 1977, 1979, and 1986, respectively. Of the original 122 active mounds, 80% (97 mounds) were still active after the 9 years (see Figure 1 for activity changes on the main plot). At least 6 of these mounds were temporarily abandoned and then reactivated by a new colony. A total of at least 36 colonies died during the study and 30 new colonies were established. Six mounds remained recognizable even after more than 9 years of inactivity. Mortality rates appeared to be associated with mound size. Approximately 50% of small, 30% of medium, and 25% of large mounds were abandoned between 1977 and 1986. This relationship suggests that colonies in small mounds are shorter lived, but this could also result because smaller mounds were less likely to be reactivated during the 5-year interval when the plots were not monitored (1981–1985).

Colony Longevity

Longevity was calculated by dividing the number of colonies alive over a specific time period by the number which died (Table 1). For example, 23 mounds on plots A and B were monitored for 3

Table 1. Estimated longevity of harvester ant colonies *(Pogonomyrmex owyheei)* in the Raft River Valley of southern Idaho.

Vegetation	Sample Dates	$\bar{x}$ Number of Mounds	Mound Years	Number of Deaths	Longevity in Years
Sagebrush and Greasewood					
Plots A & B	1977–80	20	61	4	15
Main Plot	1979–80	68	68	5	14
Shadscale	1956–58	61	121	4	30*
Saltsage	1956–58	28	56	2	28*
Depleted Saltsage	1956–58	112	223	16	14*
		Total	529	31	17

*Calculated from Sharp and Barr (1960)

years. During this time, we accumulated 61 active colony years and observed 4 deaths; thus the estimated longevity was 15 years. We also checked the activity of 68 colonies at the main plot for 1 year; 5 colonies died during this year producing an estimate of 14 years. Sharp and Barr (1960) monitored the activity of colonies over 2 years at study sites in the same valley. Their 3 sites were located in shadscale *(Atriplex confertifolia)*, saltsage *(Atriplex tridentata)*, and "depleted" or heavily foraged saltsage. Longevity estimates calculated from their data ranged from 14–30 years (Table 1).

The longevity estimates in Table 1 require the satisfaction of 3 assumptions: (1) colonies died rather than emigrated, (2) sampling frequency was sufficient to detect mortality, and (3) populations retained stable age-distributions during the study. The assumption that inactive colonies died rather than emigrated is fairly robust and acceptable. Unlike other members of its genus (Carlson and Gentry 1973, Van Pelt 1976), mature *P. owyheei* colonies rarely emigrate unless they are poisoned or severely disturbed (Willard and Crowell 1965). In 4 years of intensive study, we observed only 1 naturally occurring emigration, and it was eventually aborted. The second assumption, that sampling frequency was sufficient to detect mortality, also seems to be satisfied. Plots A and B were checked at least monthly (1977–1980) so it is highly unlikely that colony death and reestablishment could have occurred unnoticed. Other plots were surveyed once a year, but this was probably also sufficient because recolonization by founding queens could occur only in August and at least a year would be required before an incipient colony grew enough to be noticeable. Also, successful "yearling" colonies were very uncommon. The third assumption, a stable age distribution, is more questionable because we could not determine how long colonies had been at the plots prior to sampling. The main problem would be if our study populations had been founded in waves. Thus, if we sampled soon after a founding wave, the longevity estimate would have been too high, while if we sampled late in the cycle, it would have been too low. Problems with this assumption may account for some of the variation in Table 1; however, the fact that all 5 estimates exceed 10 years supports the conclusion that harvester ant colonies are very long-lived.

Mound Dimensions

Seventeen of the 22 mounds on plots A and B were active throughout the study. The average diameter of these mounds changed little during the course of our study; however, mound heights increased 20–50% between 1977–79 and 1986 (Fig. 2, repeated measures ANOVA, Scheffé F-test, $p<0.05$). This increase

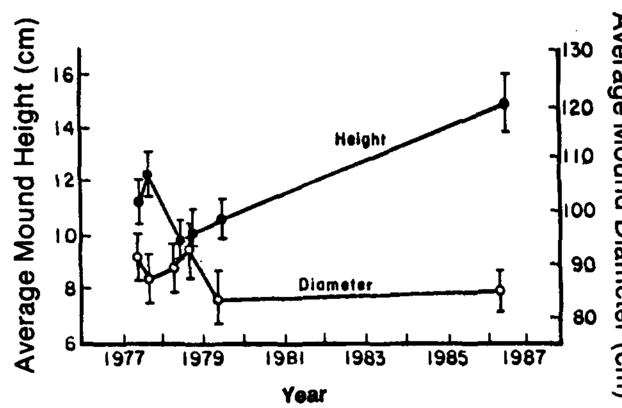

Fig. 2. *Average changes in* Pogonomyrmex owyheei *mound height and diameter of 17 mounds from 1977 to 1986. Standard errors are shown for each point.*

could be due to either a gradual accumulation of rocks over the years, or a general increase in colony size, perhaps as a result of almost 5 years of above-normal precipitation in the valley. Active mounds at the main plot also seemed to increase in size, but 70% did not change enough to switch size classes. Five mounds remained small throughout the study. Twelve mounds grew from small to medium, and another 13 from medium to large. Two mounds grew all the way from small to large. The only mounds which lost size were those in which the colony died.

Clearings

After 9 years, the size and shape of clearings on plots A and B changed very little. In fact, comparison of photographs taken in 1977 and 1986 revealed a remarkable lack of change (Fig. 3A). Many dead sticks and branches were still in the same locations they had been 9 years earlier. Most bushes were even the same general shape and size; a fact not too surprising considering sagebrush is often very long lived and slow growing (Ferguson 1964). The diameters of the clearings, however, averaged about 8% smaller in 1986 than in 1977–1979 (3.5±1.1 m versus 3.8±1.1 m; $p<0.05$, Scheffé F-test). This change may reflect increased growth of vegetation during a period of wet years, or it may simply indicate that clearings are often irregular and measuring them is difficult to standardize.

Removal Plot

The removal plot initially contained 18 active mounds. The poison treatment in 1977 was not completely effective. In 1978, almost half of the mounds were still active, albeit at rather low rates. The queens of most colonies had probably been killed the previous year, but workers in the pupal stage managed to survive. When we surveyed the plot in 1986, only 5 of the 18 mounds were still active, and 3 of these showed distinct signs of having been reactivated based on the degenerated condition of the mound and surrounding clearing. No new mounds were found in the plot. The 13 inactive mounds were still plainly visible after 8 years, but they

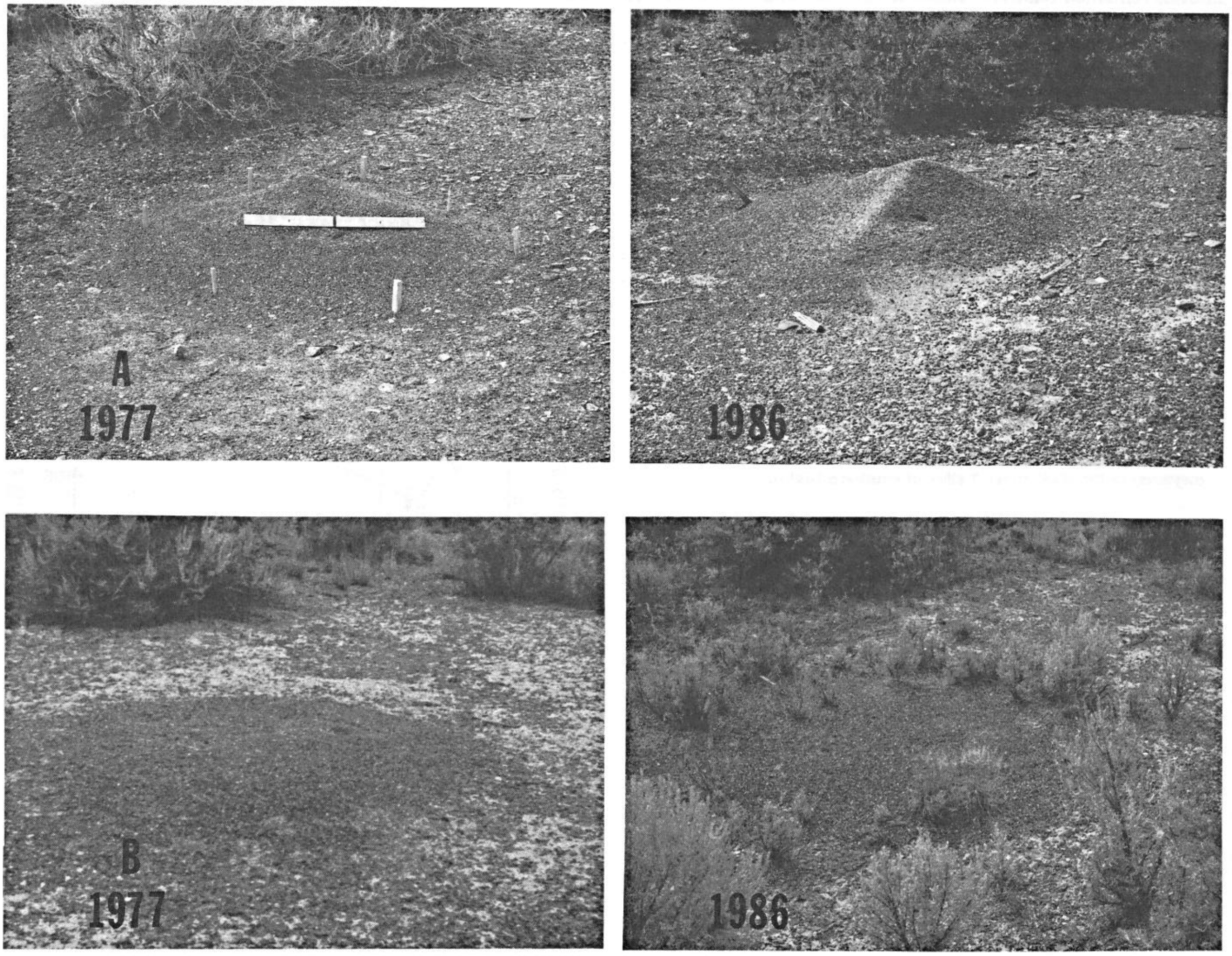

Fig. 3. *(A) An active harvester ant mound* (Pogonomyrmex owyheei) *in 1977 with a 2 ft ruler (62 cm) and the same mound again in 1986. The 1986 photograph was taken a meter or so to the right of the 1977 one. (B) A large active mound in 1977 before it was poisoned and the same mound in 1986 after 9 years of inactivity.*

were badly deteriorated and not more than 2–4 cm in height. Clearings associated with those mounds had also deteriorated, and most had young sagebrush (Fig. 3B) or perennial grasses growing on them.

Discussion

Colony Longevity

Harvester ant colonies are apparently very long lived once they become established. Estimates of longevity ranged from 14 to 30 years with a mean of about 17 years (Table 1). We were not able to determine the age distribution of these colonies, but the fact that substantial mortality occurred in all mound sizes indicates that survivorship is probably closer to a type II curve (mortality independent of age) than a type I curve (old-age mortality). If this is the case, then the age of colonies at death would vary considerably and some would easily reach 25–30 years. Colony longevity has been reported for a number of other ants, but most of these reports are fragmentary or based on single laboratory colonies. Colonies with multiple queens are potentially immortal because new queens are recruited as old ones die (Wilson 1971). Colonies with a single queen may live 5–30 years (Baroni-Urbani et al. 1978, Chew 1987, Tschinkel 1987, Weber 1972), but most species probably do not survive nearly as long in the field due to the rigors of competition, predation, pathogens, and habitat change.

Of the original mounds in our study, almost 75% (91/122) were still active 9 years later—excluding 6 which were known to have died and then been reactivated. This activity rate was almost 30% higher than would have been predicted assuming a 17-year longevity and a type II survivorship curve. Several possibilities may account for this discrepancy. The most likely one is that some active mounds probably died and then were recolonized during the 5-year period (1981–85) when data were not collected. Also, the age distribution may not have been stable or 17 years may be an underestimate of actual longevity.

Another possibility which could confuse the results would be if mature queens were replaced by young queens after they died; fortunately, this does not appear to be the case. *Pogonomyrmex* colonies are uniformly single-queened (Lavigne 1969, MacKay 1981, unpublished data) and hostile to foreign queens (Hölldobler 1976). The possibility of queen replacement was specifically tested with *P. owyheei's* sister species *P. occidentalis* (Cole 1968). We introduced 1-month-old founding queens into 8 mature laboratory colonies which had been deprived of their mother queens first for 1 week and then for 1 month. Workers in these colonies immediately attacked and eventually killed the introduced queens. In short, these colonies did not replace their mother queen when she died; consequently, colony longevity should be the same as queen longevity.

A colony longevity of 17 years indicates that founding queens have a very poor chance of success. Mature harvester ant colonies produce about 100–300 reproductive queens every year (Lavigne 1969, Rogers et al. 1972, MacKay 1981). Assuming this is also true of *P. owyheei*, the average queen would produce several thousand reproductive queens over her lifetime. Thus founding queens would have less than one chance in a thousand of successfully founding a colony in a stable population.

Mounds

Inactive harvester ant mounds are often recolonized by new colonies. reactivations accounted for 25% (8/30) of new colonies discovered during this study. This should be considered a minimum estimate because some mounds probably died and were reactivated between samples. Reactivation of old mounds probably occurs because these locations were successful in the past and offer immediate advantages associated with a preconstructed mound and clearing. The fact that mounds are recolonized indicates that some have been used by successive colonies for many decades. Recolonization of mounds may also explain why mound volume is poorly correlated with colony size (Lavigne 1969, unpublished data). The fact that abandoned mounds can be recognized for periods of a decade or more is a testament to how slowly soil crusts turn over in cold deserts.

Not all abandoned mounds are reoccupied, however. In fact, 13 of 18 mounds on the removal plot were still inactive in 1986, although at least 3 had been reactivated. It was also surprising to find that the removal plot had recovered to only 20–30% of its original population, even 7–8 years after the original mounds had been poisoned. Apparently, reinvasion of abandoned mounds and sites may take many years and is not always uniform or dependable.

Clearings

Active clearings on our study plots showed very few changes over the 9 years of our study (Fig. 3A). Workers readily removed annuals and seedling shrubs from around their mounds by gradually clipping the leaves off. Juvenile shrubs (<40 cm) were occasionally attacked, but mature shrubs were rarely attacked unless they were actually growing out of the mound or their branches were lying on the ground near the mound. This leads to the question of how mature shrubs are eliminated from clearings.

One possibility is that mounds are initially situated in naturally occurring gaps so that the shrubs do not need to be removed. This is probably true of small clearings (<3 m); however, larger clearings (5–10 m) are too large to have occurred naturally. A second possibility is that mature shrubs are attacked directly and killed by repeated defoliation. This may occur in other areas, but we observed only one instance where a mature shrub *(Atriplex)* was substantially defoliated. A third possibility is that the clearings were formed after fire or pests killed the surrounding bushes. In this case, a succession of colonies inhabiting the same clearing would simply eliminate all seedling shrubs in their clearing while the surrounding shrubs continued to mature. A fourth possibility is that the clearings are gradually enlarged as mature bushes die. In this case, the clearings could be many decades or even centuries old because sagebrush in cold deserts often lives 50–100 years (Ferguson 1964). The ages of harvester ant clearings probably vary considerably from area to area and vegetation type to vegetation type. It does seem clear, however, that at least some of these clearings are very old.

One interesting aspect of harvester ant clearings is that they increase the heterogeneity of range habitats. For instance, soil texture and algal crusts are often very different in cleared areas. These clearings also tend to accumulate both water and nutrients (Rogers and Lavigne 1974) which results in increased plant growth around the clearing perimeters (Wight and Nichols 1966). It is conceivable that harvester ant clearings may actually benefit some ranges by allowing rings of continued plant growth during droughts; this perimeter effect could also increase species diversity and perhaps even community stability by serving as temporary refugia for arthropods and other small animals.

Conclusion

Harvester ant colonies in southern Idaho appear to be extremely persistent K-selected organisms. The number of colonies in our study plots remained stable over 9 years of observations. Worker ants only live for a year or two (Porter and Jorgensen 1981), but the colonies themselves may live for several decades (Table 1). Queens apparently live as long as the colony, making them among the longest lived of rangeland animals. Harvester ant mounds and clearings can be reoccupied; consequently, some may persist for many decades.

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