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FIFTEEN YEARS OF COLONY DYNAMICS IN *POGONOMYRMEX OCCIDENTALIS*, THE WESTERN HARVESTER ANT, IN WESTERN NEBRASKA

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Ecological communities respond to environmental changes as the individuals of the component species die and are replaced. Thus, patterns of population turnover form an important aspect of community processes. Much less is known about species of long-lived individuals than of short-lived ones (Likens, 1989).

Instantaneous observations of age structure can be used to infer long-term dynamics but not all species can be aged retrospectively. Inferring life-history dynamics from current populations requires assumptions that are hard to verify. Following marked colonies of long-lived species is slow but provides direct, non-inferential data on population dynamics, although those are specific to the period observed. This note reports 15 years of observations aimed at determining survivorship of individual harvester ant colonies. Harvester ants are important arid grassland herbivores whose dynamics are crucial parameters for patterns of change in the rest of the community (Brown et al., 1979; Coffin and Lauenroth, 1990).

Fifty-six mounds of *Pogonomyrmex occidentalis* Cresson (Hymenoptera: Formicidae), the western harvester ant, were permanently marked with aluminum tags in August 1977. The ant colonies were checked each August from 1977 to 1991; colony deaths were noted and new colonies were marked. Death was determined based on the following information: absence of foragers at times in which neighboring colonies were foraging and poor condition of the mound. It was verified by deterioration of the colony site in subsequent years. Unoccupied sites remain marked for a study of succession. The site, about one hectare in extent, just south of the University of Nebraska's Cedar Point Biological Station, Keith Co., Nebraska, was within a pasture which received moderate, half-summer grazing during the period studied. The vegetation is typical of shortgrass prairie, dominated by *Buchloe dactyloides*, *Bouteloua hirsuta* and *B. gracilis*, interspersed with *Stipa comata*, *Aristida purpurea* and *A. oligantha*, and forbs such as *Artemisia* and *Psoralea* and woody pe-

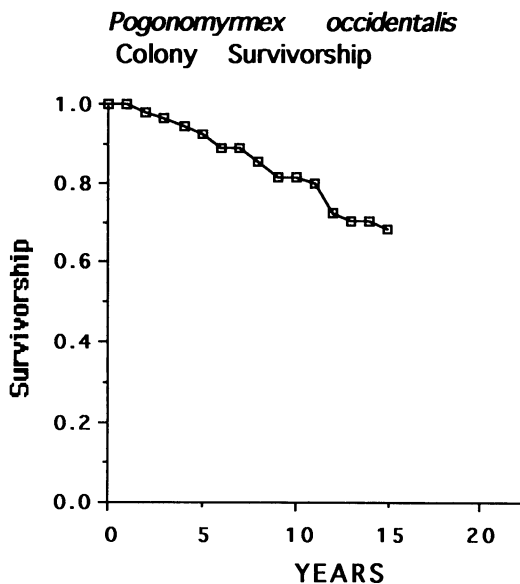


FIG. 1—Survivorship curves for colonies in a population of *Pogonomyrmex occidentalis*. Original cohort (56 colonies) marked in 1976.

rennials, including *Yucca glauca* and *Juniperus virginiana* (Kaul et al., 1983). The site lies between eroded canyons, which give the study area an irregular shape. Rock outcrops produce some areas with insufficient soil depth to support a harvester colony.

Of 56 colonies marked in 1977, 37 were alive in 1991 for an average of 1.27 colony deaths each year, (0.023 colony deaths per hundred per year). This death rate is virtually identical to the death rate calculated for this population after 10 years (Keeler, 1988). This 66.1% survival rate over 15 years projects to a colony life expectancy of 43.5 years (Fig. 1). Using the regression of survivorship vs. time, the last colony of the cohort of 56 is expected to be gone after 44.9 years.

The land use at the site has been stable throughout the 15 years of study. The number of colonies at the site rose between 1977–1981, perhaps because of discovery of overlooked colonies, but averaged 69 ($SD = 20$) from 1981 to 1991 (Table 1). If this is an equilibrium population, life expectancy can be estimated from recruitment. The term recruitment is used here to mean the discovery of a colony that had not been seen previously: the queen will have begun the nest months earlier (Gregg, 1963). Recruitment rates varied from 0.00 to 0.12 per year, between

TABLE 1—Annual colony recruitment, colony death and total number of colonies in a harvester ant population.

Year	Recruitment		Death		Total colonies
	Num-ber	Annual rate	Num-ber	Annual rate	
1977	—	—	—	—	56
1978	8	0.143	1	0.016	63
1979	4	0.064	1	0.015	66
1980	3	0.046	3	0.046	66
1981	3	0.046	1	0.015	68
1982	8	0.118	2	0.027	74
1983	3	0.040	1	0.013	77
1984	0	0.000	2	0.027	75
1985	0	0.000	5	0.071	70
1986	7	0.100	2	0.020	75
1987	6	0.080	2	0.025	79
1988	2	0.025	5	0.066	76
1989	5	0.066	1	0.012	80
1990	0	0.000	0	0.000	80
1991	2	0.025	3	0.038	79

1981 and 1991, calculated as a fraction of that year's population (Table 1). Averaging the annual recruitment rates, the mean recruitment was 4.5 colonies per hundred per year ($SE = 0.01$). If recruitment balanced death exactly, colonies in the population would have a mean life expectancy of 21.3 years.

Colony deaths ranged from 0 to 5 per year (Table 1). Calculated as mean death rates for the particular year's population, these give an average value of 2.8 deaths per hundred per year ($SE = 0.020$), which, projected to a stable population, suggests a life expectancy of 35.7 years.

The value based on death rates is lower than that from recruitment rates but not significantly different due to the high variance ($t = 0.51$, $d.f. = 28$, $P > 0.5$). The rates may in actuality differ despite statistical insensitivity since the population has shown net growth over the study period. The values for mean recruitment and death rates (Table 1) are similar to those observed in the two previous 5-year intervals (Keeler, 1981, 1988).

New colonies had higher death rates than established ones (Fig. 2). While the cohort present at the beginning of the study had a net death rate of 0.023 per year (see above), of the 51 colonies recruited since 1977, 15 have died; the death rate was calculated at 4.1 colonies per 100 per year. This projects to life spans of 24.2 years, assuming equilibrium dynamics. The regression of new col-

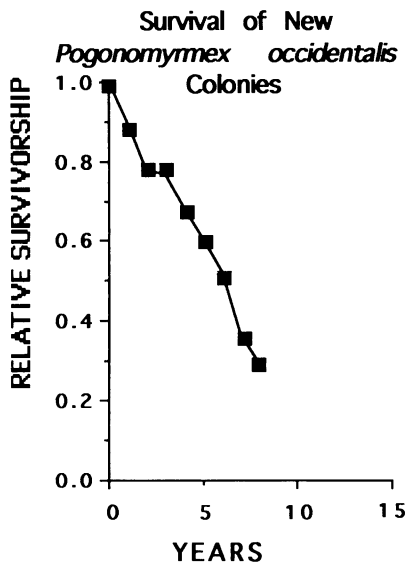


FIG. 2—Age-specific survivorship for colonies of *Pogonomyrmex occidentalis*.

ony survivorships against age suggests that the cohort of 51 will be gone after 12.7 years: the discrepancy is because this latter includes the high first-year death rate in the curve, while the former rate is influenced by the continued success of surviving colonies. The true survivorship curve must be a composite of these effects, with high initial colony mortality and very low mortality once a colony reaches some critical, currently unknown, size. These figures were calculated omitting several colonies from the margins of the population that have been followed since the 1970s but which were clearly not newly-founded when first recorded.

While there are substantial differences between the estimates, it is clear that established western harvester ant colonies live several decades and even new colonies have a life expectancy of over a decade. Once the new queen has a functioning nest, the greatest part of the risks of death are over. These long life-expectancies are consistent with values developed in other studies of harvester ants. Coffin and Lauenroth (1990) estimated similar lifespans (29 to 58 years) for *P. occidentalis* in Colorado, from the length of time colonies were in particular size classes and assuming the current distribution of size classes represented an equilibrium. A *P. badius* queen lived 17 years in the laboratory (Hölldobler and

Wilson, 1990). In eight years of direct observations, Porter and Jorgensen (1988) concluded that *P. owyheeii* in Idaho lives 14–30 years, with a mean of 15.

Porter and Jorgensen (1988) assert that recolonization of an old colony site was common for *P. owyheeii*. In contrast, only one of the 108 *P. occidentalis* colonies followed was even suspected of having been recolonized. Recolonization would be recognized by absence of ants one year, and the presence of ants within the mound the next year. Without genetic markers it is difficult to know that an unhealthy colony did not simply recover. Since long-lived colonies should be rich in commensals and subject to disease, reoccupying a nest would seem to be selected against, since suitable areas for nest building do not appear to be limiting. A more common pattern in the *P. occidentalis* population studied here was for the death of a colony to produce a space between territories which, within a few years, was the site of a new colony establishment (Fig. 3A, B). Some areas have been empty for almost 5 years, however (Fig. 3C).

There is no published report of multiple queen colonies in *P. occidentalis* but it does not appear to have been rigorously tested. Observations of inter-nest aggression and multi-colony nuptial flights in *P. occidentalis* (Hölldobler and Wilson, 1990; Keeler, unpubl.) are consistent with single-queen colonies, but the dynamics of these populations are so slow that critical interactions (e.g., successful return to the maternal nest) need only occur once a decade, making them difficult to observe. Nevertheless, it seems more probable that the colony lifespans reported here represent longevities of individual queens of *P. occidentalis*.

One critical question about the population dynamics of long-lived organisms is whether they are at equilibrium under current conditions or are driven by irregularly occurring “good” and “bad” years. This Nebraska harvester ant population 1) appears to lack a synchronized age distribution, suggesting colonies became established in different years, and 2) has had similar, although varied, recruitment and death rates throughout the 15-year period of the study. Assuming 1976–1991 was a typical period, and climatically it was not unusual (United States Department of Commerce, 1976–1991), these observations suggest that assumptions of short-term equilibrium dynamics may be valid for this species.

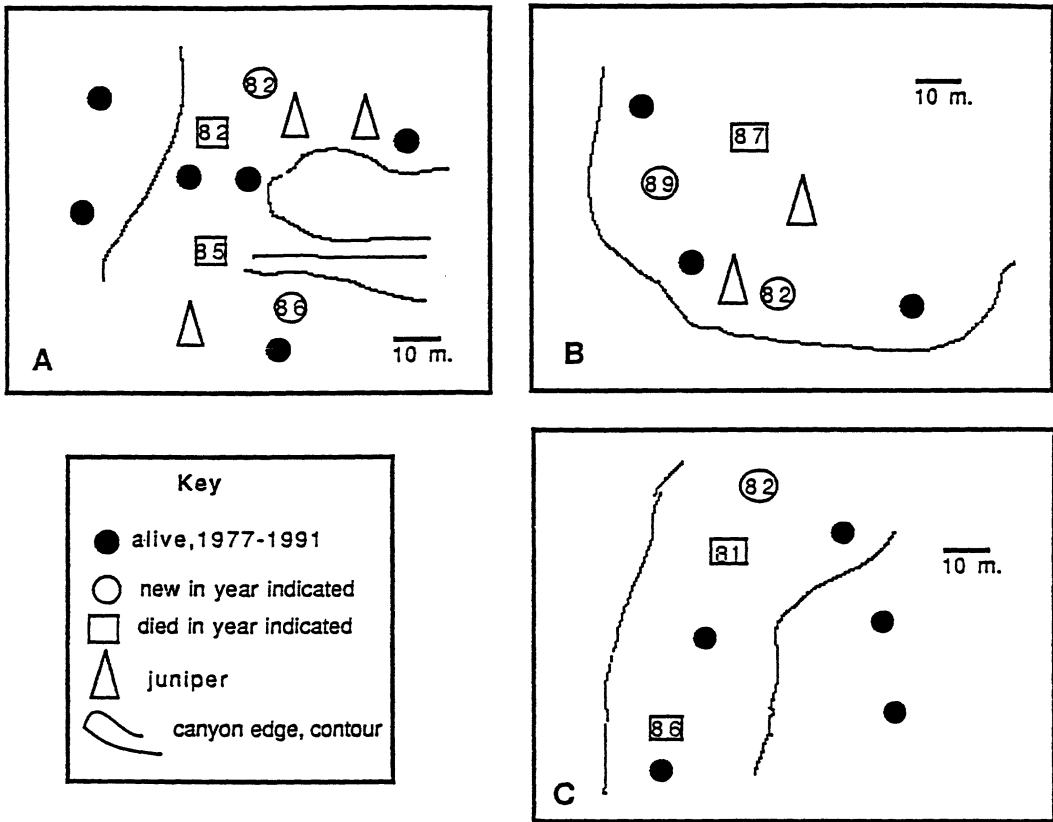


FIG. 3—Colony replacement patterns in *Pogonomyrmex occidentalis*. 3A and 3B represent areas where new colonies appeared in gaps left by colony death. 3C represents an area where a persistent gap occurred between colonies.

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