

Colony Productivity of the Fungus-Gardening Ant *Trachymyrmex septentrionalis* (Hymenoptera: Formicidae) in a Florida Pine Forest

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ABSTRACT The ecology of the fungus-gardening ant *Trachymyrmex septentrionalis* McCook (Hymenoptera: Formicidae) was investigated in a northern Florida longleaf pine, *Pinus palustris* Mill., forest. This ant is extremely abundant in pine sandhill in the Apalachicola National Forest, in north Florida; a hectare contains on average >1,000 nests, 235,000 *T. septentrionalis* workers, and 3.5 kg of fungus garden. When colony size and performance were estimated from excavations and the weight of sand in the tumulus, nests were larger and produced the most offspring in open, treeless habitats, whereas the smallest and least productive nests occurred in wooded areas. Our data suggest that the warm soils of open sites stimulate worker activity and colony growth, and cool soils of shaded, wooded sites depress performance. Moreover soils with extremely warm temperatures may have an inhibitory effect because the ants and fungus are susceptible to desiccation and excessive warmth, respectively. This suggests that *T. septentrionalis* is an indicator ant species of habitat quality in longleaf pine sandhills because its performance seems to be positively related to the natural disturbance regime—frequent fires occurring in the summer. Soil displacement is possibly a major effect that this ant has on the forest ecosystems: colonies may excavate over 1 metric ton of soil each year in a typical hectare of pine forest. The effect of this soil turnover is probably considerable in these nutrient-poor, sandy soils. Experiments are needed to determine the role of this highly abundant ant in longleaf pine forests.

RESUMEN: En un bosque de pino, *Pinus palustris* Mill., del norte de Florida se llevó a cabo la investigación de ciertos aspectos ecológicos relacionados con la producción de la hormiga *Trachymyrmex septentrionalis* McCook. Este tipo de hormiga es muy abundante en hábitats secos y arenosos (sandhills) del Bosque Nacional Apalachicola (Apalachicola National Forest); una hectárea contiene una media de 1.000 colonias, 235.000 hormigas obreras *T. septentrionalis* y 3,5 kg de jardín de hongos. Tras calcular el tamaño y la productividad de la colonia a partir de nuestras excavaciones y del peso de la arena en el túmulo, se observó que los nidos eran más grandes y que la mayor parte de las crías se producían en hábitats descubiertos, sin árboles. Por el contrario, los nidos más pequeños y menos productivos se encontraban en zonas arboladas. Nuestros datos indican que la tierra caliente de espacios abiertos estimula la actividad de la hormiga obrera y el crecimiento de la colonia, mientras que la tierra fría de zonas en sombra reduce la actividad de las mismas. Asimismo, las tierras calientes en extremo pueden llegar a ser fatales para estas hormigas y su jardín de hongos. Todo ello sugiere que la especie *T. septentrionalis* es indicadora de hábitats secos y arenosos intactos en los bosques de pino, ya que su actividad se relaciona de manera positiva con las principales alteraciones naturales del bosque; por ejemplo, los incendios que se producen con frecuencia en el verano. El desplazamiento de la tierra es uno de los principales efectos producidos por este tipo de hormiga en el ecosistema forestal—una colonia excava más de una tonelada métrica de tierra en una hectárea de bosque de pino cada año. Probablemente, esta rotación de la tierra tiene efectos significativos en estas zonas arenosas y pobres en nutrientes. Es necesario realizar experimentos para determinar cuál es el papel de este tipo de hormiga tan abundante en los bosques de pino.

KEY WORDS Attini, fungus gardening, longleaf pine, sandhills, Florida

Ants (Hymenoptera: Formicidae) are important members of nearly all terrestrial communities in temperate and tropical latitudes (Hölldobler and Wilson 1990, Agosti et al. 2000). Their ecological importance lies largely in their sheer abundance, complex social life, and the ability of individual workers to collect and

process more food than a solitary arthropod of a given size (Hölldobler and Wilson 1990). Ant colonies can be large (>1 million workers; Hölldobler and Wilson 1990) and in many cases take on characteristics of individual organisms (Tschinkel 1993, 1999). Ants play keystone roles as seed predators and dispersers (Mac-

Mahon et al. 2000), primary consumers (Tobin 1994, Davidson et al. 2003), predators (Porter and Savignano 1990, Cole et al. 1992), and ecosystem engineers (Folgarait 1998).

Attines or fungus-gardening ants occur only in the Western Hemisphere in warm temperate to tropical environments from $\approx 40^\circ$ N to 44° S (Weber 1970, Farji Brener and Ruggiero 1994). All attines are obligately dependent on specific Basidiomycete fungi (Agaricales: Lepiotaceae) that they cultivate inside their nests (Martin 1987, Mueller et al. 1998) on dead vegetation, fresh leaves, flowers, fruit pulp, or insect feces (Hölldobler and Wilson 1990, Leal and Oliveira 2000). Leaf-cutting ants (*Atta* spp. and *Acromyrmex* spp.) are conspicuous fungus gardeners and provide their fungus gardens nearly exclusively with leaves that they cut from living vegetation (Wirth et al. 2003). Additionally, these ants may be frugivores and seed dispersers (Farji Brener and Silva 1996, Dalling and Wirth 1998) and important nutrient recyclers and modifiers of soil. Species that have subterranean fungus gardens also excavate large amounts of soil (Wirth et al. 2003). Additionally, ant fungi digest soluble plant compounds, such as pectins and starch, but not the abundant, insoluble plant polymers cellulose and lignin (Silva et al. 2003). Consequently, fungus gardens produce large amounts of undigested plant matter, or refuse, which the ants place in discrete depots (Farji Brener and Medina 2000, Farji Brener and Ghermandi 2004). Fungus garden refuse is laden with rare essential minerals, especially nitrogen, phosphorous, potassium, and sulfur (Haines 1978), which may have notable effects on the plant community (Jonkman 1978; Farji Brener and Silva 1995a,b; Torres et al. 1999; Farji Brener and Medina 2000).

Although leaf-cutting ants are well studied, much remains to be explored about species in the nine remaining genera of the tribe. These species tend to have smaller ants and colonies than leaf-cutting ants, but they perform many of the same ecological functions. For example, among 19 nonleaf-cutting species, most substrate items collected by foragers were leaves, flowers, fruits, and seeds (Leal and Oliveira 2000). Eleven of these species belonged to the sister genera of the leaf-cutting ants *Trachymyrmex* and *Sericomyrmex* (Leal and Oliveira 2000). Additionally, these attines seem to disperse seeds and to increase the germination of seeds by cleaning the seed of surrounding fruit (Leal and Oliveira 1998, Pizo and Oliveira 2000). In a dry forest of Puerto Rico, *Trachymyrmex jamaicensis* (André) deposits the refuse from fungus gardens into discrete areas, which increases the germination of seeds that land in them (Torres et al. 1999). Other than these studies, there is very little information on the ecology of the nonleaf-cutting fungus-gardening ants.

Trachymyrmex septentrionalis (McCook) has the northernmost distribution of all attines. It is essentially the only higher attine found in North America east of the Mississippi River (Weber 1970, Deyrup 2003). *Trachymyrmex septentrionalis* is found from south Florida to Long Island, westward to Missouri

and southwest to Texas (Morris 1881, Wheeler 1907). In this article, we describe colony performance of *T. septentrionalis* in relation to environmental correlates in longleaf pine, *Pinus palustris* Mill., forests of the Apalachicola National Forest (ANF) in north Florida. This study was motivated by the observation that *T. septentrionalis* is among the most abundant ants in this forest with $>1,000$ nests \cdot per ha (J.N.S., unpublished data). The goal of this project was to describe the relationship among habitat characteristics, nest density, and colony performance (i.e., fitness) measures (colony size and output). We then use our results to generate hypotheses about how longleaf pine forest ecology impacts the performance of *T. septentrionalis* colonies. In turn, we also hypothesize how this ant may influence longleaf pine forest ecology, in particular through its soil-excavating activities. Finally, we place our findings in the context of other studies on populations of higher attines, especially leaf-cutting ants.

Materials and Methods

Study Site. Study populations were located in the Wakulla District of the ANF ($30^\circ 20'$ N, $84^\circ 15'$ W). The climate is humid subtropical during most of the year, except for a mild winter occurring December–February that brings occasional freezing temperatures (Chen and Gerber 1990). The growing season lasts ≈ 300 d; $>1,500$ mm rain falls each year, and the annual mean temperature is 20° C (Platt 1999, Chen and Gerber 1990, NOAA 2005).

Of the four species of Attini found in Florida (Deyrup 2003), just two occur in the ANF, *T. septentrionalis* and *Cyphomyrmex rimosus* Spinola. *T. septentrionalis* occurs throughout the longleaf pine forests of the ANF, but it is especially abundant in the so-called sandhills that lie in the northeastern section of the forest (J.N.S., unpublished data). The sandhills are remnants of Pleistocene sand dunes that form small hills interspersed by numerous sinkhole depressions (Waite 1984, Myers 1990). These soils are nutrient poor, deep, and excessively drained, making conditions very dry in the absence of frequent rain (Brown et al. 1990). Typical plants include longleaf pine; prickly-pear cactus, *Opuntia humifusa* (Raf.) Raf.; and several xeric-adapted oaks, especially turkey oak, *Quercus laevis* Walter, and bluejack oak, *Quercus incana* W. Bartram (Myers 1990). Flatwoods, in contrast, have generally less relief and a high water table (Abrahamson and Harnett 1990). In addition to containing longleaf pine, these areas generally contain plants adapted to wet soils, but areas somewhat higher in elevation (on the scale of centimeters) have deeper soils and vegetation more typical of sandhills and also carry populations of *T. septentrionalis*.

Colony Collection. Colonies were collected by excavating a 1-m^3 pit ≈ 30 cm from the nest entrance. Tunnels and fungus garden chambers were found by carefully removing soil from the face of the pit toward the entrance. All tunnels were followed until all ants had been collected. The depth and volume of each

chamber were recorded. Chamber volume was estimated by measuring the width, height, and length of the inner dimensions with a measuring tape. Thirty-nine colonies were collected from four management compartments in the ANF (compartment numbers 215 (30° 23.5' N, 84° 28' W), 216 (30° 23.6' N, 84° 27.8' W), 219 (30° 20.8' N, 84° 17.6' W), and 226 (30° 21.4' N 84° 23.7' W) in May 2002 during the period of sexual production. These compartments were 0.2–10 km apart. Colonies were collected from a fifth site within compartment 226 (called 226u), which had been recently clearcut and was an old field containing very few trees but thick underbrush. This site was different from the other part of 226, which contained many mature longleaf pines and turkey oaks. Generally, all of these sites contained sizeable populations of *T. septentrionalis* and vegetation typical of sandhills. Ten additional colonies were collected in August 2002 from compartments 219 and 226. When indicated, these data were augmented with the collection of 120 colonies during May 2003 and March 2003 and 2004 that were part of other projects (Seal 2006) and four colonies collected in October 2001 and 2003.

Before collection, the tumulus of each colony was collected to be dried and weighed later in the laboratory. Tumuli were only collected in the spring, because they weather away by midsummer. Each collected colony was returned to the laboratory in a plaster-lined box and killed by freezing. Colony contents (workers, sexual and worker brood, queen, and so on) were then sorted, counted, and weighed. We also extracted the fat of dark (old) workers, light (new) workers, and the darkest alates [visually determined as outlined by Tschinkel (1993, 1999)], giving energetic values for the standing colony biomass and the amount of colony production. Only values for dark (old) workers are reported because few of the new workers, and new sexuals were mature and thus had highly variable values. Total dry weights are used instead as an index of colony productivity. Dry, fat, and lean weights of individual workers yield measures of worker size.

Soil temperatures were measured with a four channel Hobo Pro Series eight (Onset Computer Corporation, Bourne, MA) datalogger during 2002. Temperatures were recorded at 30-min intervals for 48 h (96 measurements) at depths of 30 and 50 cm and in August an additional probe was placed at 80 cm. These depths corresponded to approximate locations of fungus gardens observed by us and by Lenczewski (1985). Temperature probes were placed in aluminum tubes and gently shoved into the ground at approximately the same time as colony collection. The exposed portions of the pipes were shaded with leaf litter. Data were recorded 5–7 May (compartment 215), 7–9 May (compartment 216), 12–14 May (219), 17–19 May (226), and 24–26 May in the field of 226 (226u). These periods spanned a longer period than anticipated because a series of cold fronts in the middle of the month lowered air temperatures considerably; consequently, data were not collected during these times. In August, probes were placed only in sites 219 (1–3 August), 226

(8–10 August), and 216 (21–24 August), for 48 h. Daily mean air temperatures did not significantly vary during August, either at the sites or at the weather station of Tallahassee Regional Airport located 1–10 km from any of the five sites.

Transects. In May 2003 and 2004, we laid out 100-by-4-m transects in three habitat types: disturbed rights of way (margins of paved roads, gas pipeline, or power line easements), undisturbed sandhills, and flatwoods sites high enough to contain *T. septentrionalis* populations. The number of nests was counted along each transect and five random tumuli were collected to provide an estimate of colony biomass. The sand was oven-dried (50°C) and weighed in the laboratory. The amount of bare sand was estimated with a sight-tube (James and Shugart 1970). Because pine biomass is thought to increase and oak biomass to decrease with frequency of fire (Glitzenstein et al. 1995), we made estimates of both by counting the numbers of trees and measuring trunk diameter at 1-m height of five to 10 randomly chosen trees occurring in each transect. The exact number of trees depended on their availability in each transect. Indices of pine and oak biomass were obtained by multiplying the average trunk diameter by the number of trees in each transect. Similarly, the number of nests was multiplied with the average tumulus weight in each transect to yield a total weight of excavated sand, producing a proxy for the amount of ant biomass in the area.

Data Analysis. Data were \log_{10} -transformed and analyzed with standard parametric analyses of variance and linear regression analysis using Statistica, version 6.1 (StatSoft 2003). Fractions were arcsine transformed (Sokal and Rohlf 1995). Visible outliers with standardized residuals >2.2 SD were excluded. When parametric assumptions were not met, nonparametric tests were used.

Results

Local Stand Characteristics, Temperature, and the Performance of *T. septentrionalis*. Compartments 215 and 216 were the poorest sites for *T. septentrionalis* colonies in terms of colony output ($F_{4,30} = 4.98$; $P < 0.01$; Fig. 1A). Only two colonies of 15 collected in these two sites produced sexual brood, whereas 15 of 23 colonies in the other three sites produced sexual brood. The three “good” sites produced nearly 10 times the amount of ant biomass (sexual and worker offspring) per colony as those in poor sites (6.55 ± 9.78 versus 64.5 ± 78.7 mg; $t = 3.33$, $df = 24$, $P < 0.05$). Colonies from the two poor sites had significantly fewer workers (152.4 ± 19.4 versus 235.2 ± 23.5 ; $t = 2.39$, $df = 34$, $P < 0.05$) and contained significantly smaller workers (average lean weight 0.369 ± 0.012 mg) than colonies from the other three sites (0.408 ± 0.012 mg; $t = 2.11$, $df = 34$, $P < 0.05$). Similarly, colonies from the poor sites had smaller fungus gardens (1740.3 ± 1102.8 versus 4591 ± 2959.1 mg; $t = 4.14$, $df = 33$, $P < 0.05$).

Differences in colony performance across sites corresponded to differences in soil temperature that seem

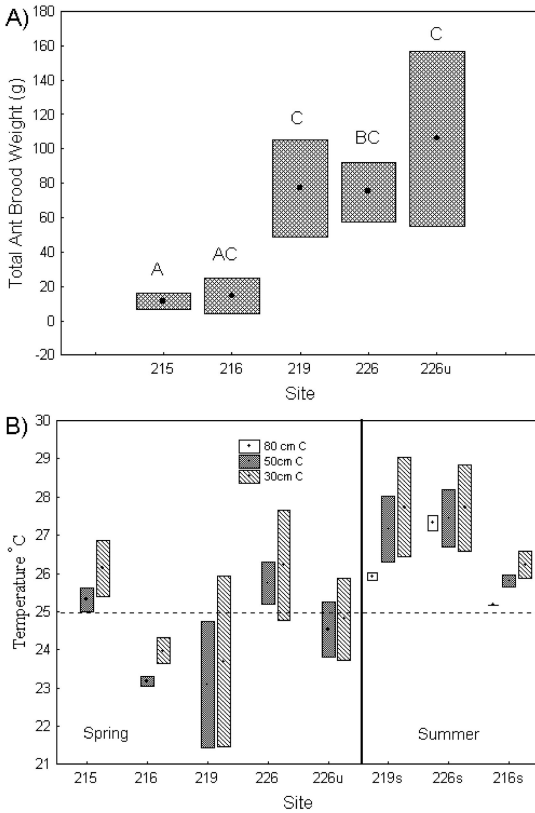


Fig. 1. (A) Weight (mean \pm 1 SD) of sexuals and workers produced per colony per site. Different letters indicate significant differences (Fisher least significant difference test, $\alpha = 0.05$). (B) Spring and summer (mean \pm 1 SD) temperature by site. The dashed horizontal line indicates 25°C, the reported optimal temperature for fungal growth (Powell and Stradling 1986).

to be functions of stand characteristics. Comparisons of soil temperature among sites were statistically significant even though differences were as little as 0.3°C. However, this difference may lie outside biological relevance. Therefore, no tests of significance are reported here. Compartments 215 and 216 were clear-cut several decades ago and now contain very few pines but possess a dense population of small-diameter oaks that in many places create an intact canopy. Compartment 216 also possessed a thick litter layer composed of oak leaves. Consequently, it is very shady and had the coolest soils in the spring and summer (Fig. 1B). In contrast, soils in compartment 215 were consistently warmer than 25°C, the reported optimal temperature for ant fungal growth (Powell and Stradling 1986) (Fig. 1B). Compartment 215 differed from 216 by experiencing a prescribed fire in July 2001. Summer burns typically cause high oak mortality (Glitzenstein et al. 1995) in addition to clearing ground litter. The productive sites had open canopies and numerous longleaf pines in the grass and pole stages in addition to mature cone-bearing trees, all of which are indicative of healthy pine forest

(Platt 1999). Oaks were common but sparsely distributed and wiregrass was abundant (an indicator of summer burns, the time of naturally occurring fires) (Myers 1990). However, only temperatures for two of these three sites approximated 25°C (Fig. 1B), compartment 226 was just as warm as compartment 215 yet still exhibited productive colonies.

Spatiotemporal Patterns of Digging Behavior and Distribution of Fungus Gardens. The ants excavate soil primarily in the spring, although some excavation occurs in the summer and autumn. In the spring, this activity more than doubles the size of their fungus garden chamber from $121.96 \pm 8.68 \text{ cm}^3$ in March to $316.72 \pm 41.02 \text{ cm}^3$ in May (Mann-Whitney $U = 98.5$, $P < 0.0001$). In March (2003 and 2004), the amount of fungus garden chamber volume per worker was smaller than in May 2003 (Kruskal-Wallis $H = 30.7$, $n = 63$, $P < 0.001$), suggesting that the workers enlarge the garden during the interval between March and May (Fig. 2). Fall digging seems to create new upper chambers that will be used in the subsequent spring.

Across the five sites used for the spring sample, the depth (mean \pm 1SD) of fungus gardens was similar (32.62 ± 3.88) ($F_{4,32} = 0.98$; $P > 0.43$). Colonies containing >300 workers may excavate a second chamber at a depth of $61.9 \pm 11.4 \text{ cm}$ ($t = 2.27$, $df = 34$, $P < 0.05$). Colonies containing more than one chamber contained more fungus garden ($5,019 \pm 3,771 \text{ mg}$; range 512–11,271) than single-chamber colonies ($2,783 \pm 1,670 \text{ mg}$; range 472–5,970 mg), but these differences were not statistically significant (Mann-Whitney $U = 91$, $P = 0.07$).

By midsummer (July–August), only the deepest chambers contained fungus garden. Of the 10 colonies excavated at this time, five had relocated all of their fungus to chambers $99 \pm 19 \text{ cm}$ in depth (range 72–115 cm). The sand from these lower chambers was apparently deposited in the upper chambers. The vertical shift in sand can be observed/verified because sand in lower strata is generally yellow and contrasts with the gray sand of upper layers (Brown et al. 1990).

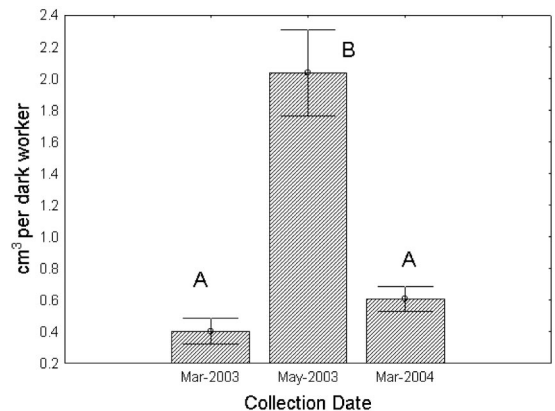


Fig. 2. Cubic centimeters (mean \pm 1 SE) of chamber volume per worker by collection date. Different letters indicate significant differences ($\alpha = 0.05$, Tukey's honestly significant difference test).

The average depth in August of the 10 colonies was not statistically greater than the spring sample of these compartments (48.78 ± 18.85 cm [summer] versus 32.13 ± 5.18 cm [spring]; Mann-Whitney $U = 39$, $P = 0.06$). It is noteworthy, however, that four of the five deepest nests were collected in compartment 226 where the deepest temperature probes were significantly warmer than the other two sites measured in the summer (Fig. 1B).

By fall (October–November), ants have moved the fungus garden back up to 37.5 ± 1.44 cm ($n = 4$). It is not likely that the ants reuse the chamber from the previous spring because it is common to find colonies that possess sand filled chambers adjacent to the chamber containing the ants. Ants probably remain in this chamber until the following spring. In November and early March, colonies contained ants clustered at the base of the chamber and an extremely small fungus garden (≈ 5 mm³).

A possible explanation of the annual vertical movement of fungus gardens is temperature. Across the five sites, the average spring temperature was $25.6 \pm 0.1^\circ\text{C}$ at 30 cm and $24.8 \pm 0.04^\circ\text{C}$ at 50 cm, or $\approx 25^\circ\text{C}$ (Fig. 1B). By summer, the temperature at these depths was $27.15 \pm 0.1^\circ\text{C}$ at 30 cm and $26.75 \pm 0.1^\circ\text{C}$ at 50 cm. At these depths, extreme highs were near 30°C (Fig. 1B). Even at 80 cm, the mean temperature was $26.11 \pm 0.05^\circ\text{C}$. At 80 cm, the variance in temperature approaches zero ($s^2 = 0.71$); the highest variation in which occurred in the open, wooded site (compartment 226), and was just 0.40°C (range 27.12 and 27.52°C) during the sampling period. Fungus gardens at the summer collection sites were 20–35 cm deeper than the deepest temperature sensor; therefore, soil temperatures surrounding the fungus garden must have been cooler and perhaps closer to 25°C . By autumn, soils seem to have cooled considerably below 25°C (30 cm, $19.68 \pm 0.05^\circ\text{C}$; 50 cm, $20.91 \pm 0.04^\circ\text{C}$), and by then colonies are dormant.

Does Tumulus Weight Describe Colony-Level Parameters? The numbers and weights of workers, fungus garden weight, and other measures of production increase significantly as tumulus weight increases (Table 1; Fig. 3A). Colonies having tumuli <150 g (or fewer than 97 old workers) did not produce sexuals. As the weight of the tumulus increases, the weight of the fungus garden and the amount of new ant biomass increase isometrically (slope = 1 on a log-log scale) across the entire range of tumulus weights (Table 1). This indicates that tumulus weight is a good surrogate measure for the amount of fungus garden and productivity of each nest. In contrast, the total weights, numbers, and energetic value of dark workers increased at a lower rate than tumulus weight. A 10-fold increase in tumulus weight resulted in only a 3.5–4-fold increase in dark worker number, total weights, and energetic value, respectively (Table 1). A 10-fold increase in tumulus weight resulted in a 1.2-fold increase in average worker weight, both before and after fat extraction (Table 1). Therefore, workers increased in size as colonies got larger. In contrast, total male biomass increased more rapidly than tumulus weight;

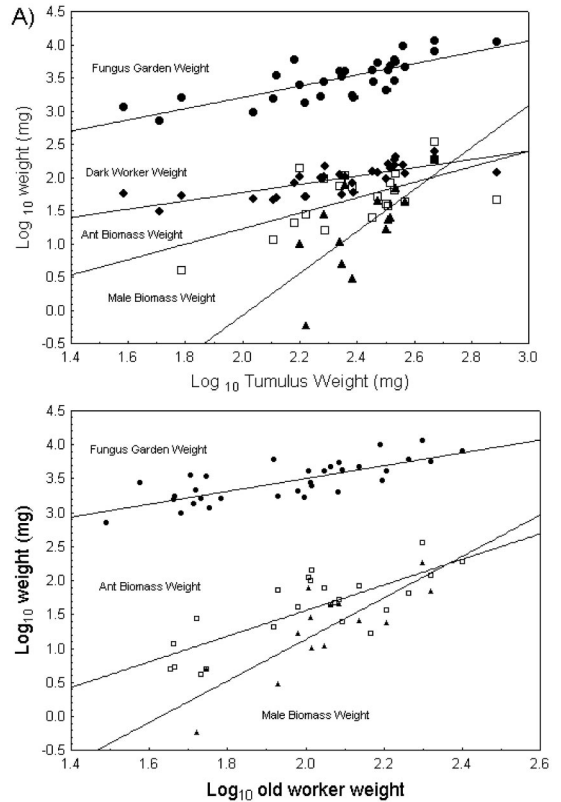


Fig. 3. (A) Log plots between tumulus weight and the weights of workers, fungus gardens, and worker number. (B) Log plots between old worker weight and fungus garden weight, new ant biomass weight, and male biomass weight. Solid circles indicate fungus garden weight; solid diamonds, weight of dark workers; open squares, total weight of all ant biomass production; and solid triangles, total weight of male biomass.

a 10-fold increase in tumulus weight resulted in a 100-fold increase in male biomass. Male number also increased with tumulus weight, but the rate was not significantly different from one ($t = 2.11$, $df = 12$, $P = 0.056$; Table 1). Neither total female weight nor number varied significantly with tumulus weight. Whereas total weight of new workers did not vary with tumulus weight, a 10-fold increase in tumulus weight resulted in a 40-fold increase in the number of new workers.

The relationships between colony size (total weight of old workers) and other colony-level measures were similar to those with tumulus weight. This relationship further supports the utility of tumulus weight as a convenient estimate of colony biomass. Colony size was positively related with all of the colony-level measures, except for the amount of worker fat and the percentage of fat of dry worker body weight (Table 2; Fig. 3B). The weights of fungus gardens, dark worker energetic value, and female and new worker investment (number and weights) increased isometrically with the weight of old workers. Similarly, large (>97 old workers) colonies also invested the same propor-

Table 1. Slope coefficients between tumulus weight and colony-level traits and tests of significance

Tumulus wt. as independent variable	r^2	B_1 (SE)	$H_0 = 0$	$H_0 = 1$
Fungus garden wt	0.61	0.849 (0.129)	$t_{28} = 6.558^{****}$	$t_{28} = 1.17^{n.s.}$
Dark worker wt.	0.60	0.622 (0.095)	$t_{29} = 6.542^{****}$	$t_{29} = 3.978^{****}$
Dark worker no.	0.61	0.561 (0.085)	$t_{28} = 6.611^{****}$	$t_{28} = 5.165^{****}$
Dark worker J	0.58	0.657 (0.104)	$t_{29} = 6.317^{****}$	$t_{29} = 3.299^{**}$
New ant biomass	0.39	1.165 (0.331)	$t_{19} = 3.517^{**}$	$t_{19} = 0.498^{n.s.}$
Total sex wt	0.21	1.945 (0.999)	$t_{14} = 1.947^{n.s.}$	$t_{14} = 0.946^{n.s.}$
Total female wt	0.023	0.683 (1.33)	$t_{11} = 0.509^{n.s.}$	$t_{11} = 0.238^{n.s.}$
Total male wt	0.47	3.157 (0.97)	$t_{12} = 2.256^{**}$	$t_{12} = 2.223^*$
New worker wt	0.00	0.02 (0.69)	$t_{14} = 0^{n.s.}$	$t_{14} = 1.42^{n.s.}$
Female no.	0.02	0.583 (1.067)	$t_{12} = 0.547^{n.s.}$	$t_{12} = 0.391^{n.s.}$
Male no.	0.46	2.933 (0.916)	$t_{12} = 3.20^{**}$	$t_{12} = 3.20^{n.s.}$
New worker no.	0.67	1.60 (0.257)	$t_{19} = 6.24^{****}$	$t_{19} = 2.349^*$
Mean worker wt	0.23	0.105 (0.035)	$t_{30} = 3.025^{**}$	$t_{30} = 25.57^{****}$
Lean wt	0.19	0.09 (0.035)	$t_{30} = 2.615^*$	$t_{30} = 26.0^{****}$
Fat	0.01	0.081 (0.139)	$t_{30} = 0.574^{n.s.}$	$t_{30} = 6.611^{****}$
% fat	0.004	0.02 (0.05)	$t_{30} = 0.361^{n.s.}$	$t_{30} = 19.6^{****}$

Data were \log_{10} transformed. The intercept was included in all analyses but is not reported here. **** $P < 0.0001$, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, and n.s., $P > 0.05$.

tion in female and new workers as small colonies. However, as colonies got larger, they invested a greater proportion (3 orders of magnitude) in the production of males and new workers (i.e., these slopes are positively allometric; Table 2). A 10-fold increase in the number of old workers resulted in a 1.6-fold increase in the average worker fat and lean weights (Table 2).

Estimated *T. septentrionalis* Production. The tumuli collected in the surveys (transects) ranged from 120 to 774 g, which is well within the range of the tumulus weights used in the calibration curves discussed above (38–774 g). This permitted the estimation of colony-level production from tumulus weight.

The average hectare in the ANF contains nearly 1,100 nests that excavate >430 kg of sand each spring. Density may exceed 2,000 nests per ha in any of the three sandhill habitat types, resulting in the excavation of >1,000 kg/ha sand (Fig. 4). Neither nest number nor the amount of sand excavated per hectare differed

among these habitats ($F_{2, 34} = 0.31$; $P > 0.72$ and $F_{2, 34} = 0.60$; $P > 0.55$, respectively; Fig. 4).

In subsequent analyses, the wooded transects (sandhills and flatwoods) were pooled and compared with transects in the open rights of way. This was justified because these areas are markedly different habitats. Rights of way lack trees and contain significantly more exposed sand than sandhills and flatwoods (58 versus 18%, Mann-Whitney $U = 28$, $P < 0.001$). Average tumulus weights (an index of colony productivity) were higher in rights of way than in intact forest (508.9 ± 31.7 versus 293.2 ± 23.6 g; $t_{35} = 5.41$, $P < 0.0001$). In wooded sites where tumuli were larger, there were also more nests. Thus, there is a positive correlation between nest number and mean tumulus weight ($r = 0.70$, $P < 0.01$). In contrast, colonies in disturbed rights of way seemed to be of similar size across all densities. There may be a slight negative trend between average tumulus weight and nest number, but this relationship is not statistically

Table 2. Slope coefficients between dark worker wt and colony-level traits and tests of significance

Dark worker wt. as independent variable	r^2	B_1 (SE)	$H_0 = 0$	$H_0 = 1$
Fungus garden wt	0.59	0.94 (0.142)	$t_{30} = 6.629^{****}$	$t_{30} = 0.4225^{n.s.}$
Dark worker no.	0.94	0.869 (0.038)	$t_{34} = 22.56^{****}$	$t_{34} = 3.45^{**}$
Dark worker J	0.96	1.041 (0.039)	$t_{32} = 29.96^{****}$	$t_{32} = 1.062^{n.s.}$
New wnt biomass	0.61	1.89 (0.321)	$t_{22} = 5.874^{****}$	$t_{22} = 2.773^*$
Total sex wt	0.61	2.54 (0.526)	$t_{15} = 4.873^{**}$	$t_{15} = 2.928^*$
Female wt	0.29	1.95 (0.874)	$t_{12} = 2.238^*$	$t_{12} = 1.087^{n.s.}$
Male wt	0.67	3.05 (0.613)	$t_{12} = 4.982^{****}$	$t_{12} = 3.344^{**}$
New worker wt	0.46	1.042 (0.325)	$t_{12} = 3.209^{**}$	$t_{12} = 0.129^{n.s.}$
Female no.	0.27	1.463 (0.676)	$t_{13} = 2.164^*$	$t_{13} = 0.685$
Male no.	0.57	2.525 (0.639)	$t_{12} = 3.949^{**}$	$t_{12} = 2.387^*$
New worker no.	0.58	1.172 (0.233)	$t_{18} = 5.026^{****}$	$t_{18} = 0.738^{n.s.}$
Mean worker wt	0.62	0.203 (0.029)	$t_{30} = 7.056^{****}$	$t_{30} = 27.48^{****}$
Lean wt	0.74	0.200 (0.023)	$t_{27} = 8.753^{****}$	$t_{27} = 34.78^{****}$
Fat	0.05	0.206 (0.153)	$t_{34} = 1.347^{n.s.}$	$t_{34} = 5.19^{****}$
Arcsine % fat	0.02	0.043 (0.057)	$t_{34} = 0.749^{n.s.}$	$t_{34} = 16.79^{***}$

Data were \log_{10} transformed. The intercept was included in all analyses but is not reported here. **** $P < 0.0001$, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, and n.s., $P > 0.05$.

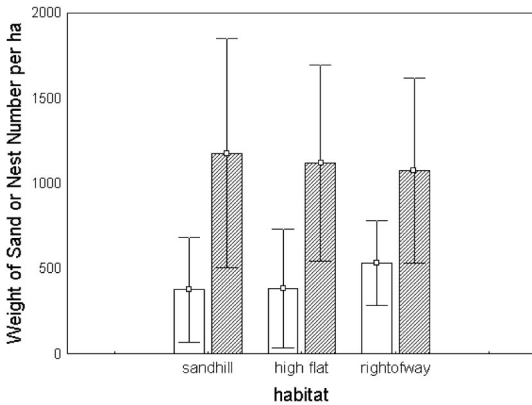


Fig. 4. Kilograms (mean \pm 1 SD) of sand excavated per hectare (unshaded bars) and the number of *T. septentrionalis* nests per hectare (shaded bars).

different from zero ($r = -0.47, P = 0.056$) (Fig. 5). Both of these trends were consistent between years and type of wooded site.

The total amount of excavated sand (nest number \times mean tumulus weight in each transect) of each transect was the greatest in transects with the least amount of oak biomass (Spearman's rank correlation = $-0.684, P < 0.05$) (Fig. 6). The two points located in the upper portion are not significant outliers (their removal does not change the correlations). In contrast, the total amount of excavated sand in each transect was greatest in those with the most pine biomass (Spearman's rank = $0.579, P < 0.05$) (Fig. 6). Oak and pine biomass were negatively correlated (Spearman's rank correlation = $-0.525, P < 0.05$). The total amount of excavated sand (and therefore ant biomass) is highest at intermediate levels (30–70%) of exposed sand and lowest at the extremes (the second order polynomial term is significant ($r^2 = 0.38; F_{2, 29} = 8.71; P < 0.001$) (Fig. 7).

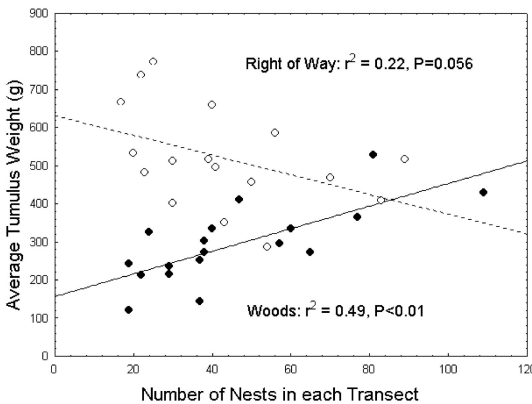


Fig. 5. Correlations between average tumulus weight and nest number in each transect. Open circles indicate right-of-ways, and solid circles indicate wooded areas.

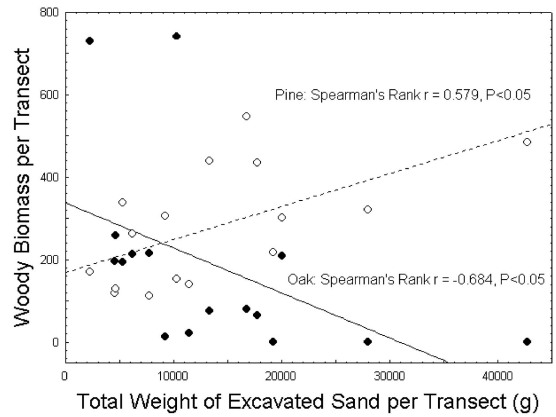


Fig. 6. Correlations between nest number and the biomass of oak and pine trees. Solid circles indicate an index of oak biomass, and open circles indicate an index of pine biomass.

Discussion

The purpose of this project was to describe the relationship between *T. septentrionalis* colony performance in relation to habitat characteristics. In areas characterized by a natural disturbance regime, i.e., where summer fires occur frequently (once every 3–5 yr), colonies contain more and larger workers, possess larger fungus gardens, and produce more offspring. Such fires tend to kill oaks and other hardwoods and thus enhance the productivity of longleaf pine and herbaceous species (Glitzenstein et al. 1995) by increasing insolation. Indeed, we found that colony biomass is positively correlated with pine biomass and negatively correlated with oak biomass. Additionally, in areas that are characterized by exposed patches of sand, *T. septentrionalis* colonies tend to be larger and more productive than areas covered with litter. These data strongly suggest that *T. septentrionalis* is an indicator insect species of intact, healthy longleaf pine sandhills.

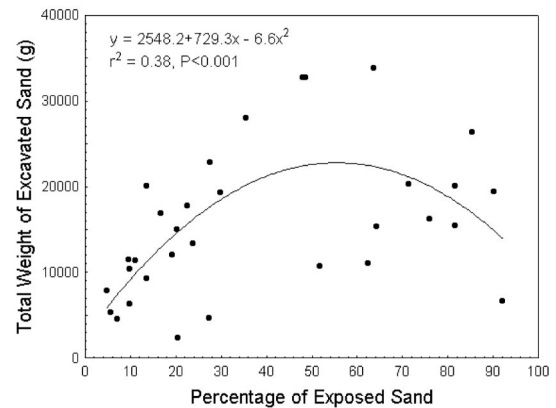


Fig. 7. Plot of the percentage of exposed sand against the total amount of excavated sand in each transect (mean tumulus weight multiplied by the number of nests).

Our results also suggest that soil temperature is the most important variable influencing the performance of *T. septentrionalis* colonies in sandhill ecosystems. The peak in the index of ant biomass at intermediate levels of exposed sand supports this conclusion. Whereas fungal growth and ant activity are probably higher in open, warm areas, extreme temperatures are lethal to the ants and fungus. *T. septentrionalis* is among the least desiccation-resistant ants in this forest (Hood and Tschinkel 1990), and attine fungi have limited tolerance to dry conditions and extreme heat (Powell and Stradling 1986). The seasonal vertical movement of fungus gardens also supports the importance of temperature and perhaps explains why this ant is not very common in longleaf pine flatwoods ecosystems where soils tend to be shallow and have a high water table (J.N.S., unpublished data). Interestingly, similar temperature-tracking behavior has been observed in leaf-cutting ants, which probably reflects similar humidity and temperature requirements across all higher attine fungi (LaPointe et al. 1998, Farji Brener 2000, Roces and Kleineidam 2000, Bollazzi and Roces 2002).

The pattern of colonies being more productive but less dense in open, sandy areas relative to colonies in shady, wooded sites also implicates temperature. This pattern may be explained by a higher rate of mortality of founding queens or incipient colonies in open areas. Foundress mortality may be high because they locate their fungus gardens ≈ 5 cm below the surface. In barren areas, temperatures approach 40°C (J.N.S., unpublished data), clearly exceeding the reported lethal temperature of ant fungus (Powell and Stradling 1986). Worker foraging may be reduced as surface temperatures are often much higher than 50°C, exceeding their lethal limit (indeed, this temperature even exceeds the tolerance of some desert ants; Cerdá et al. 1998). Larger colonies tend to be deeper, which also suggests that small colonies may not be able to dig as efficiently as larger colonies. Another important factor may be fungal substrate (food) availability. Open, warm areas may have less fungal substrate because they lack a diversity of plants, especially trees producing preferred substrates such as caterpillar frass and catkins (Seal 2006). Colonies in open, hot areas may be at significant disadvantage because of extreme heat and lack of food. Experiments will need to be conducted to determine the relative importance of soil temperature and fungal substrate availability on colony performance.

The distribution and performance of *T. septentrionalis* in the ANF is remarkably similar to available data on leaf-cutting ants. Leaf-cutting ant colonies tend to have low nest densities in primary rain forests (0.045 nests per ha) (Rockwood 1973, Fowler et al. 1984, Vasconcelos and Cherrett 1995) and densities may be 10–30 times higher in cleared areas and secondary forests (Jonkman 1979, Vasconcelos and Cherrett 1995, Wirth et al. 2003). Furthermore, the biomass totals of *T. septentrionalis* seem to be comparable with those from leaf-cutting ants in tropical systems. Using the values estimated by Weber (1972) from a colony

excavation, an *Atta colombica* (Guérin-Ménéville) colony contains 1–2.5 million workers or 7.48–9.78 kg of ant biomass. Therefore, using the densities described above for tropical forests, a hectare may contain 50,000–500,000 *Atta* workers or 330–4400 g of ants. On a per worker basis, a hectare of pine forest contains on average 88,000–600,000 *T. septentrionalis* workers. However, their workers are smaller than *Atta* workers. Thus, this amounts only to 35–780 g of *T. septentrionalis* ants per hectare, with an upper limit of nearly 2,000 g (>1.5 million workers) on the densest plots. These values assume a mean density of 1073 nests per ha (range 100–2725) that contain 205 workers (range 82–560) weighing 117 mg (range 31–728). So, even though *T. septentrionalis* are just as numerous as *Atta* ants per hectare, *Atta* ants may comprise an order of magnitude more biomass in a tropical forest than *T. septentrionalis* in pine forests. But this comparison must be placed in the context of the distribution of colonies and the features of the respective habitats. First, the main effects of an *Atta* colony on a tropical forest are probably more local. Their herbivory, for example, has the greatest impact on trees near the nest, and the effects on larger aspects of forest ecology seem to be negligible (Wirth et al. 2003). Second, pine forests are not nearly as productive as tropical rain forests. For example, pine flatwoods have a net carbon fixation rate at 860 g C m⁻² yr⁻¹ (Abrahamson and Harnett 1990), whereas the rate for climax canopy trees of tropical forests is 5,168.4 g C m⁻² yr⁻¹ (Whitmore 1990). Given the more even distribution of *T. septentrionalis* throughout the relatively unproductive southeastern pine forests, it would seem very likely that these ants are a crucial component of the function of these ecosystems.

What is the impact of *T. septentrionalis* on pine forests? The 0.5-metric ton or so of sand excavated per hectare by *T. septentrionalis* each spring goes toward the production of an average 3.5 kg of fungus garden per hectare (range 0.51–12.1 kg). Because fungus garden weight fluctuates seasonally from a minuscule amount to >10 kg each year, most of the annual production of fungus garden will be lost as metabolic heat. The metabolic heat will be transferred toward the production of ant biomass or deposited as solid waste by the time the ants become inactive in the autumn. It is possible that this represents either a significant gain or loss of nutrients to these nutrient-poor pine forests. *T. septentrionalis* ants have been observed to deposit fungus garden refuse in piles outside of nests on the surface and also in chambers that were probably used the previous spring. As in other attines, these refuse pockets could serve as reservoirs of nutrients (Haines 1978, Farji Brener and Ruggiero 1994), especially phosphorous. Phosphorous deposits from *Trachymyrmex* refuse piles almost certainly increase plant growth (Torres et al. 1999). It also has been hypothesized that leaf-cutting ants “prepare” abandoned fields and grasslands for invasion of forest plants by turning and fertilizing the soil (Jonkman 1978; Farji Brener and Silva 1995b, 1996; Garrettson et al. 1998). In a similar manner, *T. septentrionalis* might be essen-

tially "seeding its demise" by accelerating succession, which would eventually cool the soil and lower ant productivity. However, a succession from field to hardwood forest is unlikely if fires occur on a natural frequency (Platt 1999).

A contrasting possibility is that *T. septentrionalis* decreases soil fertility by bringing infertile soil to the surface. Haines (1983) hypothesized that leaf-cutting ant colonies can cause the loss of soil nutrients. Pocket gophers in pine forests have been shown to do the same (Simkin and Michener 2004). In the pine forests of the ANF >85% of the available soil nutrients occur in the top 5 cm of soil (W.R.T., unpublished data). In some areas, colonies of *T. septentrionalis* may collectively excavate more than a metric ton of soil per hectare each year. This rivals amounts reported for all other ants (420 kg–10,000 kg · ha⁻¹ yr⁻¹) in other ecosystems (Folgarait 1998). On the most productive plots where >1 metric ton of sand per hectare is excavated each spring, this amounts to an annual soil displacement of 0.0063 cm/yr. A complete displacement of the top 5 cm of soil would take ≈800 yr. This assumes a density of sand (SiO₂) of 1,600 kg/m³. This estimate on the amount of soil displacement does not include excavations for deeper chambers that the ants conduct in late spring and summer, sand from which is used to fill upper chambers. Therefore, over the course of a year these ants likely displace an amount exceeding, perhaps nearly double, the amount they displace in the spring and it would take 400 yr for complete displacement of topsoil.

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