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POLYDOMOUS *CREMATOGASTER PILOSA* (HYMENOPTERA: FORMICIDAE) COLONIES PREFER HIGHLY CONNECTED HABITATS IN A TIDAL SALT MARSH

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High productivity in salt marshes creates an attractive resource base for terrestrial consumers, but regular tidal inundation creates a harsh environment. Numerous terrestrial organisms have adapted to living in salt marshes by timing activity cycles and vertical movements to tidal cycles, while others exhibit physiological adaptations, increasing their tolerance to submersion (Foster 1983; Vaughn & Fisher 1992; Pétilion et al. 2009). One of the species able to withstand these harsh conditions is the ant *Crematogaster pilosa* (Emery) (Hymenoptera: Formicidae), which has been reported to nest in hollow stems of salt marsh vegetation ranging from Florida to North Carolina (Davis & Gray 1966; McCoy & Rey 1987), as well as in trees in mesic forests and within stems of upland plants (Teal 1962; Johnson 1988; Morgan 2010).

Little is known about *C. pilosa* (synonymous with *C. clara*; Johnson 1988) with the exception of its flexible habitat requirements. The objective of this study was to examine the basic colony attributes and habitat preferences of *C. pilosa* in a saltmarsh cordgrass [*Spartina alterniflora* Loisel (Poales: Poaceae)] dominated salt marsh on Sapelo Island, Georgia. Connectivity in the *S. alterniflora* canopy, dead and living stem densities, and maximum stem height were evaluated to examine the influence of habitat structure on ant densities.

In October 2011, two marsh transects stretching from the forest edge to the bank of a large tidal creek were demarcated and divided into fourteen 10 × 2 m sections. Ant density was sampled in 4 randomly selected 2 m² quadrats per section by sweep netting for 15 seconds. Percent vegetation cover was estimated from photographs taken from ground level and converted to binary sky/vegetation images using ImageJ software. Living and dead stem density and tallest stem height were measured in 4 haphazardly placed quadrats (0.25 m²) within a subset of 9 sections. Workers from 15 nests were enumerated, and the presence of eggs or pupae was recorded. To evaluate tidal inundation relative to nest height, 5 fence posts with cups attached at 5 cm intervals covering the lower range of observed nest heights were deployed. Flooded cups were recorded daily for 4 days, which included some of the highest local tides of 2011. The spatial extent and number of colonies examined in this study are small, limit-

ing the potential for generalization to other colonies and habitats.

Square-root transformed ant densities showed a positive correlation with percent vegetation cover (Fig. 1) when data were averaged over 20 m² transect sections ($R^2 = 0.50$, $P = 0.003$). No relationship was found between ant density and living stem density ($R^2 = 0.21$, $P = 0.22$), dead stem density ($R^2 = 0.06$, $P = 0.53$), or tallest stem height ($R^2 = 0.10$, $P = 0.42$). Mean nesting stem and entrance heights were 44.6 cm (SD = 14.4) and 35.3 cm (SD = 10.6), respectively. The maximum observed tidal height from substrate was less than 20 cm, and minimum nest entrance height was 21 cm (Fig. 2).

Nests averaged 242 workers (range: 53-1106, SD = 276), which is conservative because some workers were foraging at the time of collection. Eggs and pupae were found in 87% and 46% of the nests, respectively. Workers were observed traveling and carrying eggs among 21 nests within

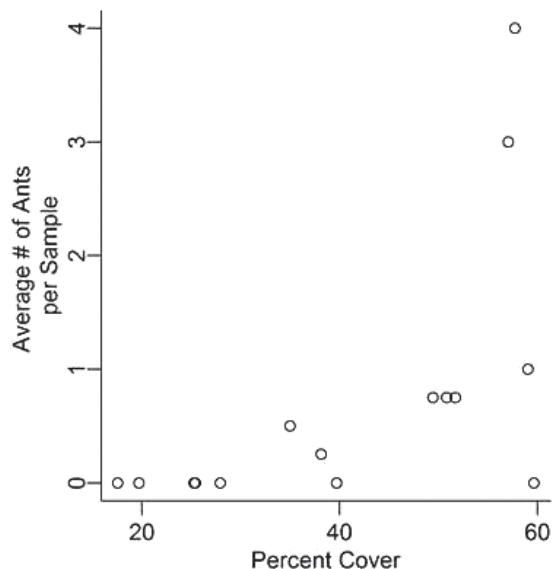


Fig. 1. Ant densities from sweep net samples over a gradient of vegetation cover. Habitat containing higher vegetation cover also tends to be more highly connected. Linear regression after square-root transforming the y-axis yielded a significant positive relationship ($R^2 = 0.50$, $P = 0.003$)

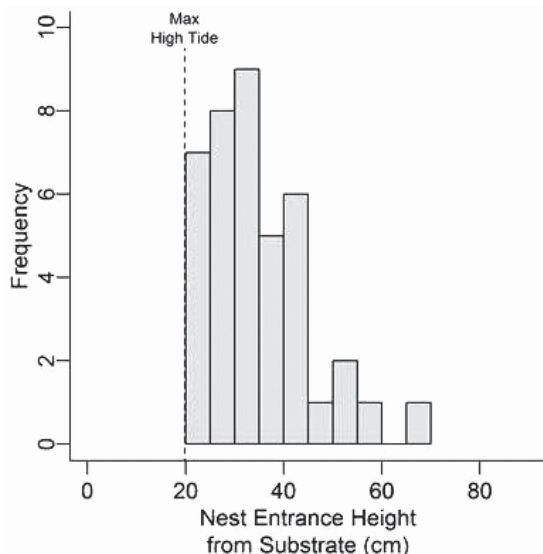


Fig. 2. Frequency histogram of the height of *C. pilosa* nest entrances in dead, standing *S. alterniflora* stems. High tide never reached above 20 cm from the substrate.

approximately 4 m², and only 1 queen was found in this colony. The search was not exhaustive and therefore represents a minimum estimate for this colony. Agonistic encounters were observed between ants that were transported 50 m across the marsh and resident ants in the new area.

The transfer of brood and individuals among nests and lack of agonism among individuals from these nests suggest *C. pilosa* is polydomous, with workers and brood distributed among many nests. Polydomy has been reported in at least two other species of *Crematogaster* with ranges in North America (Tschinkel 2002; Lanan et al. 2011). Numerous hypotheses have been presented to explain polydomy, including increased colony survival when nests are frequently destroyed (Rosengren & Pamilo 1983) and size limitations of single nests (Levings & Traniello 1981). Either hypothesis could explain polydomy in *C. pilosa*; marsh nesting sites are subject to stochastic destruction from storms and spring tides, and the observed rapid colonization of a transect marker suggests that nesting sites may be limiting.

Polydomous ants generally transport larvae and pupae among nests but do not typically exchange eggs (Debout et al. 2007). However, the eggs of *C. pilosa* were highly distributed and frequently transferred among nests. The distribution of eggs should be a viable bet-hedging strategy if the risk of single nest loss outweighs the risk of between-nest egg transport. Highly distributed brood differentiates *C. pilosa* from its polydomous congener *C. torosa*, which has concentrated brood

and uses satellite nests to increase access to foraging sites (Lanan et al. 2011).

At the study site, *C. pilosa* inhabits dead *S. alterniflora* stems above the high tide mark and is more common in areas of the marsh with dense vegetation cover. The truncated entrance height distribution (Fig. 2) suggests that ants choose nests with entrances above the high water mark or that inundated nests are destroyed by or abandoned after flooding. It was previously suggested that specialized *C. pilosa* individuals prevent nest inundation during high tide by blocking nest entrances with their head (Teal & Teal 1964); however, we found no specialized individuals, and entrance holes were much larger (mean = 1.6 mm, $n = 9$) than ant head widths (0.84 mm, $n = 8$). This previous report may have been based on a misidentification of the carpenter ant *Camponotus impressus* (Roger), which has a soldier caste with an enlarged head used to exclude intruders (Walker & Stamps 1986) and has been documented in salt marshes (Rey 1981; McCoy & Rey 1987). Of additional interest, a *C. pilosa* worker was observed carrying a dead planthopper, *Prokelisia marginata*, into a nest, and workers were attracted to both peanut butter and sugar baits.

Habitat structure plays an important role in determining *C. pilosa* distribution in the salt marsh. *Crematogaster pilosa* do not venture onto the muddy substrate, and individuals placed on the mud are unable to move. Therefore increased habitat connectivity in the canopy, as measured by vegetation cover, increases foraging area and nesting site availability. Connectivity is often provided by dead stems and dead outer leaves of living plants, though living leaves also contribute. Nest entrances all occurred above the high water mark and the availability of adequate nesting sites is likely to play a role in determining the distribution of *C. pilosa*.

SUMMARY

Habitat preference and colony characteristics of *Crematogaster pilosa* (Emery) (Hymenoptera: Formicidae) were examined in a tidal salt marsh on Sapelo Island, Georgia. The ants nest in dead *Spartina alterniflora* Loisel (Poales: Poaceae) stems and colonies exhibit polydomy, with workers and brood distributed among many nests. Connectivity of vegetative canopy and the availability of sites above the high tide mark appear to be important in determining the distribution of *C. pilosa*.

Key Words: agonistic behavior, bet-hedging strategy, connectivity, stochastic destruction, ants

RESUMEN

Se examinaron la preferencia de hábitat y las características de las colonias de *Crematogaster*

pilosa (Emery) (Hymenoptera: Formicidae) en un manglar salado en la Isla Sapelo, Georgia. Las hormigas hacen nidos en los tallos muertos de *Spartina alterniflora* Loisel. (Poales: Poaceae), y las colonias exhiben polidomia, con los trabajadores y las crías distribuidas entre muchos nidos. La conectividad de la cobertura vegetal y la disponibilidad de los sitios por encima de la línea de marea alta parecen ser importantes en la determinación de la distribución de *C. pilosa*. Palabras Clave: comportamiento agonístico, conectividad, estrategia de limitar el riesgo, destrucción estocástica

Palabras Clave: comportamiento agonístico, estrategia bet-hedging, conectividad, destrucción estocástica, hormigas

ENDNOTE

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