

Lifespan, age, size-specific mortality and dispersion of colonies of the Florida harvester ant, *Pogonomyrmex badius*

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Abstract Colonies of social insects such as ants have species-typical life history attributes that include mature colony size, mortality rate, size at first reproduction, lifespan, reproductive investment and many others. A population of over 400 colonies of the Florida harvester ant, *Pogonomyrmex badius*, was repeatedly resurveyed over 6 years, producing a record of deaths, births, colony sizes and relocations. From these data the life span, growth rate and colony-size-specific mortality rates were determined. Colonies averaged about 2500 workers and ranged from less than 500 up to 10,000. The annual mortality rate of colonies decreased from about 25% for the smallest colonies, to about 6% for mid-sized colonies. Under steady-state assumptions, these extrapolate to lifespans of about 4 and 17 year, respectively. Over 90% of the largest colonies were still alive after 6 years, so that their lifespan could not be reliably determined, but probably exceeded 30 years or more. As new colonies grew, their probability of surviving increased, but many colonies stabilized at less than maximum size, thus remaining subject to the mortality rates characteristic of their size, not age. At the level of the whole population, colonies were significantly clumped, probably as the result of habitat heterogeneity. Large colonies were associated with more open areas. Colonies with more and/or larger neighbors had moderately higher mortality rates. This rate increased as size asymmetry increased. The need

for demographic data on ant species with a range of mature colony sizes is discussed.

Keywords Lifespan · Mortality rate · Longevity · Formicidae · Spatial distribution · Colony size · Population biology · Demography

Introduction

Among many social insects, including ants, the colony is the analog of the unitary organism, in the sense that the entire colony is functionally organized to produce more colonies, and in most species, the workers that compose the colony generally have no reproductive future save by helping the colony reproduce. This reality is the basis of the superorganism concept (Hölldobler and Wilson 2009). It follows then that the colony (or superorganism) possesses life history traits parallel to those of unitary organisms, but at a higher level of organization. Thus social insect colonies of different species differ in size, reproductive output, growth rate and lifespan, among many attributes. Colony size is probably a more important variable for understanding many life history traits because colony age and size are often not strongly correlated (Tschinkel 2006). The need to describe and quantify such attributes (called sociometry, Tschinkel 1991, 1993, 1999; 2011, 2014a) underpins advances in understanding the life history and evolution of social insects.

Although the life spans of species of unitary organisms are regularly recorded, with a few exceptions, those of social insect colonies (superorganisms) remain largely unknown. The exceptions, perhaps not surprisingly, are mostly species with large, conspicuous colonies that are easily found and tracked. Estimates are usually based on

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resurveying populations over years, and calculating the lifespan from the disappearance of existing colonies and the appearance of new ones, or both (i.e. turnover), often under the assumption of steady-state dynamics. Species of *Pogonomyrmex* have been particularly attractive in this regard. Keeler (1993) tracked 56 marked colonies of *Pogonomyrmex occidentalis* for 15 years along with 51 new colonies that appeared during that period. The initial cohort projected to a lifespan of about 44 years, while the new recruits yielded a lifespan of about 13 years, and under a steady-state turnover assumption, 24 years. Porter and Jorgensen (1988) tracked a population of 122 colonies of *P. owyhee* (synonymous with *P. salinus*) for 9 years and estimated an average lifespan of 17 years. They too found lower survival rates among smaller, younger colonies. Although Gordon and Kulig (1996) and Sanders and Gordon (2004) did not specifically estimate lifespan of *P. barbatus*, their estimates of annual mortality rates suggest a lifespan of 20–25 years. Similarly, the size-specific mortality rates reported by Wiernasz and Cole (1995) for *P. occidentalis* suggest lifespans ranging from about 5 years for small colonies to about 40 for large ones. Proximity to larger colonies greatly increased the mortality of smaller colonies.

Colony lifespan estimates of a few other ant species exist. Henderson et al. (1990) tracked survival of 69 colonies of the mound-building *Formica montana* over 33 years and also found survival strongly related to colony (mound) size. Reanalysis of their data (WRT) estimated lifespans of 23 years for the original cohort and 14 years for the cohort first appearing in the second year of the study. Chew (1987) tracked cohorts of three desert ant species for up to 23 years. Lifespans of the original cohorts were about 17 years for *Myrmecocystus depilis*, 39 years for *M. mexicanus* and 8 years for *Novomessor cockerelli*. Later-founded cohorts of all species had shorter life spans. Using turnover rates, Tschinkel (2002) estimated the lifespan of mature colonies of the arboreal, pine-dwelling ant *Crematogaster ashmeadi* (now *C. pinicola*, Deyrup and Cover 2007) to be 10–15 years.

Limits on colony lifespan are mostly unknown, but because the production of diploid workers requires fertilization by sperm, and sperms are limited to the supply in the queen's spermatheca, Tschinkel (1987a) argued that sperm supply can limit colony lifespan. From the sperms remaining in queen spermathecae in colonies of increasing age, he estimated the longevity of fire ant colonies at about 7–8 years. This estimate was confirmed from population turnover rates of about 13% by Tschinkel (2006).

A few other estimates of colony lifespan have been made in the field. Rosset and Chapuisat (2007) estimated a mean longevity of monogyne nests of *Formica selysi* to be about 10 years, while that of polygyne nests was about

three times as long. Mabelis and Chardon (2006) estimated *Formica truncorum* colonies to live for “maybe” 15 years, and Forel (1948) reported lifespans of 80 and 55 years for *F. rufa* and *F. pretensis*. Using indirect genetic methods and colony mortality Pamilo (1991) estimated that colonies of *F. exsecta* live for about 27 years. Liebig and Poethke (2004) estimated the longevity of queenright field colonies of *Harpegnathus saltator* to be a year or less. Colonies of this species are much smaller (mean <100 workers) than most of those for which longevity estimates exist.

A population of over 400 colonies of the Florida harvester ant, *Pogonomyrmex badius*, presented an opportunity to add a lifespan and mortality estimate for this charismatic ant. This was carried out by repeatedly resurveying the population over 6 years, producing a record of deaths, births, colony sizes and colony relocations. From these data the life span, growth rate, colony-size-specific mortality rates and spatial distribution were determined. In addition to its comparative value, this study tracked the histories and fates of individual colonies to ask how colony size varies during the life of a colony. Does it always increase if the colony survives? Are colony size and age strongly correlated, and is either (or both) related to longevity?

Materials and methods

Study site

The study population of *Pogonomyrmex badius* occupies a 23-ha site known as Ant Heaven and numbers about 400 colonies (Tschinkel 2015). The latitude and longitude of the site are, respectively, 30.3587 and –84.4177, about 16 km southwest of Tallahassee, Florida, USA. The ecotype within the Apalachicola National Forest is classified as sandhills. The soils are excessively drained sand occupying a slope to a wetland and stream, with a water table >5 m at the maximum depth to water, creating a droughty site suitable for several drought-resistant species of ants and plants (e.g. *Opuntia* and *Nolina*). The forest is composed of longleaf pines (*Pinus palustris*) planted ca. 1975, turkey oak (*Quercus laevis*), bluejack oak (*Quercus incana*), occasional sand pines (*Pinus clausa*) and sand live oak (*Quercus geminata*). The natural ground cover of wiregrass (*Aristida stricta*) was absent, replaced by broomsedge (*Andropogon* spp.) and several other successional species of grasses, herbs and shrubs.

Survey procedure

The first survey of this population was carried out in October 2010 and included about half of the final surveyed area. The latitude and longitude coordinates of each nest were

recorded with a Trimble GeoXT GPS device. Upon completion of each survey, the file was differentially corrected using base reference files recorded by the Department of Environmental Protection in Tallahassee, FL. Accuracy averaged between 0.5 and 2 m. The data were loaded onto Google Earth as layers, each survey forming a layer. The survey area was expanded during several 2011 surveys so that by the end of that year, the survey included all areas harboring colonies and measured 23 ha. This 23-ha site was resurveyed 6–7 times a year from 2012 to 2014, with only three surveys in 2015, the last year of this study. In order to avoid overlooking colonies, especially small colonies, the areas between marked colonies were searched especially carefully.

Each colony was marked with a vinyl flag on a wire stake and numbered with an aluminum tag on a wire stake. Colonies moved on average once a year (Tschinkel 2014b). Moves were always obvious because the nest with the flag and numbered stake was inactive, but a nearby unmarked colony with a disc of newly excavated sand was active. Because colonies moved only an average of 4 m (Tschinkel 2014b), a distance much less than the average distance to neighbors (16 m), the multiple annual surveys assured the unambiguous identity of each colony over time. Further assurance derived from the rarity with which neighbors both moved in the same survey. Inactive colonies without a nearby, new active nest indicated the death of the colony. Colonies were declared dead after a year of inactivity.

The disc diameter of each colony was measured. Initially, it was remeasured only after a colony moved, but beginning in 2013, every colony was measured during every survey. Disc area is a reliable measure of nest volume and colony size (Tschinkel 2015). Depending on the analysis, the mean disc area was calculated for all surveys in which the colony was present or as the mean for the year in question.

Data analysis

Data consisted of the latitude–longitudes of each colony during each survey, its disc diameter, whether or not it had moved since the previous survey, whether it was active or inactive, as judged from surface activity and condition of the nest disc (data available in Online resources 1 and 2). Inactivity for two or more surveys indicated that the colony had died, but in most cases, inactive colonies were revisited for up to a year before a final decision on date of death was made.

Most statistical analyses were carried out using Statistica 12 (Statsoft, Inc.). The Kaplan–Meier product limit method along with a log-rank test (Kaplan and Meier 1958) was used for comparing the survival function for cohorts and size classes. This method is more appropriate than life

tables because the data were not collected at regular intervals, and because many of the data were “censored”, i.e. still alive at the end of the study. To retain adequate sample sizes, colonies were grouped into three or five size classes (of increasing disc area) for survival analysis, and homogeneity of survival was tested with a log-rank test, yielding a Chi square and p value. Post-hoc differences among groups were tested by comparing the percent alive after a designated time (usually 3 years).

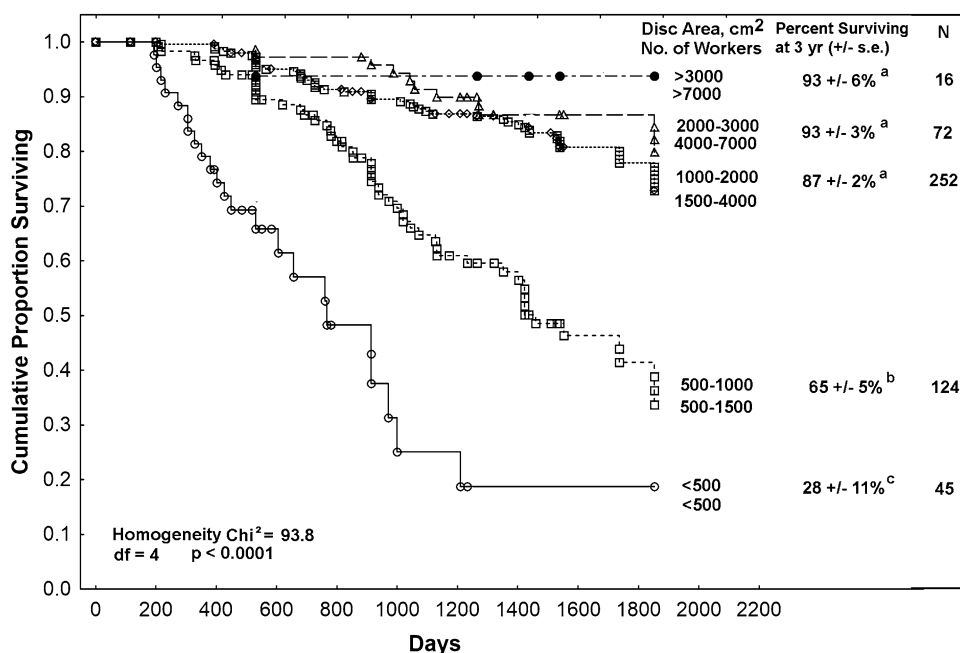
For colony size change analysis, colonies of the 2011 cohort, and thus with the longest record, were grouped into seven size classes in increments of 500 cm² and tracked until the end of the study in 2015. Analyses of variance (ANOVA) and multiple regression were also run on Statistica 12. Spatial analysis was carried out on ArcGIS using the locations of colonies at the end of each survey year. In addition to nearest neighbor distances, this produced a Moran's index whose p value and z score indicated whether colonies were randomly distributed, clustered or overdispersed. These spatial distributions were visualized through simple Voronoi tessellations. The edges of each tile in such a tessellation are the locus of points equidistant from a set of neighbors (nests). The number of sides reflects the dispersion of colonies, with more regular dispersion tending toward more six-sided tiles. When combined with colony size, the tiles allow the easy visualization of neighborhood density and colony size distribution. The spatial dispersion of colonies of specified size classes within Ant Heaven was also tested by comparing their frequency in grid units to the expected frequency determined from a Poisson distribution. Grid units were scaled to be large enough have at least a moderate expected frequency of each size class.

The effect of neighbors on focal colonies was tested by means of a “neighborhood index” computed as the sum of the mean disc area (over all surveys in which present) of each of the five closest neighbors of a focal colony divided by the square of the distance of each neighbor from the focal colony. Focal colonies at the edges of the population (i.e. those without neighbors to one side) were excluded.

Results

During every year of the survey, new colonies appeared and existing colonies ceased activity (died). The likelihood of finding a colony still alive in the following year depended strongly on its average size over the surveys in which it was alive, with survival much higher for larger colonies (Fig. 1; between group log-rank $\chi^2 = 93.8$; $df = 4$; $p < 0.00001$; this test is preferred in cases where the survival curves do not cross). Because many colonies survived beyond this study, I compared colony size classes using the percent alive at 3 years (derived from the Kaplan–Meier survival functions)

Fig. 1 Kaplan–Meier plots of colony survival in relation to their average size over all surveys in which they were active. Small colonies died at the highest rate, a rate that decreased strongly as colony size increased (Kaplan–Meier log-rank χ^2 for size class = 93.8; $df = 4$; $p < 0.00001$). Percent surviving at 3 years allowed comparison among size classes even though many colonies survived beyond the study. Size classes that were not significantly different are labeled with the same letter. Over 90% of colonies larger than 3000 cm² were still alive after 6 year. Log ranks of the size classes, in order of increasing class size: 16.1, 21.9, -21.3, -12.4, -4.6



instead of mean life span. These values and their standard errors are reported in Fig. 1. Only 28% of colonies with a mean disc size of less than 500 cm² (<500 workers) survived at 3 years, whereas over 90% of the largest two classes did so. Intermediate sized colonies (1500–4000 workers) had intermediate mean survival times. Extrapolating survival to zero, the smallest colonies will all have died in about 4 years, whereas the intermediate sized colonies (1000–2000 cm²) will have done so in about 17 years. The largest colonies (average >3000 cm²) could not be meaningfully extrapolated, but certainly live longer than 30 years. Well over 90% of these colonies (43 of 47) were still present after 6 years in 2015.

Survival also decreased with the year of first detection so that the colonies detected before the end of 2012 survived significantly longer than those detected first in 2013–2015 (ANOVA: $F_{5,523} = 62.2$; $p < 0.000001$). However, this was mostly an artifact resulting from the accumulation of detected colonies of all sizes during 2010 and 2011, followed by detection mostly of smaller, recently founded colonies thereafter. Thus, the initial surveys included colonies of all sizes, resulting in a mean disc size of 1521 cm², whereas the later surveys netted colonies whose disc size was significantly smaller, about 1000 cm² or less (Table 1; one-way ANOVA: $F_{3,506} = 26.48$; $p < 0.000001$). Most of these later detections were probably new, recently-founded colonies (a few could have been missed in earlier surveys), and these younger, smaller colonies survived less well.

In order to overcome this confounding of mean size and year of detection, survival (or time present) was related to the disc area (in arbitrary categories of 500 cm² increments) in the year the colony was first detected (Fig. 2a). For each

Table 1 Average size of newly detected colonies decreased after 2012 because new detections were mostly young, recently appeared colonies, rather than overlooked colonies

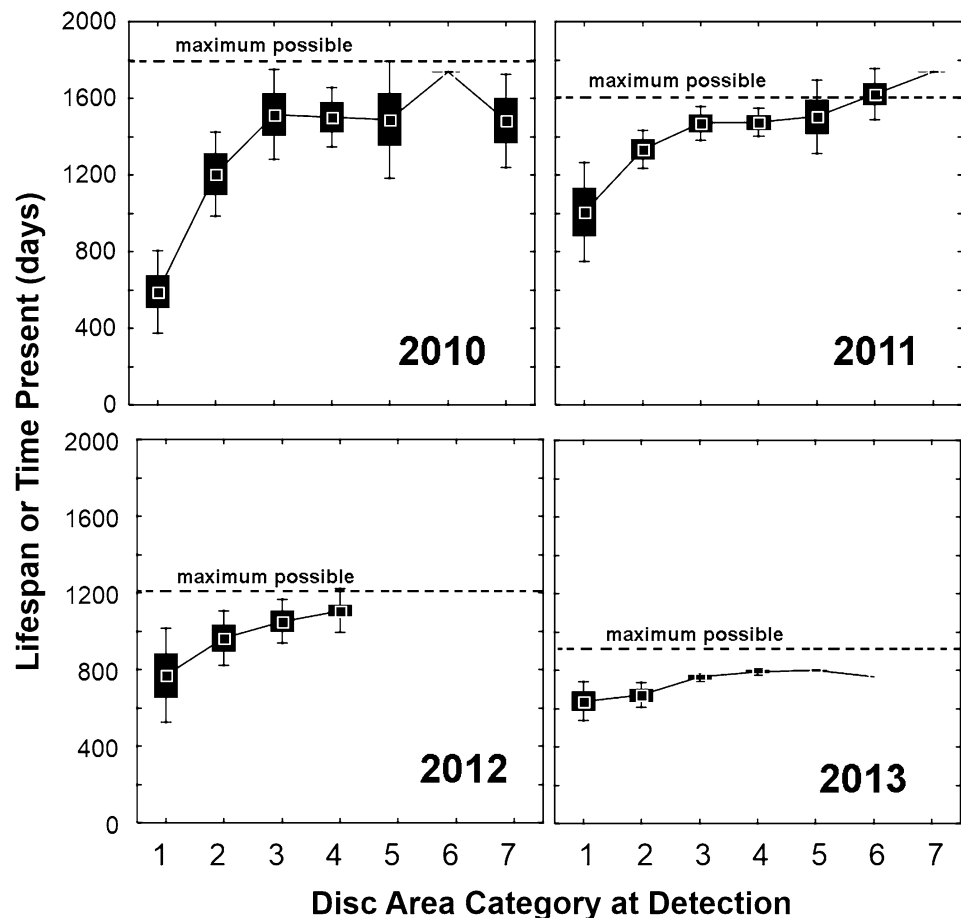
Year of detection	Mean disc area (cm ²), 2012–2015	N	SD
2012	1521 ^a	392	723
2013	1015 ^b	71	555
2014	528 ^c	37	477
2015	790 ^{bc}	15	479

Significant differences (Tukey’s HSD test) are shown by different superscripted letters

discovery year, lifespan (or time present) increased with disc area at the time of discovery (ANOVA for 2010–2014: $F_{3,498} = 10.14$; $p < 0.00001$) (Fig. 2). Between 2010 and 2013, the difference in lifespan between the largest and smallest colonies decreased from 1000 days to about 100 days. These patterns were represented by a significant year of detection by size interaction ($F_{17,498} = 1.65$; $p < 0.05$). A Kaplan–Meier survival analysis using the size class in the year of first detection (instead of overall mean) produced results very similar to those in Fig. 1, with a similar relationship of survival to colony size (between group $\chi^2 = 66.9$; $df = 4$; $p < 0.00001$). Together, these results show that whatever the effect of year of discovery on survival, it acts primarily through its effect on colony size.

Of course, the maximum time a newly discovered colony could have been present decreased from 1800 days in 2010 to 900 days in 2015, setting an upper limit, and creating the annual decrease in the asymptote in Fig. 2. For 2014 and 2015, too little time had elapsed for a meaningful analysis.

Fig. 2 Colony lifespan (or time present) in relation to size class for each year of first detection. Colonies first appearing in 2012 and 2013 had shorter lifespans than earlier-appearing colonies. The effect of size increased with elapsed time. Later-appearing colonies were also mostly small, with very few colonies larger than size class 4. The maximum possible time emphasizes that the effect of size increased with time elapsed since initial detection



It follows that the earlier a colony was detected during the 6 years of the surveys, the longer mortality factors had to act and the stronger the effect of initial size on survival. Throughout this period, smaller colonies had higher mortality rates, and mortality increased with elapsed time. To adjust for this changing asymptote, the percent of the possible maximum time that a colony was present was computed. The effect of initial size and year of detection both had large effects on this measure. The percent-of-possible increased with initial disc category (ANOVA of arcsine-square root transformed data: $F_{3,465} = 14.8$; $p < 0.00001$) and also increased with year of first detection ($F_{1,465} = 10.8$; $p < 0.002$).

It is also clear from Fig. 2 that after 2011, very few newly detected colonies were large, suggesting that the small size of new discoveries resulted from their recent appearance, not from having been overlooked in the previous surveys. When analyzed by both year of detection and colony size class, survival of small colonies ($< 500 \text{ cm}^2$) after 1 year did not differ significantly by year-of-detection—65% (C.I. 24) of 2012 colonies, 80% (C.I. 24) of 2013 colonies and 87% (C.I. 11.4) of 2014 colonies were alive at 1 year. Size class 2 colonies ($500\text{--}1000 \text{ cm}^2$) also

did not differ in survival by year of detection, but survived significantly better than class 1 in each year of detection. The year-of-detection effect on survival noted above thus resulted from detecting mostly smaller colonies in later years, colonies that survived less well.

These estimates of lifespan suggest that the turnover rate of the smallest size colonies is about 25% per year, while that of middle sized colonies is about 6% per year. If the largest colonies live for about 30 years, their annual turnover rate would be 3%.

The relationship of survival to colony size suggests the following questions: How does colony size vary during the life history of colonies? Does it always increase if the colony survives? Do some colonies fail to reach large size even though they may survive for a long time? Does mortality apply only to colony size or to size and age? To answer such questions, we must track the size of individual colonies across the surveys.

Colony size through time

Disc area is correlated to the number of workers as follows: $\log \text{wk} = -0.870 + 1.35 \log \text{area}$; Tschinkel 1999,

2015). The mean disc area over all surveys and colonies was 1440 cm² (s.d.= 811; n=529; size category 3). Thus, the mean size colony (size category 3) contained about 2500 workers, size category 1 contained <1000 workers

and categories 6–7 contained about 7000 or more workers. Although disc area (colony size) could increase or decrease, especially associated with nest relocation, it often changed little from one survey to the next. However, on a longer time scale there was a strong trend for small colonies to grow and large ones to decrease in size (Fig. 3). The pattern is most easily seen by grouping colonies present in 2011 (and thus with a long record) into disc area categories in increments of 500 cm². Colonies that were smaller than size 4 increased by an average of 1–2 size classes between 2011 and 2015, whereas colonies larger than class 4 decreased by 1 to 3 classes (one-way ANOVA: $F_{6,207} = 4.26$; $p < 0.0005$).

These size changes were not monotonic for individual colonies of each size, that is, size could either increase or decrease, as can be seen in the size-change frequencies for the 2011 cohort (Fig. 4). Size changes were tracked as the difference between the initial size class in 2011 and the final size class in 2015. On average, over this 4-year period, small colonies predominately increased in size and large ones decreased ($n = 290$) (some of this was probably simply regression to the mean). Although this effect was similar from year to year, its strength dampens from 2011 to 2014 (Fig. 5). By 2013 and 2014, this effect had weakened so that only three or four size classes were significantly different. The reason for this is probably that colonies stabilize at whatever size their intrinsic nature and their neighborhoods allow.

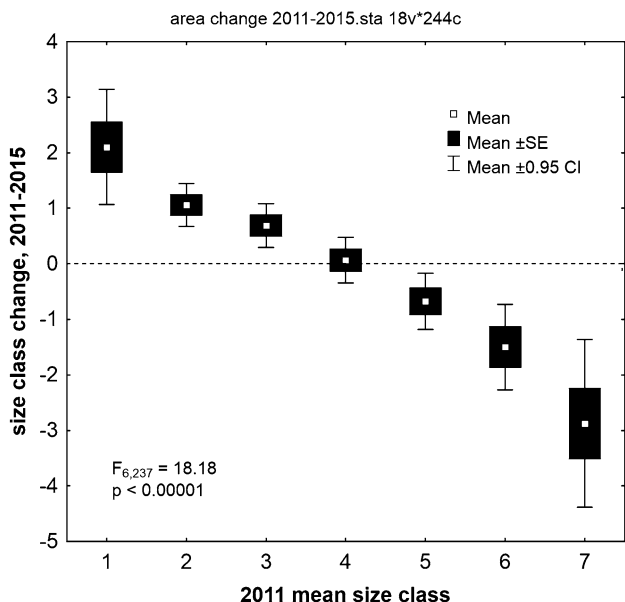


Fig. 3 The mean change in size class from 2011 to 2015 in relation to initial size class in 2011 (the year with the longest record). Small colonies grew, on average, and large ones lost size. Mid-sized colonies change little. (one-way ANOVA: $F_{6,207} = 4.26$; $p < 0.0005$)



Fig. 4 The frequency of size-class change from 2011 to 2015 for all colonies present in 2011 (the year with the longest record). Size class change was calculated by subtracting the size class in 2011 (initial size class) from the final size class in 2015. The vertical dotted lines indicate no size change, the positive values indicate colony

growth and the negative, size loss. The seven size classes were based on 500 cm² increments of the mean annual disc area. Over this 5-year period, small colonies predominately increased in size and large ones decreased ($n = 290$)

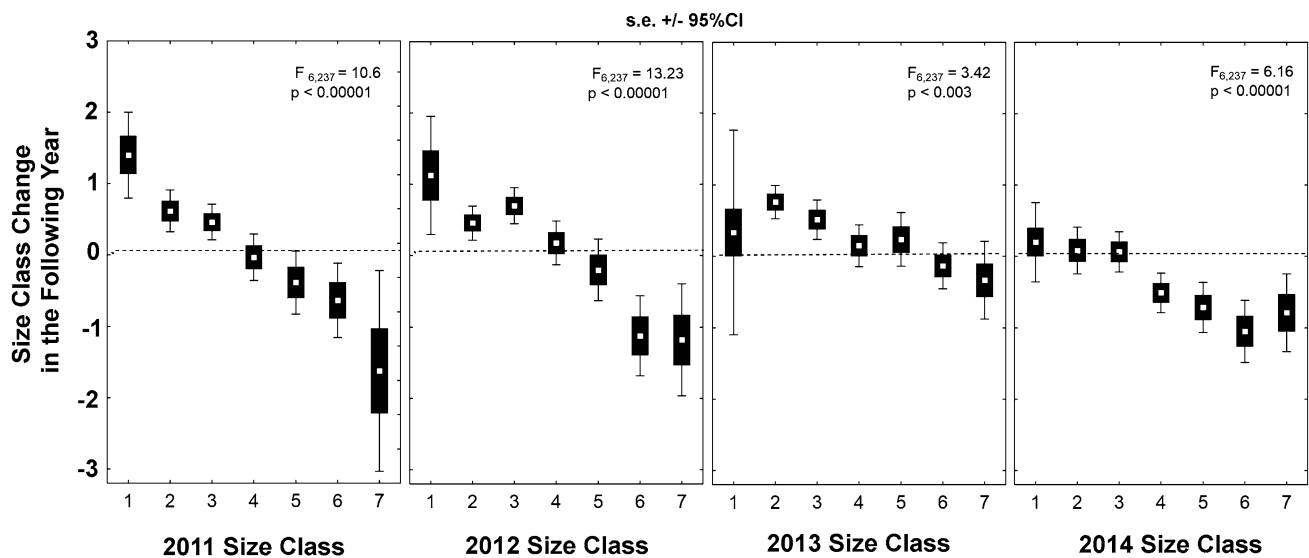


Fig. 5 The size change (in area class increments) from year to year for colonies present in 2011. Colonies that were small tended to increase in the next year, whereas large colonies tended to decrease, but both of these trends weakened with time. All colonies in this anal-

ysis were present in 2011 so that the weakening effect of size applies to this cohort, minus those that died after 2011. Size classes were constructed in disc area increments of 500 cm² increments

Spatial patterns

Colonies live in neighborhoods, and it seems possible or even likely that the fate of a focal colony depends upon its neighbors. As a result, spatial patterns are of interest. Both a nearest-neighbor analysis and Moran's index showed that the spacing of colonies was aggregated, rather than random. Taken over all years, and eliminating colonies on the edges of the population, the observed nearest neighbor distance was 16.8 m, while the expected was 15.0, resulting in a mean Z score of 3.94 and a p value < 0.0006 . Moran's index confirmed this with a mean value of 0.47, an expected of 0.0034 and a Z score of 18.05, indicating a significantly clumped spatial distribution. This is visible in a simple Voronoi tessellation as regions with larger or smaller tiles (Fig. 6). Large and very large colonies (> 2500 cm²) appeared especially clumped and a Poisson test showed that they were significantly aggregated ($p < 0.05$) and associated with more open areas that had lower canopy density and richer, denser ground cover. In contrast, smaller colonies (< 2500 cm²) did not differ from random distribution within Ant Heaven (Poisson test, $p > 0.3$). More open areas thus harbor larger colonies, probably because environmental conditions are more favorable to survival and growth, allowing colonies to achieve large size, which in turn reduces mortality and leads to greater longevity. As noted above and in Fig. 1, lifespan of colonies is strongly associated with colony size, with the largest colonies living for 30 years or more.

Effect of neighborhood and colony size on lifespan

If colonies interact with neighbors, and such interactions affect colony survival, then there should be a relationship between the density and size of neighbors and colony lifespan. Neighborhoods were characterized by distance from the focal colony to each of the first five neighbors (colonies on the population edges were not used). These distances ranged from 11 to 50 m and averaged 16 m for the first neighbor to over 30 m for the fifth (Fig. 7, inset). The fifth neighbor was between 2.2 and 14 times as far away as the first neighbor.

Reasoning that both the size and distance of neighbors might affect a focal colony, a "neighborhood index" was computed as the sum of the mean disc area (over all surveys in which present) of each of the five closest neighbors of a focal colony divided by the square of the distance of each from the focal colony. Focal colonies at the edges of the population (i.e. those without neighbors to one side) were excluded. The neighborhood index was strongly right-skewed (Fig. 7) (skewness 2.61) with a mean of 22 ($n = 389$), a minimum of 2.78 and a maximum of 110. A focal colony of average disc area (1500 cm²) had its first neighbor at about 16 m and a neighborhood index of about 23. As neighbors were closer and/or larger, the index increased. Although colonies moved on average of once a year, the distance moved was usually small relative to the distance to neighbors (Tschinkel 2014b). Moreover, the more they moved, the closer their final position was to their original position—in essence, moves are a random walk

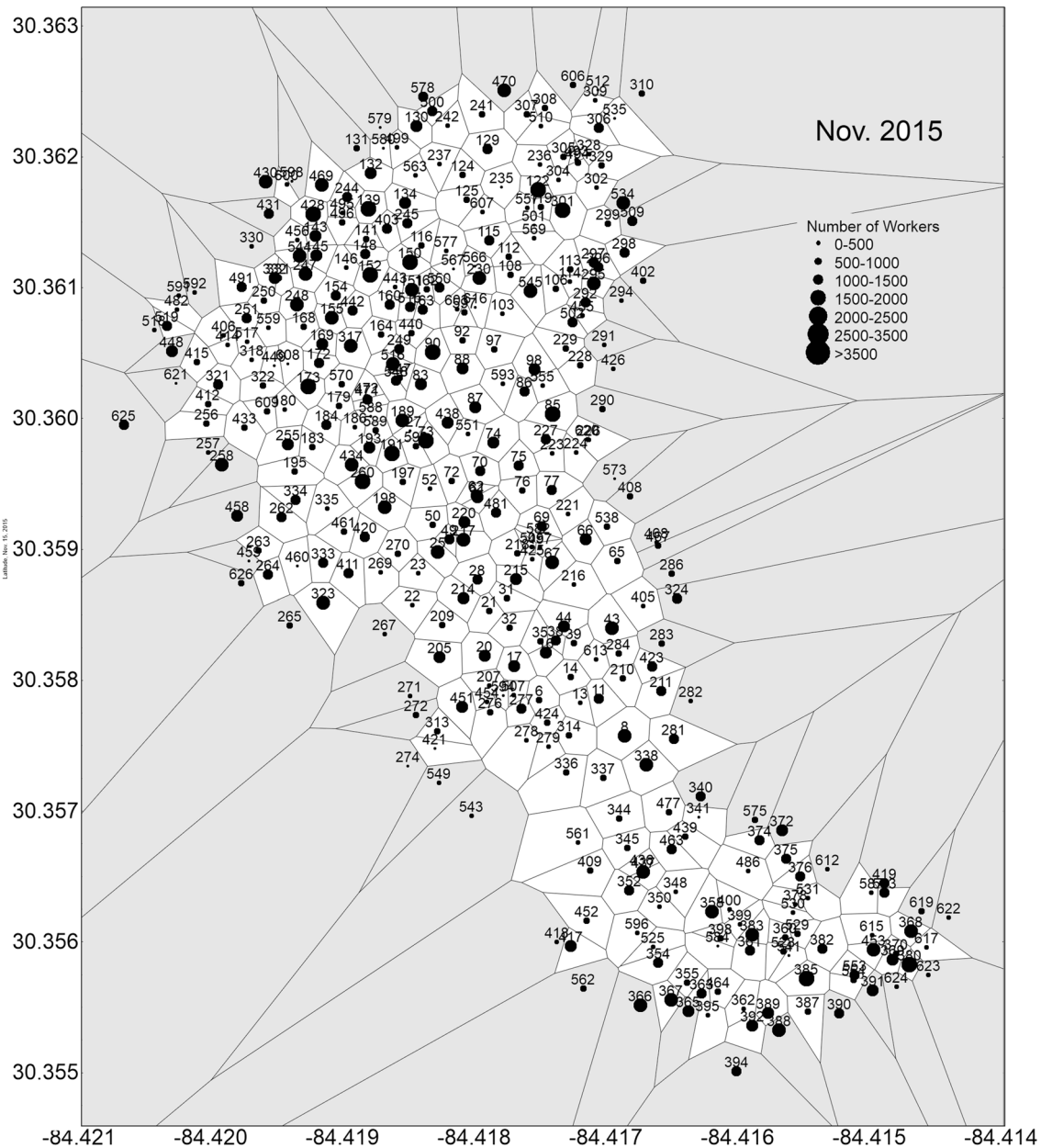


Fig. 6 Voronoi tessellation of the *P. badius* population in 2015, showing regions of larger and smaller tiles. Such variation of neighborhood density affected life span significantly. Colony size (disc area) is

indicated by the size of the symbols. Regular dispersion is associated with a higher proportion of six-sided tiles. Edge tiles in gray were not included in the analysis

around some original position (Tschinkel 2014b). Neighborhood indices were thus rather stable over time.

Testing the effect of the neighborhood index first required life span to be adjusted for the large effect of colony size so that the neighborhood index could be related to the variance in lifespan not associated with disc area, that is, to the regression residuals. The agents of interaction with neighbors are the foragers, whose number is positively related to colony size. To simplify the analysis, the

mean disc area over all years in which a colony was present was used (regression: lifespan = $-2590 + 1271 \log \text{disc area}$; $F_{1,366} = 250$; $p < 0.00001$; $R^2 = 40\%$). As the neighborhood index increased, the residuals from this regression became increasingly negative such that lifespans for the densest neighborhoods were from 250 to 570 days less than expected, given their disc area (Fig. 8; one-way ANOVA: $F_{4,479} = 6.11$; $p < 0.0001$; $R^2 = 5\%$). Although the effect is modest, higher density neighborhoods shorten the life of a

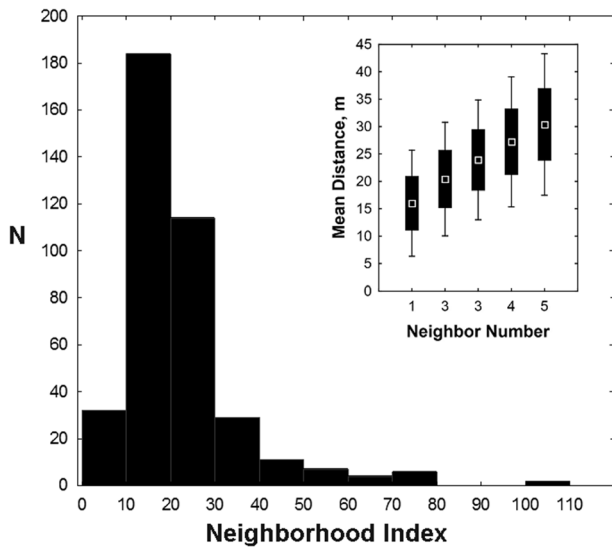


Fig. 7 Frequency distribution of the neighborhood index, and mean distance to neighbors 1 through 5 (*inset*). The index was calculated as the mean disc area of each of the five closest neighbors divided by the square of the distance (m) to each neighbor. Higher indices indicate closer and/or larger neighbors. Mean distance to neighbors increased from 16 m for the first neighbor to over 30 for the fifth. Error bars, SE, 1.96 SE

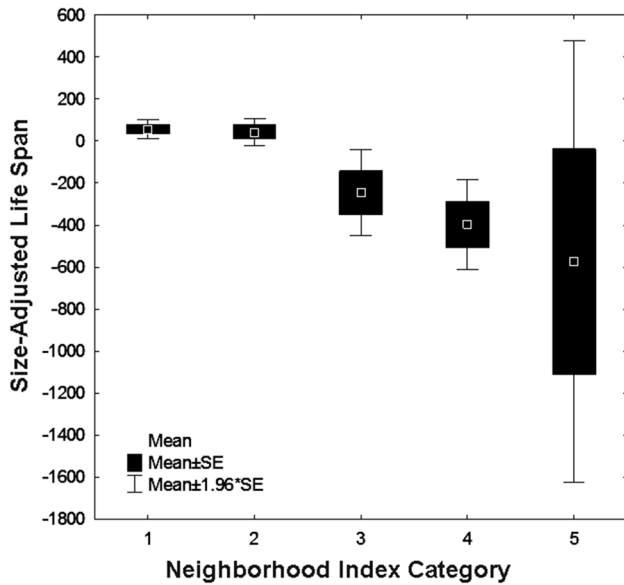


Fig. 8 Size-adjusted lifespan in relation to the density of the neighborhood. The effect of disc area on lifespan was removed by taking the residuals from the lifespan-area regression. Although the effect is modest, neighborhood density affects lifespan negatively.

focal colony, although this effect is much smaller than that of colony size.

Relative size also played a role, emphasizing the vulnerability of small colonies—lifespan decreased sharply

when the first neighbor was more than 50% larger (up to 10-fold) than the (small) focal colony (ANOVA: $F_{5,384} = 17.5; p < 0.0001$).

Discussion

Our estimate of a lifespan of 30 years or more for *Pogonomyrmex badius* colonies is similar to lifespan estimates and mortality rates for other *Pogonomyrmex* species (see Introduction). As in other *Pogonomyrmex* species, this long life is not doled out fairly, but must be earned by growing to large size. It is not primarily that longer lived colonies are able to grow to larger size, but that as they grow, colonies are less and less likely to die so that the very largest colonies have lifespans that cannot be reliably estimated with a 6-year study, but probably exceed 30 years. However, while most small colonies tend to grow, many do not grow to a large size and, therefore, continue to be subject to the mortality rate characteristic of their size. Such age-(or size)-specific mortality is probably almost universal among ants, and possibly other social insect colonies (see Introduction). This decrease in mortality rate with colony growth can be seen as a continuum that begins with the extreme mortality rates associated with colony founding (Hölldobler and Wilson 1990). During a colony’s lifetime, mortality rate decreases until the effects of advanced age once more cause it to increase.

For the few other ant species for which colony lifespans have been reported, most are in the range of decades, suggesting that perhaps ant colonies in general are long-lived. However, Cole (2009) argued that our understanding of ant colony demography and lifespan is greatly skewed by the fact that most data are of conspicuous species with large colonies and, therefore, “[i]t is important to remember that we are not in a position to make generalizations about ant demography. However, it is becoming clearer that these data are necessary for understanding the dynamics of evolutionary change.” Whereas the colonies of most ant species are small (dozens to hundreds of workers), these species are not represented in the currently available data (with the exception of *H. saltator* whose queenright colonies are small and lifespan short). This is perhaps understandable, considering the practical aspects of tracking populations of small colonies over long periods. Difficulties include detection, estimating colony size, tracking colony relocations and distinguishing these from deaths. Nevertheless, the small mature colony size range means that allometric relationships between colony size and lifespan cannot be detected, although they probably exist, much as do allometries between body size and lifespan in many taxa of

unitary animals (Schmidt-Nielsen 1984). Without reliable knowledge of such allometries, theories of the evolution of colony longevity cannot be developed.

It is not clear what sets the intrinsic, upper lifespan limit of an ant colony. To begin with, the concept of “colony lifespan” is not easily applied to polygynous social insects, whether the polygyny is primary or secondary (Feldhaar et al. 2003), for the “colony” may far outlive any of its queens. In some monogynous species, a dead queen may be replaced so that colony lifespan could greatly exceed queen lifespan, but information on queen replacement in monogynous colonies is scant. Tschinkel (1996) and McInnes and Tschinkel (1995) showed that upon the death of a colony’s queen in *Solenopsis invicta* and *S. geminata*, she may sometimes be replaced by an unrelated, and thus socially parasitic queen (replacement rates were 3 and 30%, respectively). Because such replacements are hard to detect, they may be fairly common among ants.

In monogynous ant species without queen replacement (e.g. *P. badius*), colony and queen lifespan are equivalent, and the colony dies soon after the queen. Queen longevities span a very large range, from a few years to about 30 years (Hölldobler and Wilson 1990; Keller and Genoud 1997; Schrempf and Cremer 2011; Haskins and Haskins 1992). Unfortunately, most queen lifespans have been determined in the laboratory rather than the field and thus have only a tenuous connection to realized lifespans of colonies in nature. Published queen life spans estimate possible laboratory colony lifespans, but field conditions could either increase or decrease such lifespans.

Tschinkel (1987a) pointed out that the lifetime sperm supply stored in the queen’s spermatheca is potentially an intrinsic limit to colony lifespan, for when the queen runs out of sperm, she can no longer produce workers to compensate for worker turnover. In the fire ant, *Solenopsis invicta*, each fertilized egg depleted the sperm supply by three (Tschinkel and Porter 1988). From the decrease in the number of sperm in the spermatheca of queens from colonies of increasing age, an average upper limit of colony lifespan of 7–8 year was derived (Tschinkel 1987a). This estimate was later independently confirmed from the annual turnover rate in a population of field colonies, resulting in an estimate of about 8 years (Tschinkel 2006).

Could maximum lifespan of *P. badius* colonies also be limited by sperm supply? With an initial sperm number of 2 million in newly mated queens (Tschinkel 1987b), and assuming a sperm-use efficiency of about 2:1 and an annual worker turnover of 200% in a colony of 10,000 workers, the maximum elapsed time before a queen runs out of sperm would be over 50 years, shorter for higher turnover and lower sperm-use efficiency. Having run out of sperm, she could no longer produce workers, and the colony would dwindle away and die. Whether colonies ever reach this

venerable age is not known, but the survival curves of the largest colonies suggest that they sometimes may.

What might the extrinsic mortality factors be? The modest negative effect of neighborhood density on survival suggests that interactions with neighbors might play a role, and these could be aggressive, resource competition, or both. There is no evidence that small colonies try to move away from large colonies, for the distance and direction of colony relocations are not related to colony size (Tschinkel 2014b). In any case, the distance of moves (mean 4 m, rarely more than 8 m) is much less than the distance to neighbors (mean 16 m). Wiernasz and Cole (1995), whose population of *P. occidentalis* was highly overdispersed, found the mortality rate of young colonies to depend strongly on their distance from larger colonies, but Gordon and Kulig (1996) found no such effect on *P. barbatus*. In our population of *P. badius*, large colonies were significantly clumped, rather than overdispersed, probably as a result of habitat heterogeneity with larger colonies located in more open areas. Local density within neighborhoods had a modest negative effect on mortality, more so when the focal colony was small and the neighbors large.

The improved survival rates of larger ant colonies are probably related to worker mortality rates relative to worker production rates. Perhaps larger worker populations are more buffered against catastrophe. Workers of most ant colonies are much shorter lived than the queens (and colonies) so that most of the eggs laid by the queen simply replace workers that have died. For example, mature fire ant colonies replace the entire worker population over three times per year, and small colonies six times (Tschinkel 1993; Tschinkel 2006). Colonies grow only when the annual worker production rate exceeds the death rate. Depending on climatic and ecological conditions, colonies may thus fail to grow or even lose size (Kwapich and Tschinkel 2013). Kwapich and Tschinkel (2013, 2016) showed that penning either focal colonies or their neighbors resulted in lower forager mortality rates in the focal colonies, which in turn inhibited the development of new foragers, promoting colony growth. These findings suggest that foragers die during interactions with neighbors and that this is directly linked to changes in colony size. Such interactions offer a possible mechanism for the effect of neighborhood density on longevity. Whatever the mechanism, the degree to which a colony can exceed worker production beyond simple replacement determines colony growth and size.

From a colony fitness point of view, colony size confers two benefits—greater sexual production and a longer life. Thus, colonies of intermediate size (~3000–4000 workers) have a life expectancy of approximately 20 years, while those of greater than 3000 cm² disc area (>7000 workers) may have a life expectancy of about 40 years, about twice as long. Annual sexual production is isometric with

colony size (Smith and Tschinkel 2006) so that the larger colonies will produce twice the sexuals as the smaller ones for twice as long, i.e. four times as many. Assuming that success in colony founding does not depend on the colony of birth, the larger colonies will leave behind four times as many daughter colonies as the smaller ones, providing very strong selection on size and longevity.

A similarly lop-sided apportionment of population-level reproduction occurred in the fire ant, *S. invicta* (Tschinkel 2006, Chap. 31), in which the largest 15% of colonies were capable of producing over half of the total sexuals, and the largest 5% produced 20% of the total. Genetic studies showed that only a small minority of colonies of *P. barbatus* successfully produced daughter colonies (Ingram et al. 2013). Given that sexual production (and probably longevity) is likely to be positively related to colony size across many if not most ant species (e.g. Tschinkel 1993; Elmes 1987; Cole and Wiernasz 2000; Smith and Tschinkel 2006), it would appear that positive selection for large colony size should be widespread among ants. The puzzle is why the great majority of ant species have small colonies (Hölldobler and Wilson 1990).

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References

- Brian MV (1972). Population turnover in wild colonies of the ant *Myrmica*. *Ecol Pol* 20: 43–53
- Chew RM (1987) Population dynamics of colonies of three species of ants in desertified grassland, southeastern Arizona, 1958–1981. *Am Midl Nat* 118(1):177–188
- Cole BJ (2009) The ecological setting of social evolution: the demography of ant populations. Organization of insect societies—from genome to sociocomplexity. In: Gadau J, Fewell J (eds) Harvard University Press, Cambridge, pp 74–104
- Cole BJ, Wiernasz DC (2000) Colony size and reproduction in the western harvester ant, *Pogonomyrmex occidentalis*. *Insect Soc* 47:249–255
- Deyrup M, Cover SP (2007) A new species of *Crematogaster* from the pinelands of the southeastern United States. In: Snelling RR, Fisher BL, Ward PS (eds) Advances in ant systematics: homage to E.O. Wilson— 50 years of contributions. *Memoirs of the American Entomological Institute* 80:100–112
- Elmes GW (1987) Temporal variation in colony populations of the ant *Myrmica sulcinodis*. II. Sexual production and sex ratios. *J Anim Ecol* 56:573–583
- Feldhaar H, Fiala B et al (2003) Patterns of the *Crematogaster*-Macaranga association: the ant partner makes the difference. *Insect Soc* 50(1):9–19
- Forel A (1948) *Die Welt der Ameisen*. Translated by Kutter H. Rotapfel Verlag, Zürich
- Gordon DM, Kulig A (1996) The effect of neighbors on the mortality of harvester ant colonies. *J Anim Ecol* 67(1):141–148
- Haskins CP, Haskins E (1992) Note on extraordinary longevity in a queen of the formicine ant genus *Camponotus*. *Psyche* 99:31–34
- Henderson G, Wagner RO, Jeanne RL (1990) Prairie ant colony longevity and mound growth. *Psyche* 96:257–268
- Hölldobler B, Wilson EO (1990) *The ants*. Harvard/Belknap Press, Cambridge, MA, USA
- Hölldobler B, Wilson EO (2009) *The superorganism: the beauty, elegance, and strangeness of insect societies*. WW Norton & Company, NY, London
- Ingram KK, Pilko A, Heer J, Gordon DM (2013) Colony life history and lifetime reproductive success of red harvester ant colonies. *J Anim Ecol* 82:540–550
- Kaplan E, Meier P (1958) Nonparametric estimation from incomplete observations. *J Amer Stat Assoc* 53:457–481
- Keeler KH (1993) Fifteen years of colony dynamics in *Pogonomyrmex occidentalis*, the western harvester ant, in western Nebraska. *Southw Nat* 38: 286–289
- Keller L, Genoud M (1997) Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature* 389:958–960
- Kwapich CL, Tschinkel WR (2013) Demography, demand, death, and the seasonal allocation of labor in the Florida harvester ant (*Pogonomyrmex badius*). *Behav Ecol Sociobiol* 67:2011–2027
- Kwapich CL, Tschinkel WR (2016) Limited flexibility and unusual longevity shape forager allocation in the Florida harvester ant (*Pogonomyrmex badius*). *Behav Ecol Sociobiol* 70:221–235
- Liebig J, Poethke HJ (2004) Queen lifespan and colony longevity in the ant *Harpegnathos saltator*. *Ecol Entomol* 29(2): 203–207
- Mabelis AA, Chardon JP (2006) Survival of the trunk ant (*Formica truncorum* Fabricius, 1804; Hymenoptera: Formicidae) in a fragmented habitat. *Myrmecol Nachr* 9: 1–11
- McInnes DA, Tschinkel WR (1995) Mermithid nematode parasitism of *Solenopsis* ants (Hymenoptera: Formicidae) of northern Florida. *Ann Entomol Soc Amer* 89:231–237
- Pamilo P (1991) Life span of queens in the ant *Formica exsecta*. *Insect Soc* 38:111–119
- Porter JD, Jorgensen CD (1988) Longevity of harvester ant colonies in southern Idaho. *J Range Manage* 41:104–107
- Rosset H, Chapuisat M (2007) Alternative life-histories in a socially polymorphic ant. *Evol Ecol* 21(5):577–588
- Sanders NJ, Gordon DM (2004) The interactive effects of climate, life history, and interspecific neighbours on mortality in a population of seed harvester ants. *Ecol Entomol* 29(5):632–637
- Schmidt-Nielsen K (1984) *Why is animal size so important?* Cambridge Univ. Press, Cambridge
- Schrempf A, Cremer S et al (2011) Social influence on age and reproduction: reduced lifespan and fecundity in multi-queen ant colonies. *J Evol Biol* 24(7):1455–1461
- Smith CR, Tschinkel WR (2006) The sociometry and sociogenesis of reproduction in the Florida harvester ant (*Pogonomyrmex badius*). *J Insect Sci* 6: 32. <http://jinsectscience.oxfordjournals.org/content/6/1/32>
- Tschinkel WR (1987a) Fire ant queen longevity and age: estimation by sperm depletion. *Ann Entomol Soc Amer* 80:263–266
- Tschinkel WR (1987b) The relationship between ovariole number and spermathecal sperm count in ant queens: a new allometry. *Ann Entomol Soc Amer* 80:208–211
- Tschinkel WR (1991) Insect sociometry, a field in search of data. *Insect Soc* 38(1):77–82
- Tschinkel WR (1993) Sociometry and sociogenesis in colonies of the fire ant, *Solenopsis invicta* during one annual cycle. *Ecol Monogr* 63:425–457

- Tschinkel WR (1996) A newly-discovered mode of colony founding among fire ants. *Insect Soc* 43:267–276
- Tschinkel WR (1999) Sociometry and sociogenesis of colony-level attributes of the Florida harvester ant (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 92:80–89
- Tschinkel WR (2002) The natural history of the arboreal ant, *Crematogaster ashmeadi*. *J Insect Sci* 2(12):15
- Tschinkel WR (2006) *The fire ants*. Harvard/Belknap, Cambridge, MA
- Tschinkel WR (2011) Back to basics: sociometry and sociogenesis of ant societies (Hymenoptera: Formicidae). *Myrmecol News* 14: 49–54
- Tschinkel WR (2014a) Scientific natural history: telling the epics of nature. *Bioscience* 64:438–443. doi:[10.1093/biosci/biu033](https://doi.org/10.1093/biosci/biu033)
- Tschinkel WR (2014b) Nest relocation and excavation in the Florida harvester ant, *Pogonomyrmex badius*. *PLoS One* 9(11):e112981. doi:[10.1371/journal.pone.0120407](https://doi.org/10.1371/journal.pone.0120407)
- Tschinkel WR (2015) Biomantling and bioturbation by colonies of the Florida harvester ant, *Pogonomyrmex badius*. *PLoS One* 10(3):e0120407. doi:[10.1371/journal.pone.0120407](https://doi.org/10.1371/journal.pone.0120407)
- Tschinkel WR, Porter SD (1988) Efficiency of sperm use in queens of the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). *Ann Entomol Soc Amer* 81:777–781
- Wiernasz DC, Cole BJ (1995) Spatial distribution of *Pogonomyrmex occidentalis*: Recruitment, mortality and overdispersion. *J Anim Ecol* 64:519–527
- Wiernasz DC, Hines J, Parker DG, Cole BJ (2008) Mating for variety increases foraging activity in the harvester ant, *Pogonomyrmex occidentalis*. *Mol Ecol* 17(4):1137–1144