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Suburban sprawl: environmental features affect colony social and spatial structure in the black carpenter ant, *Camponotus pennsylvanicus*

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Abstract. 1. In social insects, the number of nests that a colony inhabits may have important consequences for colony genetic structure, the number of queens, sex allocation, foraging efficiency, and nestmate recognition. Within the ants, colonies may either occupy a single nest (monodomy) or may be organised into a complex network of nests and trails, a condition known as polydomy.

2. The current study is a large-scale, long-term, comprehensive field examination of various features of colony social and spatial structure in the facultatively polydomous black carpenter ant, *Camponotus pennsylvanicus* (DeGeer). The study examined the density, persistence, and the spatiotemporal distribution of colonies across a gradient of land disturbance associated with urban development. The temporal and spatial pattern of nest use was compared between fragmented landscapes where nesting sites were interspersed among human-built structures (urban plots) and less disturbed landscapes with higher tree density (suburban plots). In addition, nesting site fidelity and changes in colony spatial structure were monitored over 7 years.

3. Long-term monitoring and extensive sampling over a large spatial area allowed the first comprehensive insight into the spatiotemporal dynamics of colony and population structure in *C. pennsylvanicus*. A total of 1113 trees were inspected over 233 ha. *Camponotus pennsylvanicus* were active on 348 of the 1113 trees (31%) and these represented 182 distinct colonies. The colonisation rate remained relatively stable over 7 years suggesting that an equilibrium point had been reached. Relative to the suburban plots, tree density was 65% lower in the urban plots. The proportion of trees colonised by *C. pennsylvanicus* was significantly higher in the urban plots suggesting that intraspecific competition for nesting sites may be especially high in areas with lower tree density. Colony spatial structure also differed significantly between habitats and a higher incidence of monodomy was observed in the urban environment. The average number of trees per colony across all subplots was 1.95 (range 1–4) indicating that *C. pennsylvanicus* are weakly polydomous.

4. The composite picture that emerges for *C. pennsylvanicus* colonies in the urban habitat is a chain reaction of events: (i) the urban habitat has a lower tree density, (ii) lower tree density results in higher tree colonisation rate, (iii) higher tree colonisation rate results in simpler colony spatial structure (i.e. higher incidence of monodomy), and (iv) simpler colony spatial structure results in numerically smaller colonies. Long-term monitoring of the spatiotemporal pattern of nest site use in selected colonies revealed a unique trend. While worker counts in selected colonies remained relatively stable throughout the course of the study, colony spatial structure changed considerably with 28% of colonies experiencing a change. Furthermore, the likelihood of detecting a

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change in colony spatial structure increased with the amount of time passing from the initial inspection.

5. In conclusion, tree density has a significant effect on a number of important colony features in *C. pennsylvanicus*. Besides tree density, other environmental features such as human-built structures cause habitat fragmentation and may act as natural barriers to worker dispersal and/or foraging. Such barriers may ultimately affect the social and/or spatial structure at both the colony and the population level.

Key words. Black carpenter ant, *Camponotus pennsylvanicus*, colony spatial structure, foraging, nest fidelity, polydomy.

Introduction

Polydomy, defined as the presence of multiple nests within a more or less genetically homogeneous colony (reviewed in Debout *et al*., 2007), is a unique feature of two eusocial insect groups: ants and termites. In contrast to other eusocial insects, such as bees and wasps, the terrestrial nature of workers facilitates social contact between nests via trails and promotes colony cohesion and cooperation. In ants, the extent of polydomy is extremely variable and may depend on various social and ecological factors (Debout *et al*., 2007). The continuum ranges from small colonies that are monodomous and monogynous to extremely large supercolonies that are highly polydomous and polygynous (reviewed in Holway *et al*., 2002). In monogynous species living in relatively small colonies, polydomy may be closely tied to ecological factors such as foraging strategy (Hölldobler & Lumsden, 1980; McIver, 1991) and/or may be a consequence of strong queen–worker conflict (Backus, 1993; Herbers *et al*., 2001). In highly polygynous species living in dense and spatially vast supercolonies, polydomy may be a result of various social factors, such as overcrowding (e.g. red imported fire ants: Tschinkel *et al*., 1995), colony reproduction by budding (e.g. Pharaoh ants: Buczkowski & Bennett, 2009), or even intracolony competition for resources (e.g. odorous house ants: Buczkowski & Bennett, 2006). Ultimately, the colony's spatial structure is shaped by a complex interaction between social and ecological factors producing a seemingly endless array of possibilities found within the Formicidae.

Polydomous colonies are organised into complex and constantly changing networks of nests and trails and numerous factors may affect the establishment and the extent of polydomy. Approximately 84% of polydomous ant species examined to date are facultatively polydomous (Debout *et al*., 2007) demonstrating the potential for extensive variation in the degree of polydomy even within a single species. Monodomous colonies may become polydomous in response to various environmental factors such as the discovery of attractive nesting and/or feeding locations (Buczkowski & Bennett, 2006), response to variation in patch quality within a territory (Pfeiffer & Linsenmair, 1998; Heller & Gordon, 2006), or simply a constraint on nest size (Levings & Traniello, 1981). Likewise, polydomous colonies may revert to monodomy due to conflicts among reproductive females, the destruction of alternative nesting sites, exhaustion of local food sources, or seasonal weather cycles (Herbers & Grieco, 1994; Buczkowski & Bennett, 2008). Some species may be seasonally polydomous (Alloway *et al*., 1982; Snyder & Herbers, 1991; Dillier & Wehner, 2004; Elias *et al*., 2005; Heller & Gordon, 2006; Buczkowski & Bennett, 2008), whereby the colony undergoes an annual fission–fusion cycle depending on ambient temperature and the seasonal availability of food. Furthermore, polydomy in certain species, such as the odorous house ant, may be regulated by environmental characteristics such as urbanisation (Buczkowski, 2010).

Despite numerous theoretical predictions concerning polydomy (reviewed in Debout *et al*., 2007) and a handful of empirical studies, the ecology of polydomy remains relatively unexplored (Debout *et al*., 2007). To advance our understanding of polydomy, the present study investigated various features of colony social and spatial structure in the facultatively polydomous black carpenter ant, *Camponotus pennsylvanicus* (DeGeer). *Camponotus* is the second largest ant genus (Hölldobler & Wilson, 1990; Bolton, 1995; Brady *et al*., 2000), with approximately 900 species worldwide, of which 50 are found in the U.S.A. and Canada (Bolton, 1995). *Camponotus* spp., collectively known as carpenter ants, are an important ecological component of most forest environments, where they serve as predators, scavengers, and food for other animals (Hansen & Klotz, 2005). Of the Nearctic species, *C. pennsylvanicus* is one of the most widespread species and one that is ecologically and economically important. The black carpenter ant, *C. pennsylvanicus*, is the most common *Camponotus* species in central and eastern U.S.A. (Wheeler, 1910) and is the principal structural pest in urban areas (Fowler, 1986).

Mature carpenter ant colonies are monogynous and may be partitioned into parent and satellite nests (Sanders, 1964; Hansen & Klotz, 2005). Nests are connected by trails that facilitate the exchange of workers, brood, and food and help maintain colony integrity. The queen, eggs, early-instar larvae, and workers are located in the parent nest, usually in a standing live tree. Workers, mature larvae, pupae, and winged reproductives are found in satellite nests, which are often excavated in drier, solid wood. The number of satellite nests per colony varies, as does their demographic composition (Hansen & Klotz, 2005). Furthermore, the distribution and location of carpenter ant nests vary among species and habitat. Unlike tramp ants that often build shallow, ephemeral nests, carpenter ants invest heavily into nest construction and excavate permanent nesting sites that are initially founded by individual mated females. Thus, the colonies are initially monogynous and monodomous, but may become polydomous as the colony grows and the colony's spatial and nutritional requirements change. While the location of the primary nesting site is generally decided by the founding female, the location and number of satellite nests is affected by various biotic (e.g. tree species, local intra- and interspecific competition) and abiotic (e.g. temperature, humidity) factors (Hansen & Akre, 1985; Hansen & Klotz, 2005).

The current study is a large-scale, long-term, comprehensive examination of *C. pennsylvanicus* colony and population dynamics within an urban habitat. The study examined the density, persistence, and the spatiotemporal distribution of colonies across a gradient of land disturbance associated with urban development. The dynamics of colonies were compared between fragmented landscapes where nesting sites were interspersed among human-built structures (e.g. buildings, streets, parking lots) and less disturbed landscapes with higher tree density (e.g. city parks, suburban forest remnants, nature preserves). The main goal of the study was to compare colony spatial and social structure in *C. pennsylvanicus* colonies living in highly disturbed urban habitats and less disturbed suburban habitats and to test the hypothesis that the degree of habitat disturbance has an effect on colony structure and colony size. Specifically, based on preliminary observations of colonies in both habitats, I predicted that urban colonies would have a simpler colony spatial structure and would be numerically smaller. In addition, nesting site and foraging trail fidelity and changes in colony spatial structure were monitored over the course of the study to detect possible changes in spatiotemporal pattern of nest site use in *C. pennsylvanicus*.

Materials and methods

Study site

The abundance and spatial distribution of *C. pennsylvanicus* colonies was characterised within a large plot on the campus of Purdue University, West Lafayette, Indiana, U.S.A. (Fig. 1). The habitat is a managed urban landscape with numerous buildings, streets, and landscaping consisting of an abundance of trees and shrubs, park-like areas, lawns, and mulched beds. The plot totalled approximately 1 mi^2 (233 ha; Table 1) and was divided into six subplots: Hilltop Apartments (#1; 34 ha, initially examined in 2009), Horticulture Park (#2; 21 ha, initially examined in 2004), Purdue Village (#3; 46 ha, initially examined in 2005), Jischke Drive (#4, 39 ha, initially examined in 2008), McCormick Road (#5; 54 ha, initially

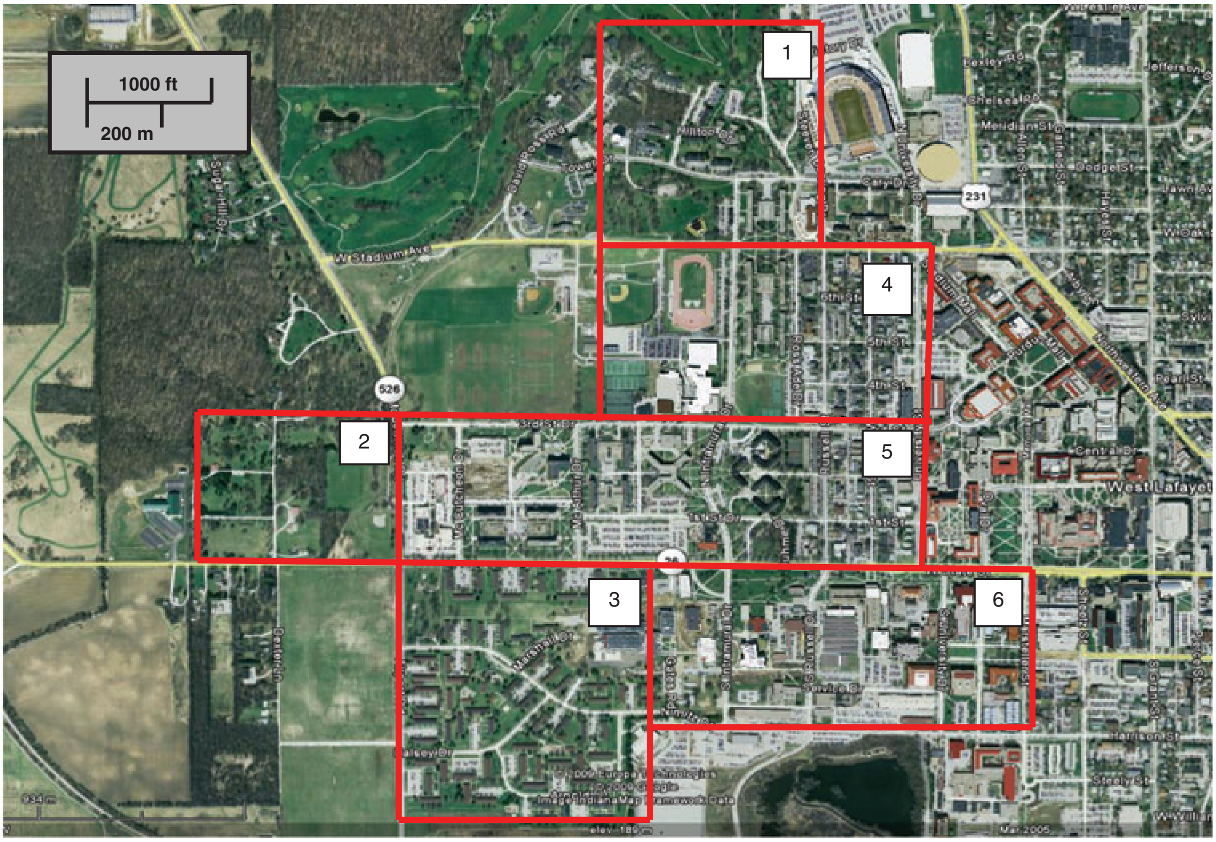

Fig. 1. Aerial orthophoto of the research site – Purdue University campus and surrounding areas. Numbers represent urban and suburban plots examined in the study: (1) Hilltop Apartments, (2) Horticulture Park, (3) Purdue Village, (4) Jischke Drive, (5) McCormick Road, and (6) State Street.

Table 1. Habitat attributes and the prevalence of black carpenter ants within the study sites.

Site name and number	Site type	Area (ha)	Trees inspected	Trees colonised	% trees colonised	Total colonies	Tree density
Hilltop Apartments (1)	Suburban	34	148	36	24%	18 (36)	4.3
Horticulture Park (2)	Suburban	21	209	50	25%	24 (50)	10.0
Purdue Village (3)	Suburban	46	256	84	33%	43 (84)	5.6
	Total	101	613	170	—	85 (170)	—
	Mean ± SEM	34 ± 7	204 ± 31	57 ± 14	27 ± 3%	28 ± 8	6.6 ± 1.7
Jischke Drive (4)	Urban	39	158	55	35%	30 (55)	4.1
McCormick Road (5)	Urban	54	122	38	31%	23 (38)	2.2
State Street (6)	Urban	39	220	85	36%	44 (85)	5.6
	Total	132	500	178	—	97 (178)	—
	Mean ± SEM	44 ± 5	167 ± 29	59 ± 14	35 ± 2%	32 ± 6	4.0 ± 1.0
All sites	Cumulative total	233	1113	348	—	182 (348)	—
All sites	Cumulative mean ± SEM	39 ± 5	186 ± 21	58 ± 9	31 ± 2%	—	5.3 ± 1.1

Total colonies indicates the total number of colonies discovered within the study plot. The total number of trees that the colonies occupied is given in parentheses. Tree density is the number of trees per hectares.

examined in 2007), and State Street (#6; 39 ha, initially examined in 2006). The subplots were categorised as either having a relatively low level of urbanisation (plots 1, 2, and 3; ‘suburban plots’, Fig. 1) or a high level of urbanisation (plots 4, 5, and 6; ‘urban plots’). This distinction was made based on satellite imagery (Fig. 1) and preliminary on-the-ground inspections to estimate habitat characteristics such as tree distribution and density and the degree of urbanisation. Suburban plots were on the periphery of town and were generally bordered by agricultural fields or forests, had relatively few streets and buildings, and consisted of park-like areas with a relatively high tree density (Table 1). In contrast, urban plots contained numerous human-built structures such as buildings, parking lots, and roads and had fewer green areas. Availability of green areas such as lawns and fields was an important feature as green areas allowed for colony connectivity and dispersal between potential nesting sites. Specifically, carpenter ants readily trailed over grassy areas and generally avoided trailing over man-made structures such as buildings or roads. Plot size and boundaries were determined based on a combination of two factors: habitat characteristics (i.e. the degree of urbanisation) and the location of major roads, which constituted plot boundaries.

Spatial organisation of colonies

Visual inspections were performed to identify trees occupied by the black carpenter ant, *Camponotus pennsylvanicus*, the predominant carpenter ant species in urbanised areas in central U.S.A. (Hansen & Klotz, 2005). The ants were identified to species based on worker morphology (Hansen & Klotz, 2005) and other *Camponotus* species were rarely encountered. The study was comprehensive in that all trees greater than 5 cm diameter were inspected within the research site. Preliminary inspections of newly planted, young trees (<5 cm diameter) revealed that such trees were not suitable nesting sites and did not contain colonies. All trees colonised by the ants were identified to genus level based on leaf and bark characteristics and different species within the same genus were placed in the same common name category. For example, all *Quercus* species were broadly categorised as oaks. Carpenter ants nest almost exclusively in wood and will inhabit both living and dead trees, as well as rotting logs and stumps and wood material inside of human-built structures.

Mature carpenter ant colonies are generally polydomous and colonies consist of a focal parent nest and one or more satellite nests. The degree of polydomy (i.e. the number of trees occupied by each colony) was determined for all colonies within each plot. This was accomplished by inspecting the ground for ant trailing activity and any trees connected by a clearly defined foraging trail were classified as belonging to the same colony. In rare instances when colony boundaries could not be easily determined, aggression assays were performed in the field to determine colony membership. A foraging worker was collected on one tree and was paired up with a worker from another tree. The two workers were held for 1 min in a glass vial (25 mm diameter by 55 mm tall) coated with Fluon halfway down. The aggressive responses were so strong that they were scored as either 0 = no display of aggression or 1 = intense aggression with prolonged biting and formic acid spraying. Three replications were performed for each pairing. The results of the aggression tests were then used to help determine individual colony boundaries. In addition to recording the colony spatial structure I also estimated colony size as indicated by the number of foraging workers present on each tree. The total number of workers present on the trunk, the main branches, and the ground 1.5 m around each tree was recorded. *Camponotus pennsylvanicus* are nocturnal and all inspections were performed with the aid of a flashlight starting 1 h after sunset and continued through the night until all trees were inspected. All surveys were conducted from May to August when the colonies are the most active. In addition, the distance between nests (trees) was recorded to help estimate the size of each colony’s territory. The location of all colonised trees was recorded using a GPS unit and a numbered metal identification tag (Forestry Suppliers Inc., Jackson, Mississippi) was nailed to the base of each tree to help locate specific trees over the course of the study.

Nesting site and foraging trail fidelity

Changes in various biotic and abiotic factors can alter the suitability of a nesting location and many ant species respond by moving nests to a more favourable location. Carpenter ants, however, invest a substantial amount of effort into constructing and maintaining the nest and alternative nesting sites may not be readily available and may be subject of intense competition from conspecifics. To assess the temporal and spatial patterns of nest use in *C. pennsylvanicus* short-term and long-term changes in nest site use were monitored by censusing selected colonies within each experimental plot. In the first series of inspections (short-term changes), spatial and temporal nest fidelity was determined by re-inspecting all nests approximately 1 year after the initial inspection dates listed above. Nine colonies were censused in each plot: three colonies nesting in single trees, three colonies nesting in pairs (two trees per colony), and three colonies nesting in triplets (three trees per colony). Thus, 54 colonies occupying a total of 108 trees were inspected. In a second series of inspections (long-term changes), all colonies mentioned above were inspected again in 2010 (with the exception of Hilltop Apartments where the 2010 inspection coincided with the 1 year inspection). During both short-term and long-term inspections worker counts were taken again at each tree to determine possible changes in colony activity. Any changes in colony spatial structure such as abandoning or adding nesting sites were noted.

Statistical analysis

All data analyses were performed using SAS 9.2 statistical software (SAS Institute, 2008). Logistic regression (PROC GENMOD) was used to examine whether tree colonisation rate differed between habitats. A t-test (PROC TTEST) was used to examine whether the average worker count differed between habitats. Differences in trail length and colony nesting structure were examined by using χ^2 analysis (PROC FREQ). A proportional Z-test was used to examine the evenness of worker distribution among the nests. ANOVA tests were conducted to determine the effect of habitat type, time, and colony spatial structure on worker counts. In addition an ANOVA test was used to analyse the relationship between colony spatial structure (total number of nests per colony) and colony size (total number of workers per colony). This was accomplished by using the PROC MIXED procedure on log transformed data. The ANOVA was followed by post-hoc Tukey's HSD tests to separate the means.

Results

A total of 1113 trees were inspected over 233 ha and 348 trees (31%) were colonised by *C. pennsylvanicus* (Table 1). The 348 trees represented 182 distinct colonies, of which 85 (47%) were found in the suburban habitat and 97 (53%) in the urban habitat. The average tree density was 6.6 ± 1.7 trees ha^{-1} in the suburban plots (low level of urbanisation) and 4.0 ± 1.0 trees ha^{-1} in the urban plots (high level of urbanisation). Thus, tree density was 65% lower in the urban plots where more land was dedicated to human-built structures such as buildings, streets, and parking lots. The suburban plots contained a total of 613 trees of which 170 were colonised (27%). In contrast, the urban plots had a significantly higher proportion of trees occupied by carpenter ants and 35% of all trees (178 out of 500) were colonised (d.f. = 1, $\chi^2 = 7.90$, $P = 0.005$). Overall, trees in the urban plots were 1.4 times more likely to be colonised by carpenter ants relative to trees in the suburban plots.

The average number of workers observed on the trees within the whole study site was 42 ± 3 and the median was 34 (Table 2). The counts ranged from five workers to 230 workers per tree and 72% of all trees had fewer than 50 workers, 22% had counts ranging from 51 to 100 workers, and 7% had counts greater than 100 workers (Fig. 2a). This breakdown is rather arbitrary, but our experience indicates that colonies with fewer than 50 active foragers are generally small, colonies with 50–100 foragers can be considered medium, and colonies where >100 active foragers are observed can be considered large. The average ant count was 40 ± 4 workers per tree in the suburban habitat. Within the urban habitat, the average ant count was slightly higher, 45 ± 5 workers

Table 2. Trailing activity in black carpenter ants and colony nesting structure.

	Trailing activity and trail length					Colony nesting structure			
Site	Average ant count	Average trail length (m)	% trails <5 m	% trails 5–15 m	% trails >5 m	% single	% double	% triple	% quadruple
Hilltop Apartments	33 ± 4	11 ± 2 (4–27)	17	61	22	28	44	28	0
Horticulture Park	48 ± 5	12 ± 2 (1–32)	27	46	27	25	42	33	0
Purdue Village	38 ± 3	12 ± 1 (2–30)	20	56	24	28	49	23	0
Mean ± SEM	40 ± 4	12.0 ± 0.8	21 ± 3	54 ± 4	25 ± 1	27 ± 1	45 ± 2	28 ± 3	0 ± 0
Jischke Drive	54 ± 5	12 ± 1 (2–23)	4	65	31	33	43	17	3
McCormick Road	38 ± 5	13 ± 1 (5–22)	7	60	33	48	39	13	0
State Street	43 ± 4	14 ± 1 (5–34)	5	57	38	27	55	16	2
Mean ± SEM	45 ± 5	13.3 ± 0.7	5 ± 1	61 ± 2	34 ± 2	36 ± 6	46 ± 5	15 ± 1	2 ± 1
Cumulative mean ± SEM	42 ± 3	12.6 ± 0.4	13 ± 4	58 ± 3	29 ± 2	32 ± 3	45 ± 2	22 ± 3	1 ± 1

All values reported as mean ± SEM. Average ant count is the mean number of foraging workers observed on trees within the plot. For trail length, ranges are given in parentheses. Colony nesting structure refers to the percentage of colonies nesting in one, two, three, or four nests (trees).

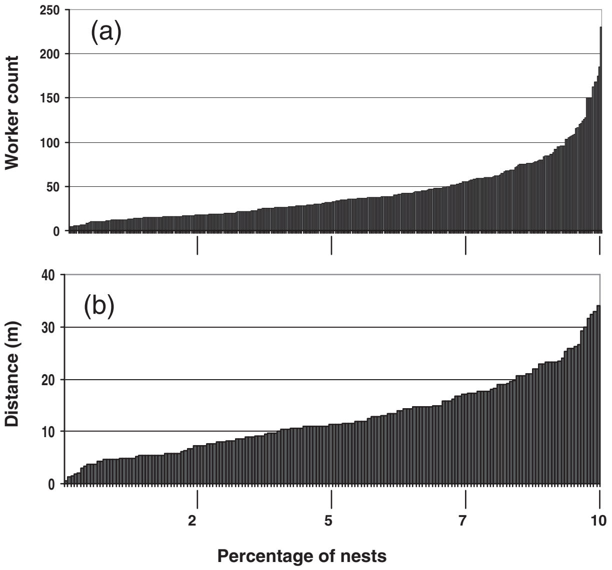

Fig. 2. Distribution charts showing (a) worker counts on individual trees ($n = 348$) and (b) length of trails (in metres) separating the individual trees ($n = 166$). For both charts, data are summarised over all urban and suburban plots.

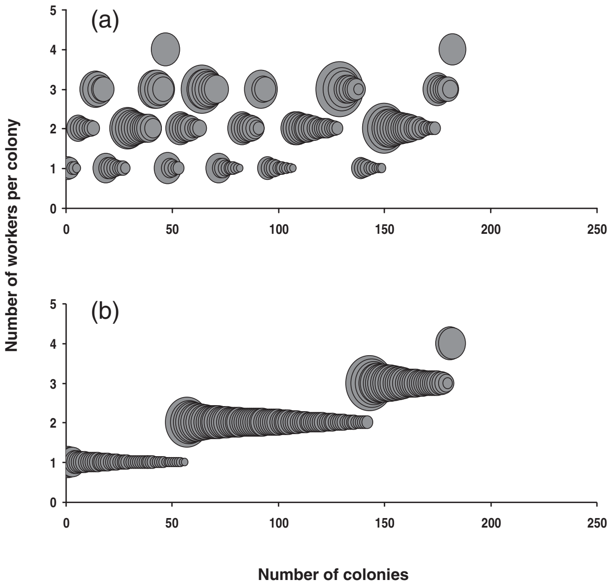

Fig. 3. The relationship between colony spatial structure (total number of nests per colony) and colony size (total number of workers per colony). (a) Data sorted by plot, from left to right, the six bubble groupings represent individual plots, Hilltop Apartments, Jischke Drive, Horticulture Park, McCormick Woods, Purdue Village, and State Street. (b) Data sorted by nest number (combined for all plots). For both charts, each bubble represents a single colony and bubble size is proportional to the actual colony size (total worker count). Data for all 182 colonies is presented.

per tree, but not significantly different from the suburban habitat (d.f. = 84, $F = 1.52$, $P = 0.07$). The average length of trail(s) between trees was measured to determine to extent of the colony's foraging range and foraging distance (Fig. 2b). Overall, the average distance between colonised trees (i.e. colony's nests) was 12.6 ± 0.4 m. The distance ranged from less than 1 m to 34 m and 13% of all nests were separated by trails less than 5 m, 58% were separated by trails between 5 and 15 m, and 29% were separated by trails longer than 15 m (Table 2 and Fig. 2). The average distance between nests was 12.0 ± 0.8 m within the suburban plots. Within the urban plots, the average distance was slightly higher, 13.3 ± 0.7 m, but not significantly different from the suburban plots (d.f. = 5, $F = 0.53$, $P = 0.75$). However, the distribution of trail lengths [defined as short (<5 m), medium (5–15 m), or long (>15 m)] was uneven between habitat types and trees within the suburban plot were more likely to be separated by a shorter foraging trail (d.f. = 1, $\chi^2 = 6.16$, $P = 0.013$). This was largely due to colonies within the suburban habitat having a much greater proportion of short trails, 21 ± 3%, relative to colonies in the urban habitat where short trails comprised only 5 ± 1% of all trails. Colony spatial structure (defined as the number of trees occupied by a colony) also differed significantly between habitats types (d.f. = 1, $\chi^2 = 2.12$, $P = 0.015$) and colonies nesting in the urban environment were more likely to nest in fewer trees. In the urban environment, 36 ± 6% of all colonies were monodomous vs. 27 ± 1% in the suburban environment (Table 2). Further, only 15 ± 1% of colonies in the urban environment nested in three trees vs. 28 ± 3% in the suburban environment. Across all study plots, 56 (32 ± 3%) colonies nested in single trees, 86 (45 ± 2%) nested in two trees, 38 (22 ± 3%) nested in three trees, and 2 (1 ± 1%) nested in four trees. The average number of trees per colony was 1.95 ± 0.06 (range 1–4).

The analysis of the relationship between colony spatial structure (total number of nests per colony) and colony size (total number of foraging workers per colony) revealed that colonies with more nests had significantly greater worker counts (d.f. = 2, $F = 60.62$, $P \leq 0.0001$; Fig. 3). Across all plots, monodomous colonies had an average of 37 ± 3 workers, two nest colonies 90 ± 6 workers, three nest colonies 127 ± 11 workers, and four nest colonies 134 ± 3 workers. Two nest colonies had significantly higher worker counts relative to single nest colonies (d.f. = 177, $t = -8.77$, $P \leq 0.0001$) and three nest colonies had significantly higher worker counts relative to two nest colonies (d.f. = 177, $t = 3.18$, $P = 0.005$). Furthermore, proportional Z-test analysis revealed that the distribution of workers among the trees (nests) was uneven with one tree generally having a much higher worker count relative to the remaining trees. Worker distribution among the trees was uneven in 74% of two nest colonies and 95% of three nest colonies.

Colony activity as indicated by the number of workers foraging on trees selected for multiple year inspections remained relatively stable over the course of the study (Table 3). The initial worker count across all six subplots was 40 ± 4 workers per tree during the initial inspection, not significantly different from the 1 year inspection when 39 ± 2 workers were observed (d.f. = 283, $t = -1.17$, $P = 0.241$) or the

Table 3. Spatiotemporal changes in colony activity and spatial structure.

Site	Year of initial inspection	Worker count initial	Worker count 1 year	Worker count 2010	Changes in colony spatial structure
Hilltop Apartments	2009	35 ± 11	37 ± 11	N/A	1 (11%)
Horticulture Park	2004	48 ± 19	45 ± 17	39 ± 20	4 (44%)
Purdue Village	2005	31 ± 11	36 ± 14	32 ± 13	2 (22%)
	Mean ± SEM	38 ± 5	39 ± 3	36 ± 5	2.3 (26%)
Jischke Drive	2008	34 ± 7	44 ± 10	41 ± 13	2 (22%)
McCormick Road	2007	31 ± 13	32 ± 9	27 ± 11	3 (33%)
State Street	2006	45 ± 25	44 ± 22	45 ± 25	3 (33%)
	Mean ± SEM	42 ± 6	40 ± 4	38 ± 4	2.7 (29%)
All sites	Cumulative mean ± SEM	40 ± 4	39 ± 2	37 ± 3	2.5 (28%)

All values reported as mean ± SEM. Means within each site are an average of nine colonies (three single nest, three double nest, and three triple nest). Changes in colony spatial structure indicate the number of colonies that experienced an increase or a decrease in the number of nests.

2010 inspection when 37 ± 3 workers were observed (d.f. = 283, $t = -1.39$, $P = 0.164$). Similarly, worker counts did not change significantly within each habitat type (suburban vs. urban) and ANOVA analysis indicated that habitat type had no effect on colony activity as indicated by worker counts (d.f. = 1, $F = 0.46$, $P = 0.499$). The effect of time (initial vs. 1 year vs. 2010 inspection) was also not significant (d.f. = 2, $F = 1.16$, $P = 0.315$). While worker counts remained relatively stable throughout the course of the study, colony spatial structure changed considerably. Changes in colony spatial structure (i.e. the degree of polydomy) were tracked in nine colonies in each of the six subplots for a total of 54 colonies (Table 3). Colonies in all six plots experienced changes in colony spatial structure with 26% of suburban colonies and 29% of urban colonies experiencing a change (d.f. = 14, $t = -2.29$, $P = 0.282$). Colony spatial structure changed in 15/54 (28%) colonies: three single nest colonies became double nest colonies, five double nest colonies became single nest colonies, and seven triple nest colonies became double nest colonies. The overall trend was for the colonies to lose nesting sites and become less spatially complex. The likelihood of detecting a change in colony spatial structure increased with the amount of time passing from the initial inspection. For example, colony spatial structure changed in 4/9 colonies in Horticulture Park, which were monitored for 6 years, but only in 1/9 colonies in Hilltop Apartments, which were monitored for only 1 year.

The ants nested in 24 different types of trees with 97% of all nests in hardwoods and 3% in conifers. Five types of trees accounted for 70% of all nests: 29% were in oaks, 18% in maples, 10% in locusts, 7% walnuts, and 6% in ash trees. The remaining 30% of nests were in 19 other types of trees with each type comprising less than 5% of the total. The majority of nests (29%) were in oak trees; however, this does not necessarily mean that carpenter ants prefer oaks over other trees. Oaks were simply the most abundant trees within the study site and carpenter ants nested in any and all types of trees including conifers and hardwoods. No relationship was detected between tree type and worker counts (d.f. = 9, $F = 1.36$, $P = 0.204$) suggesting that colony size in *C. pennsylvanicus* is determined by factors other than the type of tree the colonies are nesting in.

Discussion

Long-term monitoring and extensive sampling over a large spatial area allowed a comprehensive insight into the spatiotemporal dynamics of colony and population structure in *C. pennsylvanicus*. Carpenter ant colonies were active on 348 of the 1113 trees inspected and these represented 182 distinct colonies. This highlights two main features of *C. pennsylvanicus* colonies in the urban/suburban habitat. First, approximately one-third of all available nesting sites are utilised by carpenter ants. On average, 31% of all trees were colonised and the colonisation rate remained relatively stable over time, suggesting that an equilibrium point had been reached. The equilibrium point is likely shaped by a dynamic interaction between various biotic and abiotic factors. Given that carpenter ants nest almost exclusively in trees and intraspecific competition for nesting sites is thought to be high (Hansen & Klotz, 2005), the 31% colonisation rate seems rather low. Indeed, many colonies within the study site were observed to produce new alate queens at least once a year, suggesting a high reproductive potential of the established colonies. A relatively low and stable tree colonisation rate despite an apparently high reproductive rate suggests that the alate queens either disperse far from natal nests and set up colonies in areas with lower competition or die as a result of intraspecific fighting or predation. Other factors such as intraspecific competition for food (access to trees harbouring honeydew-producing Hemiptera), competition with other arboreal species, and lack of trees that present a suitable nesting site may also be important in limiting the number of trees colonised by *C. pennsylvanicus*. A second feature of *C. pennsylvanicus* is that colonies appear to be weakly polydomous with an average of 1.95 nests per colony (range 1–4), lower than a previous study by Klotz *et al.* (1998) who reported an average of 3.8 trees per colony. In the current study, 32% of colonies were monodomous and 68% were polydomous (45% double nest, 22% triple nest, and 1% quadruple nest). Furthermore, colonies with more nests had significantly higher worker counts and the relationship between the number of nests and the average total worker count was linear. This suggests that younger, smaller colonies generally maintain a monodomous colony structure and later become polydomous depending on the colony's size and nutritional needs. The data also suggests that older colonies may be spatially more complex and maintain larger territories as has been demonstrated in numerous other ant species (e.g. Gordon & Kulig, 1996; Kenne & Dejean, 1999). In *C. pennsylvanicus* and other carpenter ants colony size is an indicator of colony age and older colonies are generally larger (Akre *et al*., 1994; Hansen & Klotz, 2005).

Carpenter ants nest almost exclusively in trees and tree density might be an important factor regulating colony density and colony social and/or spatial structure. The proportion of trees colonised by *C. pennsylvanicus* was significantly higher in the urban plots, 35 ± 2% vs. 27 ± 2% in the suburban plots and trees in the urban plots were 1.4 times more likely to be colonised by carpenter ants. This is despite the fact that tree density was 65% lower in the urban plots. This suggests that intraspecific competition for nesting sites may be especially high in areas with lower tree density due to a limited number of nesting sites. The habitats also differed significantly with respect to two other important features: colony spatial structure (defined as the total number of trees per colony) and colony size (defined as the total number of foraging workers observed on the trees). Overall, colony spatial structure was simpler in the urban habitat where a higher incidence of monodomy was observed. Furthermore, colonies in the urban habitat were only half as likely to nest in three trees relative to colonies in the suburban habitat. As a result of nesting in fewer trees and thus having smaller territories, colonies in the urban habitat also had significantly lower worker counts. The composite picture that emerges for *C. pennsylvanicus* colonies in the urban habitat is a chain reaction of events: (i) the urban habitat has a lower tree density, (ii) lower tree density results in higher tree colonisation rate, (iii) higher tree colonisation rate results in simpler colony spatial structure (i.e. higher incidence of monodomy), and (iv) simpler colony spatial structure results in numerically smaller colonies. Therefore, it appears that tree density has a significant effect on a number of important colony features in *C. pennsylvanicus* and most likely other arboreal ant species. Besides tree density, other environmental features may have an effect on colony spatial structure in the urban environment. For example, artificial barriers in the form of human-built structures (e.g. streets, sidewalks, etc.) may cause habitat fragmentation and act as natural barriers to worker dispersal and may ultimately affect social and/or spatial structure at both the colony and the population level. In other ant species, habitat fragmentation had an effect on various colony features including colony social (Braschler & Baur, 2003) and genetic structure (Bickel *et al*., 2006). In contrast to urban colonies, *C. pennsylvanicus* in the suburban habitat are subject to 'suburban sprawl': higher tree density allows the colonies to maintain larger territories, which ultimately leads to numerically larger colonies. While the average number of workers per tree was comparable in both habitats with 40 ± 4 workers in the suburban habitat and 45 ± 5 workers in the urban habitat, suburban colonies tended to be significantly more numerous as they nested in more trees relative to colonies in the urban habitat. Previous studies demonstrate a positive effect of nesting site availability on colony dynamics in ants (Foitzik *et al*., 2004). In carpenter ants, trees are an especially important resource because they serve a dual purpose. In addition to being permanent nesting sites, trees also serve as feeding sites because honeydew-producing Hemiptera often inhabit the trees that the ants are nesting in. Ant communities are mainly structured by intra- and interspecific competition for nesting and feeding sites and the availability of nesting and feeding resources affects numerous dimensions of ant colonies (Banschbach & Herbers, 1999; Foitzik *et al*., 2004). Furthermore, other studies demonstrate that ecological factors can cause a long-term shift in colony social organisation and life history traits (DeHeer *et al*., 2001; Buczkowski, 2010).

The prevalence of satellite nests in *C. pennsylvanicus* enables colonies to expand their territory. While the area of the individual territories was not estimated in this study, the distance between trees was measured and is indicative of the overall territory size. On average, nests in the suburban environment were separated by a shorter distance, most likely because of the higher tree density. Despite shorter distance between nests, suburban colonies nested in more trees and thus maintained larger territories, which allowed them to monopolise vital resources such as nesting and feeding sites. In other ants, larger territories were important for securing access to foraging sites (Levings & Traniello, 1981; Ryti & Case, 1984; Crist & Wiens, 1996).

Long-term monitoring of the spatiotemporal pattern of nest site use in *C. pennsylvanicus* revealed a unique trend. On the one hand, colonies in both habitats experienced substantial changes in colony spatial structure. Across all test sites, colony spatial structure changed in 28% of the colonies and the majority of colonies lost nesting sites and became less spatially complex. On the other hand, the average total worker count within the affected colonies remained virtually unchanged. This indicates that reductions in nest site use do not translate into reductions in colony size and suggests that ants in the satellite nests did not die out, but simply joined other existing nests. Furthermore, the likelihood of detecting a change in colony spatial structure increased with the amount of time passing from the initial inspection. For example, colony spatial structure changed in 4/9 colonies in Horticulture Park, which were monitored for 6 years, but only in 1/9 colonies in Hilltop Apartments, which were monitored for only 1 year. Numerous factors such as physical deterioration of nesting structure, competition with other animals, exhaustion of food supplies, seasonal polydomy, or discovery of more attractive nesting sites may be driving the shift in nesting strategies. In other cases, ants move their nests to avoid predation (Droual, 1984; Yamaguchi, 1992; McGlynn *et al*., 2004; Dahbi *et al*., 2008), to escape from unfavourable environmental conditions (Yamaguchi, 1992; Gibb & Hochuli, 2003), to increase access to food (McGlynn *et al*., 2004), to maximise foraging efficiency (Holway & Case, 2000), or to avoid overcrowding (Gobin *et al*., 1998; Buczkowski & Bennett, 2009). *Camponotus pennsylvanicus* nests are generally found in live trees and most likely remain in good physical condition throughout the life of the colony. This suggests that factors other than nest condition drive nest movement in *C. pennsylvanicus*, with high intraspecific and interspecific competition for food resources a likely factor.

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