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LONGITUDINAL STUDY OF *POGONOMYRMEX OCCIDENTALIS* (HYMENOPTERA: FORMICIDAE), WESTERN HARVESTER ANT, COLONY SURVIVAL IN WESTERN NEBRASKA

KATHLEEN H. KEELER

School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588
Correspondent: kkeeler1@unl.edu

ABSTRACT—I observed individual western harvester ant (*Pogonomyrmex occidentalis*) colonies, marked between 1977 and 1994, to live a mean of 15.65 years ($n = 112$). The longest-lived colony lived 42 years.

RESUMEN—Observé que colonias de hormigas cosechadoras occidentales (*Pogonomyrmex occidentalis*), marcadas entre 1977 y 1994, sobrevivieron una media de 15.65 años ($n = 112$). La colonia que vivió más tiempo sobrevivió 42 años.

Western harvester ants, *Pogonomyrmex occidentalis*, are granivores that build conspicuous mounds in grasslands and forest openings from Nebraska and Kansas west to eastern California, and from southern North Dakota to north Texas, New Mexico, and Arizona. Colonies may contain 8,000 workers (Lavigne, 1969) and persist many years (Keeler, 1982, 1993; Coffin and Lauenroth, 1990). This study reports colony survival on the basis of completion of a longitudinal study of *P. occidentalis* colonies marked between 1977 and 1994.

In *The Insect Societies*, Wilson (1971) published a table (21-4) of the longevities of established colonies of social insects, which included only three entries, all of them *Formica* species and, because of queen replacement, potentially immortal. The conspicuous colonies of *P. occidentalis* in the shortgrass prairie of western Nebraska looked easy to mark and recapture to determine colony longevity. Colony longevity is an important part of the dynamics of both the species and its community and informative for interspecific comparisons (e.g., Keller, 1998).

MATERIALS AND METHODS—*Study Site*—The site was an area of approximately 400 × 100 m on a plateau of nearly level ground above Cedar Point Biological Station, Ogallala, Nebraska, site elevation 1,036 m, 41°7'22.7994"N, 101°23'16.8"W. The edges of the site dropped abruptly into deep canyons largely uninhabited by *P. occidentalis*. Vegetation was shortgrass prairie, dominated by *Bouteloua gracilis*, *Carex filifolia*, and *Heterostipa comata* (Kaul et al., 1983; McKenzie, 2005) on Sully–Dix coarse well-drained loess soil (National Resources Conservation Services, 1990). Rainfall averaged 481.5 mm annually ($SD = 108.8$) over 38 years taken at the Lake McConaughy station (3 km distant; missing were years 1985, 1993–1994, 2009, and 2011). At the same station, the 30-year mean temperature (1981–2010) for July was 24.3°C, and for January it was –3°C (United States Department of Commerce,

1977–2020). Cattle had been grazing the site for part of each year for at least a decade when I initiated the study and continued in the same pattern until 2010. The site owners excluded cattle in 2010–2012 and then restored them in a pattern similar to the historic one during 2013–2019 (pers. observ.).

Sampling Design—In late July 1977, I marked every colony in the study area with a metal tag, initially numbers stamped into a square cut from a steel soda can, then cut from an aluminum soda can, and finally, written onto double-layered commercial aluminum tags, secured by a nail in the ground at the east point of the outside edge of the disc. I described colony location initially, mapped it by hand in 1978, and determined it using a global positioning system in 2010.

Each year on about 1 August, I walked the study area, relocating marked colonies and searching intensively for unmarked colonies. Until 1994 I marked all newly discovered colonies to follow every colony within the study area. After 1994 I merely followed attrition. Annually, I recorded observations of colony condition. Initially I measured the largest diameter of the colony's disc (cleared area) and the mound within it. Both disc and mound were circular on open ground, variously distorted ovals on slopes or near obstacles. I discontinued the measurements in 1985. Throughout the study I estimated the condition of disc and mound (excellent, good, fair, poor) and the size class of the disc and mound (large, medium, small, tiny). *Pogonomyrmex occidentalis* colonies clear the area around the nest of both living and dead plant material. Workers create an elevated mound over the nest entrance and cover it with pebbles. Both the level of clearing of the disc and the arrangement of the pebbles on the mound degenerated in poor-condition colonies and, of course, upon the death of the colony. I checked for *P. occidentalis* workers entering and leaving the mound. If I thought the colony had died, I confirmed it the following year. Lavigne (1969) noted that *P. occidentalis* ants are active only at warm temperatures, 29.4–47.3°C at 1,371 m in Wyoming, and my population behaved similarly; I adjusted my observations accordingly.

TABLE 1—Comparison of disc (cleared zone) diameter of established and newly observed *Pogonomyrmex occidentalis* colonies showing increase in diameter with age. Given are mean, standard deviation (in parentheses), number of colonies, and significance (*t* test comparing added colonies to established ones each year). Significance values are <0.001***, 0.001–0.01**, 0.01–0.05*, and >0.05, not significant (ns). Variation in number of colonies is due to attrition and missing data.

Year seen	1978	1979	1980	1981	1982	1983	1984
Established in 1977	112.20 (29.82) 48	130.30 (36.18) 52	120.77 (29.05) 52	120.87 (29.04) 52	123.92 (34.78) 51	127.67 (34.75) 51	116.0 (31.24) 44
Marked 1978	97.1 (42.0) 7 ns	125.9 (57.2) 8 ns	93.30 (32.66) 9 ns	102.78 (38.81) 9 ns	107.50 (21.36) 8 ns	110.63 (29.20) 8 ns	105.0 (29.03) 7 ns
Marked 1979		43.3 (12.5) 3***	70.0 (21.6) 3 ns	80.0 (18.71) 4*	78.75 (18.41) 3***	100.50 (20.69) 4 ns	95.0 (25.0) 4 ns
Marked 1980			Not recorded	56.67 (23.21) 3 ns	71.67 (6.24) 3***	76.67 (32.34) 3 ns	85.0 (27.81) 2 ns
Marked 1981				45.0 (22.73) 3*	113.33 (33.03) 3 ns	148.33 (70.04) 3 ns	127.50 (52.50) 2 ns
Marked 1982					56.67 (23.57) 9***	62.50 (10.0) 8***	58.0 (14.70) 8***
Marked 1983						65.0 (35.0) 2 ns	40.0 (20.0) 2 ns
Marked 1984							None added

Statistical Methods—I compared mean sizes and ages for groups of different cohorts using Student's *t* test. To evaluate the size of colonies at death, I compared the size of the colonies that died to the range of two standard deviations around the mean of the surviving population.

Missing Data—Throughout the data there are missing values, so that *n* varies. Some colonies were missed during a survey; other measurements or conditions were either not recorded or the records have been lost. I collected no data in 1994 or in 1997–2001. In the analysis, I assumed the colonies found dead when observations resumed died in 1994 and 1997, respectively, under- rather than overestimating longevity.

RESULTS—Colony Establishment—*Pogonomyrmex occidentalis* mating flights are in late July or August (Mull and Crist, 1993; Cole and Wiernasz, 2000); I watched for them after a heavy rain starting in the last week of July. Mated queens initiated a colony shortly thereafter, but there was no disc (cleared zone) or mound until the following year. That year, workers began clearing plant material to create the disc and piling dirt and pebbles (2–3 mm in diameter) over the nest to build the distinctive mound (Cole and Wiernasz, 2002). I first noted the colony when there was at least a small disc or stone-covered mound. Consequently, I detected colonies in the first summer after the queen established the colony. Forty-one of 49 colonies added after 1978 (83.67%) were small, new colonies on the basis of my comments in the field notes, and 14 of those lacked a defined disc or mound; I recorded eight

colonies as having a medium-sized disc or mound the first time I observed them. Rather than inflate the numbers by adding the unknown first year or years, I report years of observation, which are at minimum one less than the actual colony age.

Colony Size Dynamics—In 1977–1984, I measured disc and mound diameters. Disc diameters averaged 112.20 cm (Table 1) and mound diameters averaged 52.65 cm (*SD* = 14.4, *n* = 54, data not shown) in 1977. Subsequent years showed moderate fluctuation in mean diameters (Table 1), which was presumably a function of climate. The discs and mounds of newly observed colonies were noticeably smaller than the established population, and their mean size increased annually (Table 1; mound data not shown), in some cases significantly. My measurements do not address whether increase in size continued throughout colony life. Topography determined the size of the disc and mound of some colonies, limiting size or distorting the shape. Most mature colonies were similar in disc and mound size and remained that size for years.

Colonies rarely showed signs of senescence until the year before they died. In the measurements from 1978 to 1984, the 12 colonies that died during that period were not significantly different in size from the colonies that survived, comparing disc and mound diameter to the mean plus or minus two standard deviations (data not shown), except one that had a particularly large mound diameter the year before it died. The dead colonies were rather evenly split in size; for disc diameter, seven were

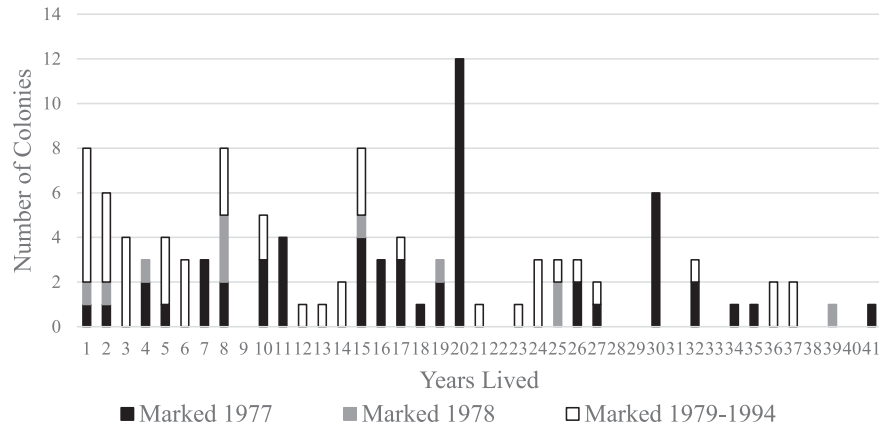


FIG. 1.—Distribution of *Pogonomyrmex occidentalis* life spans observed in western Nebraska, 1977–2019. For those marked in 1977 of unknown age, mean years lived was 18.13; colonies marked in 1978 included some missed in 1977 and some new colonies, mean years lived 15.3; for those marked in 1979–1994, mainly 1-year-old colonies, mean life span was 15.30 years. See text for details.

larger and four smaller than the mean of surviving colonies, and for mound diameter, four were larger, two right at the mean, and three smaller. For 45 colonies, I had 3 years of condition records before they died. In only two cases (4.26%) did I observe a colony in poorer and poorer condition for 2 years before it died. Twenty-two colonies (46.81%) were in excellent condition one year and dead the next year. Twenty-three colonies (48.93%) were in good to excellent condition, then a year of fair or poor condition, after which they died. I recorded colonies as in poor condition 26 times. Of these, only 14 (53.85%) died the next year; the rest lived on for at least 2 years. Colony deaths were difficult to predict. Most colonies quickly reached adult size and remained there relatively unchanged for years before quickly declining to death.

Of 12 deaths I could evaluate spatially, 4 (25%) were replaced; a new colony appeared within a year in a position that would have made it a nearest neighbor of the dead colony. I learned to look for new colonies most carefully in the region around a dead colony and in areas equidistant from existing colonies, not close to healthy colonies. In four other cases, colonies that died I subsequently recorded as alive; that is, after a year or two, a live colony occupied the tagged nest site. I considered these recolonized and treated them as separate colonies in the data.

Colony Longevity—Colonies lived a mean of 15.65 years ($SD = 10.57$, $n = 112$; Fig. 1). I observed the colonies marked in 1977, of unknown age, to live a mean of 18.13 additional years ($SD = 9.16$, $n = 56$). Ten colonies discovered and marked in 1978 lived an average of 15.3 additional years ($SD = 11.08$). Five of these colonies were small, like new colonies, but three were medium sized in comparison with the size of the colonies marked in 1977 (Table 1) and two were above the mean size, so the 1978 group included both new colonies and ones I missed in 1977. Between 1979 and 1994 newly observed colonies were generally in their first year. Of them, I noted 8 of 49

(16.3%) as “medium” or “not small” in my field notes, not “tiny,” “small,” or “new,” which suggests that I discovered them after 2 years rather than 1 year. I observed these colonies to live a mean of 12.83 additional years ($SD = 11.24$, $n = 46$). Comparing the longevity of the group of colonies established in 1977 with the two groups of colonies observed later, the mean life span of the colonies from 1978 was not significantly different (t test, $P = 0.483$, 1 df), whereas the additions from 1979 to 1994 had significantly shorter life spans (t test, $P = 0.013$, 1 df).

In 2018, no colonies marked before 1980 were alive. In Fig. 2, those marked in 1977 form a natural survivorship curve, whereas for comparison, colonies added later were plotted as if I first observed them in 1977. In the curve for 1977 the effect of not visiting the site in 1997–2001 and assigning all deaths in that period to 1997 is visible as a substantial drop. There is an accumulation of deaths in 1997 in the added colonies but it is not visible because of standardization of their longevities.

The longest-lived colony, marked in 1977, died after 41 years of observation (Fig. 1). That colony was relatively small (disc 70 cm, mound 25 cm compared with means, including it, of 112.2 and 52.65 cm that year for disc and mound, respectively), so probably quite young. I am calling its age at death to be 42 years. The longest-lived colony of known age lived from 1978 to 2017, 39 years. It was even smaller, disc 35 cm, mound 20 cm when first seen in 1978, so likely founded the previous year, making it 40 years old at death.

DISCUSSION—I began this study to directly determine how long *P. occidentalis* colonies live. These are the first direct observations of colony survivorship in this species, with a mean life span of 16–19 years (including the unobserved establishment year). The longest-lived colonies lived 40 and 42 years.

In previous articles, I estimated colony survivorship for

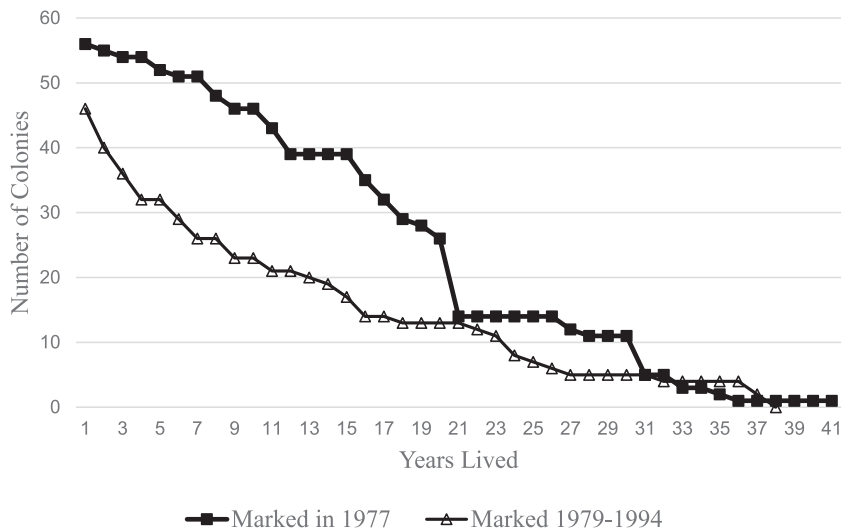


FIG. 2—Observed survival of *Pogonomyrmex occidentalis* colonies in western Nebraska. For colonies marked in 1977, observed years lived can be read as 1 = 1978, 2 = 1979, etc. For those marked in 1979–1994, the survivorship curve was created by setting the first observation of all colonies to year 0. See text for details.

this population three times. After 5 years, assuming equilibrium, estimates from death rates projected that an established colony lived 43 years, and from the rate of recruitment, 22 years (Keeler, 1982). After 10 years, the expectation from death rates was that established colonies lived 35.7 or 50.9 years, and from recruitment rates 17.8 years, although the population grew between 1977 and 1987, inflating mortality-based estimates (Keeler, 1988). After 15 years, from the survivorship curve I projected that the last of the colonies observed in 1977 would be gone after 43 years (2020). Assuming a stable age distribution, death rates projected a mean life span of 21.3 years and the recruitment rates 12.7 years. The population was stable between 1981 and 1991. These estimates reflect the wide range of life spans that creates the mean *P. occidentalis* life span.

Other researchers' observations of *P. occidentalis* survivorship were in the same range. Coffin and Lauenroth (1990) estimated colony life spans of 29–58 years from the age distribution changes in 2 years in Colorado. In western Colorado, after high initial mortality, Wiernasz and Cole (1995) projected that colonies would live an additional 30 years. Porter and Jorgensen (1988) followed colonies of *P. owylei* (also called *P. salinus*), a close congener of *P. occidentalis*, for 10 years in Idaho and estimated colony life spans of 14–30 years, with a mean of about 17 years.

Colony survival is known from several ant species. In *P. badius* in Florida, Tschinkel (2017) found a 4-year life span for small colonies and 17 years for medium-sized colonies and estimated the life span of large colonies to be >30 years. In *P. barbatus* in New Mexico, Gordon (1991) estimated that colonies live 15–20 years. Colonies with multiple queens and queen replacement are potentially immortal, as in *Formica pratensis*, *F. rufa*, and

F. ulkei, with record ages of 56, 60, and 25 years, respectively (Wilson, 1971). Czechowski and Vespäläinen (2009) followed an artificially introduced colony of *F. polyctena* on a Baltic Island for 22 years. On the other extreme, colonies of *Harpegnathos saltator* lived 0.43–0.78 years in the field (Liebig and Poethke, 2004). Keller (1998) summarized studies, most with queens kept in a laboratory, of ant longevity. In those data, *Pogonomyrmex* species are among the longest lived.

This study found that older colonies lived longer than new colonies. This is a consistent observation of *Pogonomyrmex* populations (for *P. occidentalis*, Wiernasz and Cole, 1995; *P. barbatus*, Gordon, 1991; and *P. badius*, Tschinkel, 2017). Since old colonies must have been young colonies, this reflects the winnowing of weaker colonies over time, and should apply broadly to ant colony survival.

The marked colonies declined gradually to extinction; there is no sudden drop in old age typical of a type III survivorship curve (Fig. 2). It seems logical that there is a biological limit to the queen's life span, and that should ultimately limit single-queen colonies. I know of no reports of the longevity of *P. occidentalis* queens in a laboratory colony that might suggest that limit. For now, we have only the 11 colonies I observed to live 30–42 years (Fig. 1), which suggests that the limit is slightly over 40 years.

The survivorships reported here depend upon a series of assumptions: that the colonies were observed when new, that colonies do not migrate, and that colonies do not replace each other in the same nest. Projecting to queen survivorship requires the assumption that these are single-queen colonies without replacement.

I hoped to discover colonies the summer after the mated queen began the colony. I have no direct test of that. The fact that additions in 1979–1994 were smaller

than the initially marked population (Table 1) and that 83.67% of the new colonies were noted as small is consistent with that. The 16.33% of colonies added after 1978 that were noted in my field notes as medium size or too large to be new suggest the rate at which I missed tiny colonies. In sum, all colonies were 1 year old when observed and some were 2 years old.

I never observed a case of colony migration. Lavigne (1966), applying insecticide and following the site thereafter, saw 4 of 220 colonies migrate. Wiernasz and Cole (2003), studying undisturbed populations in western Colorado, wrote that colony movement was less than 2.5% per year. According to Lavigne (1969), migrating colonies leave a large, obvious path. I never saw anything like that. However, returning only once a year, it is impossible to exclude that possibility.

I assumed initially that new queens did not establish their colony within the mound of a dead colony. Established colonies are hostile to each other and attack by workers is an important source of mortality for new queens (Wiernasz and Cole, 1995; Cole and Wiernasz, 2002). Excavations of nests showed large numbers of parasites and commensals (Lavigne, 1969) and disease avoidance is a major factor in social insect behavior (Fefferman et al., 2007; Zelagin et al., 2018). Balanced against these factors is the possibility that good nest sites are in short supply (Wiernasz and Cole, 1995). Of the 112 colonies I followed, I saw four (3.57%) cases of colonization of a dead nest by a new queen, and in the data, I treated those colonies, although at the same site, as separate. Between 1977 and 1994, the period I followed all colonies, 4 (33%) of 12 colonies that died had a new colony establish in the dead colony's territory within a year, close enough to be a nearest neighbor but not inside the dead colony's disc. I considered these cases of replacement. Both recolonization and replacement, if undetected, would change (reduce) my longevity estimates, but they appear to occur infrequently.

The assumption that each colony has a single queen and that when she dies the colony dies does not affect colony survivorship patterns but is important for understanding *P. occidentalis* biology. Colonies of *P. occidentalis* are founded by a single, multiply mated queen (Cole and Wiernasz, 2000, 2002; Wiernasz et al., 2004). Excavations of *P. occidentalis* nests have routinely found only one queen (Lavigne, 1969). So far there is no evidence of multiple queens in a colony at any stage (Cole and Wiernasz, 2000). Thus, this study presumably followed survival of individual ant queens who lived a mean of 16–19 years, with the longest-lived living 42 years. Despite similar ages having been projected in other *Pogonomyrmex* species, it remains an impressive life span.

My site in Ogallala, Nebraska, is close to the eastern limit of the range of *P. occidentalis*. It is lower in elevation and wetter than other sites studied. Discs and mounds seem relatively small compared with Colorado and

Wyoming populations; in Colorado the discs of mature colonies averaged 1.4 m² (Coffin and Lauenroth, 1990), whereas my largest mean, when converted to area, was 1.33 m² (Table 1). The means for mound diameters given by Lavigne (1966, 1969, calculated from Lavigne 1969:Tables 1 and 2, as 54.61 and 63.67 cm, respectively) are consistent with mine, but discs ranged up 500 cm in diameter and mine averaged at most 130 cm (Table 1). Because Wiernasz and Cole converted mound (nest cone) sizes to the log of length × width × height, and I did not record height, I cannot compare with their data. Mound differences could be due to a variety of factors but disc differences probably point to western Nebraska as a more productive habitat.

The light grazing of my site appeared to facilitate the ant colonies, favoring the shortgrass prairie species and reducing the impact of shading by taller plants such as *Heterostipa comata*. Colonies became active later in the morning and were harder to find during the three summers without grazing because of the height of the vegetation (pers. observ.). Cattle were an additional source of disturbance by occasionally trampling my tags beyond recognition or stepping directly onto the colony mound, collapsing it, just before I arrived to record condition. Lavigne (1966) worked on private land that was almost certainly grazed but does not mention land use for his excavations (Lavigne, 1969). The site of Coffin and Lauenroth (1990) was grazed, in some areas heavily. Wiernasz and Cole (1995) imply that their Bureau of Land Management site was ungrazed. Grazing, both as a form of disturbance and for its impact on availability of seeds, is certainly an important variable for harvester ant colony dynamics.

Pogonomyrmex occidentalis colonies are conspicuous features of grasslands in much of the American West. Not only do they appear to be long lasting, they are. This is the first longitudinal demographic study of *P. occidentalis*, possibly of any long-lived ant, directly observing colony survivorship. Colonies were observed to live an average of 15.65 years, with colonies once established living slightly longer. This would be the parameter, compared with instantaneous survivorship estimates, were it not for the fact that the climate has changed (warmed) over the course of this study. It is not clear what estimates of longevity of a decade—4 decades for the longest-lived colonies—mean in a rapidly changing climate.

Good data on the survival of ant colonies, which collectively are big predators, scavengers, and in the case of harvester ants, granivores, are important to understanding the dynamics and structure of ecosystems. *Pogonomyrmex occidentalis* is a consumer that forages outward from the same point for decades. Its long colony life also has implications for adaptation to climate change, especially in light of the complexities of mating and nest establishment for this ant (e.g., Cole and Wiernasz, 2002).

Even after projecting survivorship at 5, 10, and 15 years (Keeler, 1982, 1988, 1993), I did not grasp what was involved in following a population for 42 years. I am grateful to Cedar Point Biological Station management, past and present, for logistical support. Before it was purchased by Cedar Point Biological Station, the Gainsforth family kindly let me establish and maintain my study on their property. I thank the students who helped me locate colonies over the years. I especially want to express my appreciation to J. Garbish for assistance with data collection in the 2010s.

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