

PRAIRIE ANT COLONY LONGEVITY AND MOUND GROWTH

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INTRODUCTION

Of the social Hymenoptera (ants, some bees, and some wasps), colonies of ants appear to live longest. However, little information bearing on ant colony longevity exists (Wilson, 1971; Tschinkel, 1988), and much of it is anecdotal. Darwin (1859), for example, commented that some ant colonies must live as long as a human generation, and Forel (1928), fascinated by a colony of *Formica pratensis* in his childhood, found the nest still active 56 years later. Donisthorpe (1915) knew of a *rufa* nest in Weybridge, England, that was active for at least 20 years.

More recently, long-term monitoring of mound growth has been conducted in an attempt to understand colony population dynamics (Andrews, 1925; Dreyer and Park, 1932; Dreyer, 1942; Scherba, 1958; Talbot, 1961). Dreyer (1942) projected a 25- to 30-year maximum colony lifetime for *Formica ulkei* Emery, based on average changes in mound size for a population of colonies. Andrews (1925) took mound measurements for 19 years on a single nest of *Formica exsectoides* Forel, showing a clear exponential growth in mound size in the first half of the colony's life. Recently Tschinkel (1988) found that colony growth in *Solenopsis invicta* Buren fits a logistic curve, supporting the hypothesis that the growth of social insect colonies is regulated by density-dependent negative feedback mechanisms (Wilson, 1971; Oster and Wilson, 1978; Levings and Traunielo, 1981; Hölldobler, 1986; Rissing, 1987; Tschinkel, 1988).

Individual ant-mounds of the prairie ant, *Formica montana* Emery, discovered in a prairie remnant in southwestern Wisconsin, were mapped in 1956. Here we report on the survivorship of 69 nests during the next 33 years. We also present 31 years (1957–1987) of data on growth patterns of eight of the original mounds that were

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Manuscript received by the editor August 6, 1989.

still active in 1988. This represents the most extensive longitudinal study on a population of social insect colonies to date.

FORMICA MONTANA

F. montana is a mound-building member of the *fusca* group that prefers sunny places and damp soil (Francoeur, 1973). Insolation of the relatively bare mound helps to regulate temperatures inside to levels that are optimal for brood development (Andrews, 1927; Scherba, 1958, 1961; Wilson, 1971; Bruskewitz, 1981). Gregg (1948) regarded the prairie ant, *F. montana*, a subdominant species, if not a true ecological dominant. *F. montana* builds mounds of excavated soil that may occupy up to 1.7% of the surface area of a prairie, and are considered to be one of the most important biotic forces in the prairie environment (Baxter and Hole, 1967; Fig. 1). Homopteran honeydew, a major dietary constituent for *F. montana*, is supplied by a complex of prairie plants on which the homopterans reside throughout the foraging season (Henderson, in preparation).

STUDY SITE

Ipswich Prairie is a 1500 m by 10 m prairie remnant located along a railroad right-of-way on the Grant-LaFayette County line in southwestern Wisconsin. Over 120 native prairie plant species are located at Ipswich Prairie, and of Curtis' (1955) 50 prairie plant indicator species, 31 are present (Wagner, 1960). The Wisconsin Scientific Areas Preservation Council (Natural Areas now) initiated acquisition of Ipswich Prairie about 1979 and now has it listed as one of over 200 such areas.

METHODS

In 1956, four 150 m × 1 m transects along the 1500 m length of Ipswich Prairie were established by one of us (ROW) and all nests of *F. montana* located within their boundaries were mapped. The presence of ants entering or exiting nest holes and/or the condition of the nest (e.g., whether the nest showed signs of recent excavation) were used as indicators of nest activity. Abandoned nests lacked recently excavated entrances and other signs of ant activity.

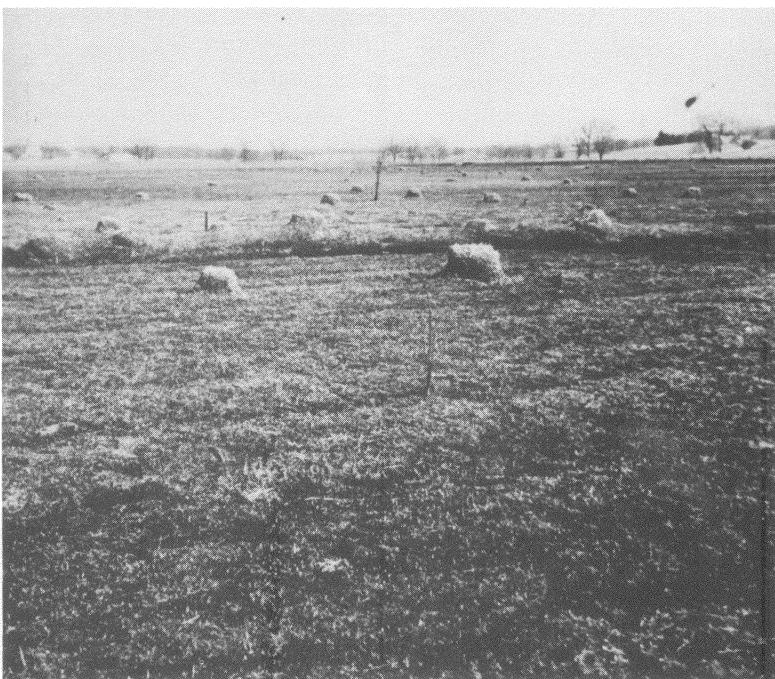


Fig. 1. *Formica montana* mounds in Green Prairie (University of Wisconsin Arboretum, Madison, WI), after a prairie fire. Photograph taken in 1940s.

As a non-destructive estimator of colony size, mound measurements were taken in mid-summer or early fall every year between 1957 and 1962, and intermittently thereafter through 1987. The volume of each mound was estimated by using its length, width and height to compute the volume of a cylinder.

To establish the correlation between mound volume and colony size in *F. montana*, forty ant colonies were dug in 1957 and 1958 (outside of the four transects) and the ants counted. Colonies having mounds of rather uniform size (15 cm \times 15 cm \times 13 cm, length, width and height) were selected, and the dry weight and volume of soil in each mound was determined. The number of workers inhabiting a colony positively correlated with mound volume at the 1% level (J. T. Medler, unpublished data). Mound size for other ant

species is also considered a good approximation of colony population size (Andrews, 1925; Weber, 1935; Scherba, 1958; Talbot, 1961; Wilson, 1971; Tschinkel, 1988; but see Porter and Jorgensen, 1988).

Multiple regression analyses (via Minitab) were used to evaluate the pattern of mound volume changes for the eight longest-lived nests. We used indicator variables ($X_2 = 1$ if a mound had not yet reached maximum volume, $X_2 = 0$ for each subsequent year after reaching maximum volume) to determine if the data points for each nest best fit a line that showed 1) a significant growth phase and decline phase, 2) a growth phase with no subsequent decline, or 3) no significant change in volume throughout the 31-year period.

Regression equation: $y = B_0 + B_1X_1 + B_2X_2 + B_3(X_1X_2)$, where Y = mound volume, B_0 , B_1 , B_2 , B_3 , = constants, X_1 = year, X_2 = indicator variable; Minitab automatically eliminated the (X_1X_2) combination if it was highly correlated with the other X variables.

RESULTS

From observations of nests outside of the transects it was apparent that prairie ants initiate two kinds of new colonies, permanent and temporary, or food-source mounds. Food-source mounds were often located about the stems of prairie plants, found most commonly associated with the prairie rose, *Rosa arkansana* and the cone flower, *Ratibida pinnata*. Excavations of these nests showed that about two dozen workers and a species of aphid they were tending were in residence. Food-source mounds were most often initiated in June, but did not grow in size and often disappeared by late season.

Of 58 *F. montana* colonies in the four 150 m \times 1 m transects in 1956, survivorship was 40 (69%) after 10 years, 28 (48%) after 23 years, and 8 (14%) after 33 years (Fig. 2). Three of the 18 nests that disappeared between 1956 and 1966 lost their identities through merging with closely adjacent colonies, indicating that polydomy occurs in this species. Most of the 58 mounds were already of moderate size (mean = 38 cm \times 39 cm \times 25 cm) in 1957 and had probably been founded several years before 1956. Between 1956 and 1959 mounds ranged in size from the newly initiated (measuring less than 5 cm \times 5 cm \times 5 cm) to some of the largest (1 m \times 1 m \times 23 cm).

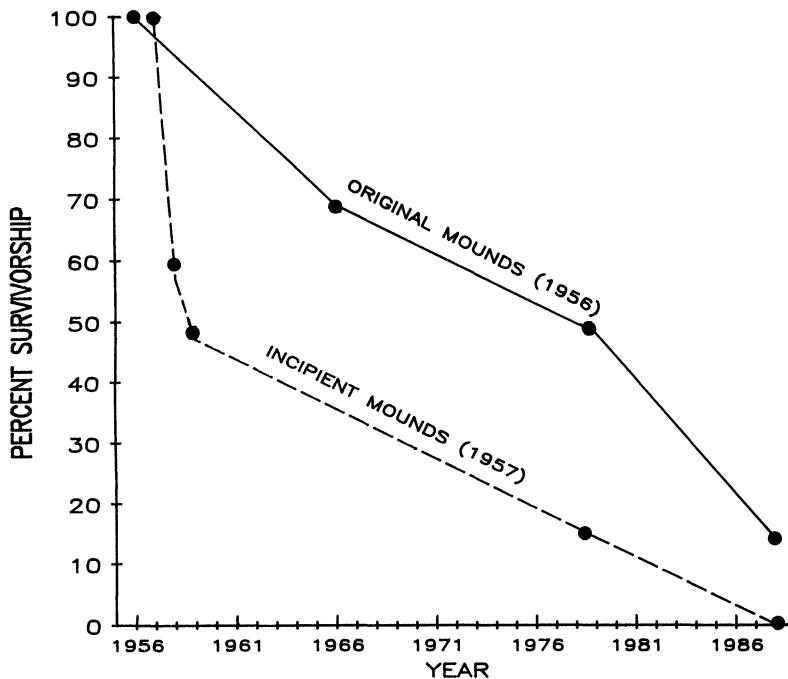


Fig. 2. Comparison of survivorship curves of established *F. montana* mounds with incipient mounds. Lines are interpolated from data points. See text for details.

In 1957, 21 new mounds were recorded. Of these, 12 (57%) were active in 1958, 10 (47%) in 1959, three (14%) in 1979, and none were active in 1988 (Fig. 2). In contrast, of 40 food-source mounds recorded in June 1959, 38 (95%) disappeared by the end of August 1959.

The relatively large volumes of six of the eight mounds in 1957 (all except nests *c* and *g*) indicated that they were initiated some years before recordings started (Fig. 3; Appendix I). Nest mound *h* grew very little over the 31-year census (Fig. 3h; Table I). Volumes of nest mounds *a*, *b*, *c*, and *f* increased rapidly and then declined, the decline starting between 1973 and 1979. Part of colony decline was coincident with the beginning of a reduced burning schedule for the prairie. Following the last regular burning of Ipswich Prairie in 1964 woody species (especially sumac and black cherry) began to invade

the prairie, and by 1979 these had completely displaced native prairie plants in some locations. In 1979, ROW noted that in one invaded area 76% of the colonies died out, whereas 39% die-out was recorded in a relatively little-affected portion.

The dramatic mound volume increase by nest *a* in 1973 was due to its merger with a nearby mound. The next measurement year however, mound volume dropped just as dramatically. Nest mounds *d* and *e* showed a positive growth at first, then leveled off. Nest *g* grew in mound volume throughout the observation period. 92% of the variance in nest *g*'s volume can be explained by the year.

Nest mounds showing a significant change in volume were collectively analyzed in two groups according to year of colony founding. Since nest mounds *a* and *h* had essentially no sustained growth phase (Table I; Fig. 3) they were omitted from the analysis. Nest mounds *c* and *g*, whose small initial mound volumes in 1957 indicated they were probably incipient colonies in 1956, were analyzed together (group I). Nest mounds *b*, *d*, *e* and *f* had larger mound volumes in 1957, suggesting they were all initiated at some earlier date than nests *c* and *g*. We analyzed these nest mounds as group II.

For each group, mound volume was regressed on year to determine if the pattern growth was logistic (an S-shaped curve), or more like a truncated S curve (such that the bottom of the S was cut off). Data were transformed using the guidelines given by Chatterjee and Price (1977: 29):

Logistic Equation Transformation: $Y = \ln(Y/1-Y)$;

Truncated S Transformation: $X = \ln(X)$;

where \ln = natural logs, Y = volume, X = year.

The truncated S transformation gave the better fit for both groups (Table I). However, only data for group I are valid for evaluating mound growth for newly initiated colonies, since start-up year for colonies of group II was not known. Nests of group II may have had a phase of exponential growth prior to 1956.

DISCUSSION

Interpreting the growth pattern of *F. montana* colonies requires that we consider the constraints that help shape it. To do this we must know some of the biology of *F. montana*. *F. montana* is multicolonial: workers distinguish nestmates from alien conspecifics and they aggressively defend food-territories from nearby colonies

Table 1. Best fit regression line for mound a-h growth patterns. Nest groups I and II show fit of data to a logistic growth model and a truncated S growth model. Y = mound volume, X = year, I = indicator variable, ln = natural logs, P = significance level, R²(%) = Percent of variance in mound volume explained by the X-axis variables.

| Nest | Regression equation | R ² (%) | P |
|----------|--|---------------------|----------|
| a | y = 0.103 - 0.0001X - 0.06I + 0.005(XI) | 45 | >.10 |
| b | y = 0.27 - 0.005X - 0.24I + 0.01(XI) | 86 | <.001 |
| c | y = 0.09 - 0.0001X - 0.105I + 0.006(XI) | 96 | <.001 |
| d | y = 0.02 + 0.003X + 0.013I | 80 | <.001 |
| e | y = -0.007 + 0.003X + 0.038I | 84 | >.05<.10 |
| f | y = 0.08 + 0.00002X - 0.046I + 0.005(XI) | 68 | <.05 |
| g | y = 0.00065 + 0.0036X | 92 | <.001 |
| h | y = 0.06 + 0.0003X - 0.01I + 0.002(XI) | 51 | >.10 |
| Group I | {ln(X)} | y = -0.045 + 0.039X | >.05<.10 |
| | {ln(y/1-y)} | y = -5.88 + 0.15X | >.10 |
| Group II | {ln(X)} | y = 0.012 + 0.029X | >.05<.10 |
| | {ln(y/1-y)} | y = -3.09 + 0.036X | >.10 |

of conspecifics (Henderson, in preparation). Nevertheless, several other attributes of *F. montana* are normally associated with a uniclonal species (sensu Wilson, 1971; Hölldobler and Wilson, 1977; but see Rissing and Pollock, 1988): they occur in patchily distributed habitats, monopolize the habitat by excluding other ant species, build large, aggregated populations of colonies through budding, and are polygynous (Henderson, in preparation).

Ant colony growth most often appears governed by the food limitations of the habitat, a density-dependent controlling mechanism (Brian, 1953, 1957; Wilson, 1971; Rissing, 1978; Tschinkel, 1988). This may be going on in *F. montana* as well. That is, the behavior of territoriality between *F. montana* colonies limits a colony's access to food and thus governs the density-dependent negative feedback that regulates colony growth. This provides a means by which a single species may populate a habitat and not over-exploit its food supply.

While the carrying capacity of the prairie habitat for *F. montana* may be set by food resources accessible to the territorial colonies, density-independent factors affecting habitat quality also appear to influence colony size and density in this population. The correlation of the decline of *F. montana* colonies with the cessation of annual

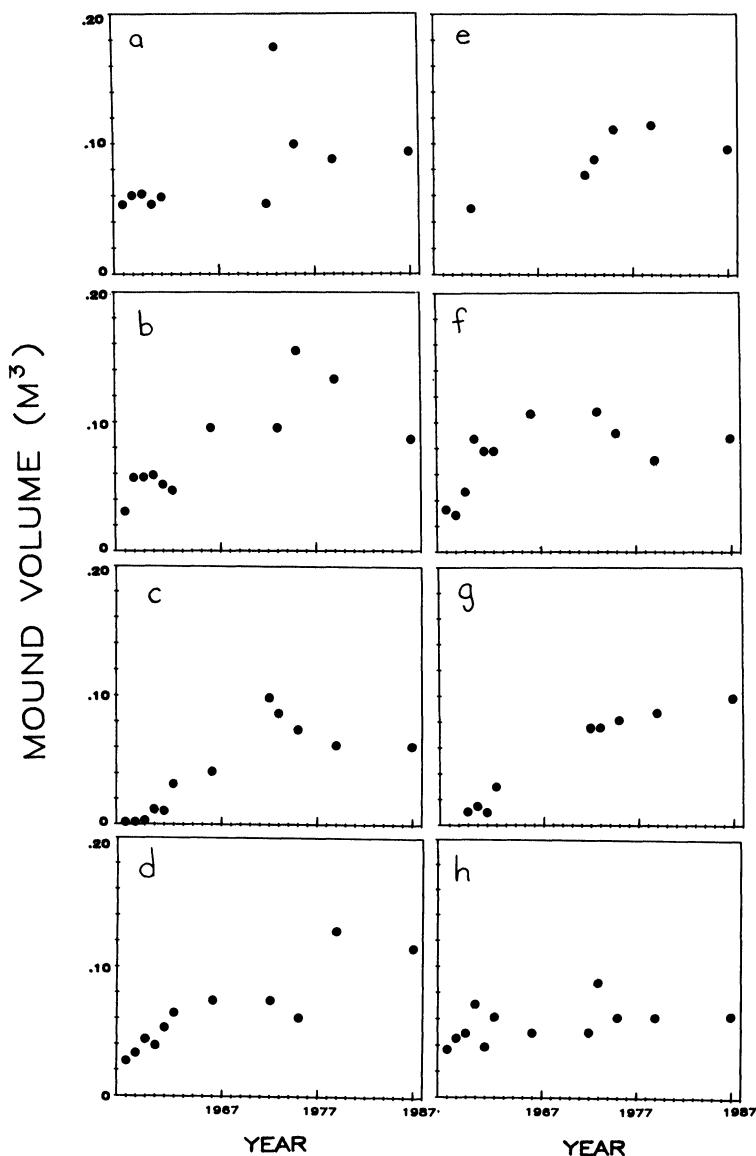


Fig. 3. Mound volume (m^3) as a function of year for eight *Formica montana* colonies censused over a 31-year period.

burning and the subsequent invasion of woody plant species at Ipswich Prairie suggests that the one was the effect of the other. The increasing shade imposed by the invading species could well have reduced the quality of the habitat, either directly by its negative effects on nest mound temperature, or indirectly via its influence on the growth of the prairie plant species harboring the homopterans whose honeydew is an important food source for this ant.

SUMMARY

Nest mound growth of a population of *F. montana* colonies was systematically measured over a 31-year period. Some nests were still active 33 years later and one nest was still in the growth phase in 1987. Regression analysis revealed that mounds grew quickly in the first years of life, suggesting that colony initiation through budding provides an efficient means of rapid growth at the point when colony survival is most in jeopardy. It is hypothesized that colony growth is mediated by intraspecific territoriality which limits a colony's access to food. Decline of the colony is correlated with density-independent factors.

ACKNOWLEDGMENTS

We are especially grateful to J. T. Medler for his expert contribution and interest in the earlier phases of this study. Joan M. Herbers, Sean O'Donnell, Edward O. Wilson and two anonymous reviewers are thanked for critically reading earlier drafts of this paper. The College of Agriculture and Life Sciences (CALS) Statistical Consulting Service provided us with advice on statistical procedures. This work was supported by: the Research Committee of the Graduate School of the University of Wisconsin and funds from the National Science Foundation (G-13320) to ROW and J. T. Medler (principal investigator), Federal Hatch Support Project No. 2588 to RLJ, grants from the Friends of the Arboretum, University of Wisconsin, to GH, and a grant from the Roger Tory Peterson Institute of Natural History to GH. The writers express their appreciation to W. L. Brown Jr. and A. Francouer for helpful determination of the ant species.

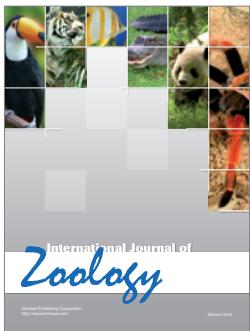
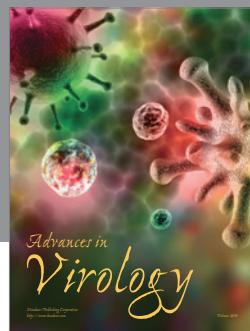
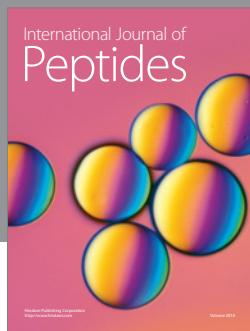
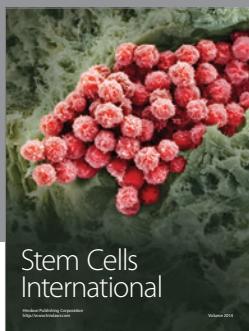
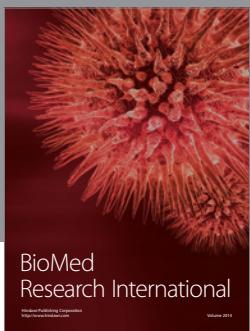
Appendix I. Volume measurement (m^3) of eight *Formica montana* mounds over a 31-year census.

| nest | Year | | | | | | |
|------|-------|-------|-------|-------|-------|-------|-------|
| | 1957 | 1958 | 1959 | 1960 | 1961 | 1962 | 1966 |
| a | 0.054 | 0.061 | 0.062 | 0.054 | 0.059 | 0.067 | — |
| b | 0.031 | 0.058 | 0.058 | 0.059 | 0.052 | 0.047 | 0.096 |
| c | .0001 | .0009 | 0.003 | 0.012 | 0.011 | 0.032 | 0.042 |
| d | 0.028 | 0.033 | 0.044 | 0.039 | 0.053 | 0.064 | 0.074 |
| e | — | — | — | 0.051 | — | — | 0.076 |
| f | 0.034 | 0.029 | 0.047 | 0.088 | 0.078 | 0.078 | 0.107 |
| g | — | — | 0.011 | 0.015 | 0.010 | 0.030 | — |
| h | 0.037 | 0.046 | 0.049 | 0.071 | 0.039 | 0.061 | 0.050 |

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