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Habitat Requirements and Occurrence of Crematogaster pilosa (Hymenoptera: Formicidae) Ants within Intertidal Salt Marshes

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Luke C. Loken* and Samantha K. Oliver

Abstract

Spartina alterniflora Loisel. (Poales: Poaceae) salt marshes provide unique conditions for organisms to develop specialized morphological and behavioral traits. *Crematogaster pilosa* Emery (Hymenoptera: Formicidae) ants nest in *S. alterniflora* stems and display polydomy (i.e., multiple nests per colony), which has not been observed in terrestrial populations of this species. We identified new colonies of *C. pilosa* in *S. alterniflora* dominated salt marshes of Sapelo Island, Georgia (USA), and characterized the vegetation structure associated with ant presence. *Crematogaster pilosa* colonies were found most often 2 to 10 m from tidal creek channels in areas with expansive intermediate-height *S. alterniflora*. Marsh patches with abundant brown leaf vegetation above the high water level were most likely to have ants present ($P = 0.03$). These areas have extensive vegetation that remains dry during tidal advances, are protected from tidal surges, and most often occur along depositional banks of tidal creeks. Ant populations do not occur in the upland portion of the *S. alterniflora* marsh, presumably due to a lack of elevated habitat. Persistence of *C. pilosa* within *S. alterniflora* salt marshes is tied to the availability of connected habitat that avoids tidal submersion. The narrow band of intermediate-height *S. alterniflora* plants along tidal creeks provides both the needed horizontal structure and dry vegetation, allowing a terrestrial ant to colonize this seemingly atypical environment.

Key Words: *Spartina alterniflora*; Sapelo Island; niche; connectivity

Resumen

Las marismas de *Spartina alterniflora* Loisel. (Poales: Poaceae) proveen condiciones únicas a los organismos para el desarrollo de rasgos morfológicos y de comportamiento especializado. La hormiga, *Crematogaster pilosa* Emery (Hymenoptera: Formicidae) anidan en los tallos *de S. alterniflora* y demuestran la polidomia (nidos múltiples por colonia), que no se ha observado en las poblaciones terrestres de esta especie. Identificamos nuevas colonias de *C. pilosa* en marismas dominadas por *S. alterniflora* en la Isla Sapelo, Georgia (EE.UU.), y caracteriza la estructura de la vegetación asociada a la presencia de hormigas. Se encontraron las colonias de *Crematogaster pilosa* con mayor frecuencia de 2 a 10 m de los canales de las quebradas de marea en zonas con amplia *S. alterniflora* de intermedio-alto altura. Las áreas de las marismas con una abundancia de vegetación de hojas de color café por encima del nivel de agua fueron más propensas a tener hormigas presentes ($P = 0.03$). Estas áreas tienen una amplia vegetación que permanece seca durante los avances de marea, están protegidos por marejadas, y más a menudo se producen a lo largo de los bancos de deposición de canales de la marisma. Las poblaciones de hormigas no se presentan en la parte de las tierras altas de la marismae de *S. alterniflora*, presumiblemente debido a la falta de hábitat de altura. La persistencia de *C. pilosa* dentro de las marismas de *S. alterniflora* está ligada a la disponibilidad de hábitat conectadas que evite la inmersión de las mareas. La banda estrecha de las plantas de *S. alterniflora* de altura intermedia a lo largo de canales de marea provee tanto la estructura horizontal necesaria como la vegetación seca, lo que le permite una hormiga terrestre el colonizar este ambiente aparentemente atípico.

Palabras Clave: *Spartina alterniflora*; Isla Sapelo; nicho; conectividad

Salt marsh ecosystems are attractive resources for terrestrial consumers if adapted for their harsh environmental conditions. *Spartina alterniflora* Loisel. (Poales: Poaceae) salt marshes dominate much of the Atlantic and Gulf Coasts of the USA, are highly productive ecosystems (Odum 1988; Mcleod et al. 2011), and host a diverse assemblage of organisms, including over 100 species of invertebrates (Preiffer & Wiegert 1981). Terrestrial inhabitants often develop unique adaptations and behaviors to tolerate alternating wet/dry conditions (e.g., Foster & Moreton 1981; Foster 1983; Pétillon et al. 2009; Nielsen 2011). Mobile species can migrate horizontally or vertically with the advancing tide (e.g., Vaughn & Fisher 1992). Some species of salt marsh spiders endure inundation by entering a hypoxic coma when submerged

(Pétillon et al. 2009). If adapted, these organisms likely benefit because biological competition may be reduced (Foster & Treherne 1976 and references within) as only a limited number of species can withstand the environmental pressures. Those adapted are rewarded with exclusive access to a desirable resource.

Crematogaster pilosa Emery (Hymenoptera: Formicidae) is a common terrestrial ant that has been observed in salt marshes of the southeastern USA (Davis & Gray 1966; McCoy & Rey 1987; Childress & Koning 2013). *Crematogaster pilosa* (also cited as *C. clara*; Johnson 1988) nests in a variety of habitats, which include mesic and montane forests, under rocks, and in stems of plants (Teal 1962; McCoy & Rey 1987; Johnson 1988). To our knowledge, *C. pilosa* is the only

ant species found in *S. alterniflora* salt marshes of the southeastern USA. Salt marsh *C. pilosa* populations have adapted specialized survival behaviors, allowing them to exploit this wet environment. Colonies of *C. pilosa* establish multiple nests (i.e., polydomy) within hollow *S. alterniflora* stems and use a network of horizontal grasses and debris to connect nests and foraging habitat (Childress & Koning 2013). Childress & Koning (2013) also observed that *C. pilosa* nest entrances were positioned above the high water level, keeping them dry during high tides. Other unpublished observations suggest that the ants do not travel on the ground and avoid submersion by remaining in the *S. alterniflora* canopy. Therefore, *C. pilosa* should not be ubiquitous across the entire marsh, rather restricted to locations with sufficient canopy that remains above tidal surges.

Given that *C. pilosa* require dry and well-connected habitats (Childress & Koning 2013)*,* salt marsh heterogeneity may restrict the distribution of *C. pilosa* to locations with adequate resources that lack recurrent environmental destruction. Storms, tides, and winter ice disturb marsh habitats, which have been shown to influence invertebrate distributions (e.g., Denno et al. 1996 and reference within). Tidal advances flood lower elevations of the marsh through a network of tidal creeks and occasionally deposit floating wracks of dead vegetation on the marsh surface. Wrack deposition occurs more frequently on creek shores, where it can cause vegetation diebacks (Reidenbaugh & Banta 1983) and reduce vegetation biomass (Tolley & Christian 1999). Additionally, tidal currents disrupt vegetation by bending and completely submerging plant stems growing along the channel. Although *S. alterniflora* growing further upland also floods with advancing tides, water levels rise and fall without the destructive forces of strong currents. Therefore, *C. pilosa* may not persist proximate to tidal creeks due to the higher risk of flooding and damage to nests.

In addition to a gradient in tidal disruption, hydrologic exchange varies across the marsh, resulting in a gradient of *S. alterniflora* growth that is dependent upon the availability of nutrients and redox conditions within the soil (Valiela et al. 1978; Howes et al. 1981). *Spartina alterniflora* comprises nearly 100% of the low and intermediate marsh plant community (Pennings et al. 2005). Plants grow tall (max. height 1–3 m) and dense in the lower marsh along tidal creeks where nutrients and dissolved oxygen are more available (Fox et al. 2012). Shorter plants (max. height <1 m) persist in backwater areas of the high marsh that are relatively nutrient depleted and lack efficient drainage (Fox et al. 2012). Typically, there is an abrupt transition between the height classes less than 5 m from creek channels. However, more gradual transitions are common on slightly elevated levees (Teal 1958) and prominent along depositional (i.e., inside) bends of tidal creeks. Although tall *S. alterniflora* growing proximate to creeks may be the most attractive resource for consumers due to its higher productivity (Odum 1988; Mcleod et al. 2011), greater abundance of standing biomass (Gallagher et al. 1980), and better nutritional quality (Burkholder 1956), the potential for submersion or wrack deposition may restrict ants to the higher marsh. The benefit of fewer disturbances in the high marsh, however, may be counteracted by sparse vegetation that is too short to provide sufficient dry habitat and does not allow for adequate connectivity among nests. Expanses of intermediate-height *S. alterniflora* in transition zones may represent the optimum habitat for *C. pilosa*, where vegetation is sufficiently tall and dense but is not subject to the destructive forces associated with tidal creeks.

Our study focused on the distribution and habitat requirements of *C. pilosa* ants living in *S. alterniflora* dominated salt marshes on Sapelo Island, Georgia (USA). Although reports of salt marsh populations of *C. pilosa* span from Florida (McCoy & Rey 1987) to North Carolina (Davis & Gray 1966), all accounts from Sapelo Island, Georgia (Marples 1966; Childress & Koning 2013) come from a single location less than 100 m wide.

We specifically asked, 1) do populations of *C. pilosa* exist in other locations on Sapelo Island? And 2) what features of the *S. alterniflora* habitat predict ant presence? We expected *C. pilosa* colonies to be widespread but restricted to areas of intermediate-height *S. alterniflora*.

Materials and Methods

Fieldwork was conducted in *S. alterniflora* dominated salt marshes of Sapelo Island, Georgia, in Oct 2013 (Fig. 1). To identify populations of *C. pilosa* outside of those previously reported (Marples 1966; Childress & Koning 2013), we surveyed depositional and erosional sides of creek meanders because we expected differences in the vegetation pattern to affect ant occurrence. Ant presence/absence was recorded at 13 sites along 2 km of a tidal creek (Lighthouse Creek, Fig. 1B). We visited each location twice on 20 Oct 2013 during the daytime high and low tides. From a canoe at high tide, 1 person visually searched for ant presence at each site for 1 min and cut and surveyed 3 *S. alterniflora* stems. We clipped baited traps (paper plates with peanut butter and honey) to *S. alterniflora* stems 1 to 3 m from the edge of the creek channel above the high water line and arranged vegetation to facilitate ant access to traps. At the subsequent low tide, we returned to each site on foot, visually assessed each site for 1 min, and counted the number of ants at each trap.

Beyond our formal creek survey, we identified 2 salt marsh patches that contained *C. pilosa*. One patch (Odum's Marsh) was previously known to support ant populations (Fig. 1A; Marples 1966; Childress & Koning 2013), whereas the other (Dean Creek) harbored a newly identified population in a neighboring drainage (Fig. 1C). Both patches were within 50 m of tidal channels and spanned the transition in *S. alterniflora* growth form. At each patch, a subset of ants were collected and confirmed to be *C. pilosa* (Fisher & Cover 2007).

We assessed ant abundance and vegetation characteristics at plots in Odum's Marsh (*n* = 9) and Dean Creek (*n* = 8) (Fig. 1A and 1C). We selected plots to span the height range of *S. alterniflora*, with the majority of plots located near the transition from tall to short plants. Plots were delineated by joining four 1 m PVC segments that were fed through the vegetation just above the soil surface. We arranged the 1 m² quadrat on the ground to minimize disturbance to the vegetation arrangement. Each plot was first visually assessed for ant presence by 2 people simultaneously for 2 min.

In each plot, we classified the relative amount of vegetation available to ants at explicit height intervals. Vegetation density was determined using a modified Robel pole (Robel et al. 1970) constructed from a 2 m stake 0.01 m in diameter. The pole was taped at 0.2 m intervals and dropped vertically into the plot, resting the bottom on the marsh surface. The pole was held vertical while vegetation touching it was counted at each height interval (i.e., 0–0.20 m, 0.21–0.40 m, etc.) and classified as green leaf, brown leaf, green stem, or brown stem. We dropped the pole 20 times per plot and averaged the counts within each height-type, creating 40 classes per plot (i.e., green leaf 0–0.20 m, brown leaf 0–0.20 m, etc.). Counts were divided by interval height (i.e., 0.2 m) and recorded as vegetation density (# per vertical m). While conducting vegetation assessments, we limited the amount of physical disturbance to plots to prevent any ant reaction.

Immediately after assessing vegetation structure, we thoroughly searched each plot for ants and nests. We cut open all *S. alterniflora* stems within the plot and collected all stems containing ants (i.e., nests) in Ziploc bags. Nests were frozen within 6 h of collection. Within 1 mo, we opened all nests and counted adults, pupae, and larvae. Because all nests from a single plot were stored in a common container, ant abundance metrics were summarized per plot.
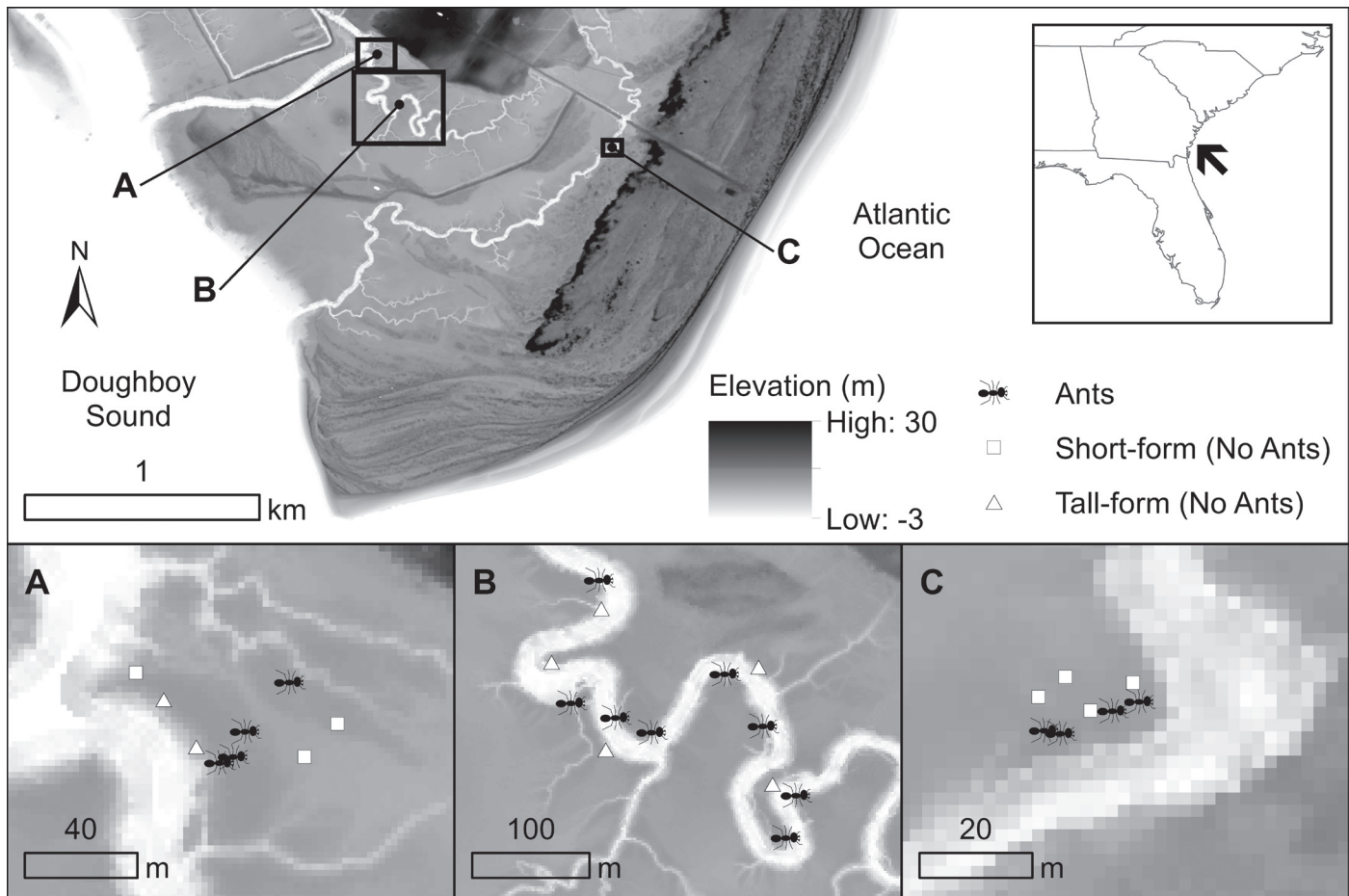
Fig. 1. Southern tip of Sapelo Island, Georgia (USA). Location of *Crematogaster pilosa* observations and vegetation assessments in Odum's Marsh (A) and Dean Creek (C). Presence/absence of ants along Lighthouse Creek (B) from canoe and baited trap survey. Sites containing *C. pilosa* were labeled "ants", those not containing ants were labeled by their vegetation (i.e., short or tall) based on maximum vegetation height.

We compared vegetation structure among plots containing *C. pilosa* with those without ants. We summarized vegetation density metrics based on ant presence and vegetation type. First, plots containing ants were aggregated together. Then, plots not containing ants were further categorized based on vegetation growth form. We did this because plots spanned the range of *S. alterniflora* growth form, and we predicted that ants would be restricted from tall vegetation along the creek and short vegetation growing upland. Plots with a maximum vegetation height taller than 1.60 m were assigned "tall"; those shorter than 1.21 m were labeled "short". All plots with maximum vegetation heights between 1.21 and 1.60 m contained ants. In total, we produced 3 plot classifications: those containing ants (ants), those not containing ants and dominated by shorter *S. alterniflora* (short), and those not containing ants and dominated by taller plants (tall). Within each plot classification, vegetation densities were averaged. Differences among mean vegetation densities were assessed using a 1-way ANOVA followed by a Tukey's honest significant difference (HSD) test to determine pairwise differences.

We used logistic regressions to determine which type of vegetation best predicted ant presence. First, ant presence was regressed against each vegetation density category (i.e., height-types) individually generating 34 regression models. Only regressions using brown leaf densities between 0.61 and 1.20 m were positively ($P < 0.1$) related to ant presence (see results). Because these categories were all the same vegetation type (i.e., brown leaf) and from adjacent height intervals, their vegetation densities were combined and then regressed against

ant presence. Logistic models were fit in R (R Core Team 2015) using the generalized linear model function.

To identify the maximum inundation height, we deployed 3 water level gauges in Odum's Marsh and Dean Creek. We constructed water level gauges by attaching open 1.5 mL Eppendorf tubes to a sturdy stake at 0.01 m intervals. Water level gauges were placed near vegetation plots and checked after the 22 Oct 2013 daytime high tide. The high water level for that tide was recorded as the height of the highest inundated tube. We calculated the maximum inundation height by comparing the recorded high water level to the 2 wk maximum high tide observed at Old Tower, Sapelo Island Station (NOAA Station: 8675622).

Results

We found *C. pilosa* at 8 of 13 sites along Lighthouse Creek (Fig. 1B). All sites with ants were along depositional banks where intermediate-height *S. alterniflora* occurred. We also found ant populations in Odum's Marsh (4 of 9 plots) and Dean Creek (4 of 8 plots) (Fig. 1). In plots containing ants, there was a range of 1 to 9 nests m^{-2} and 20 to 2,281 adults m^{-2} (Table 1). We did not find other species of ants, and all *C. pilosa* nests were found within stems of *S. alterniflora*. In both Lighthouse Creek and Dean Creek, we observed ants on small islets completely separated from the mainland by the stream channel.

Plots containing ants had a different vegetation structure than those not containing ants. The mean vegetation height was significant-

Table 1. Mean and standard deviations of nests, adults, pupae, and larvae for 1 m² plots (*n* = 8) containing *Crematogaster pilosa* ants.

Parameter	Mean (range)	Standard deviation
Nests per plot	4 (1–9)	3.1
Adults per plot	807 (20–2,281)	878
Pupae per plot	18 (0–128)	45
Larvae per plot	333 (0–1,926)	653

ly different between plots (*F* = 6.639; df = 2,13; *P* = 0.01). Tukey's HSD comparison identified that vegetation in short plots was significantly (*P* < 0.05) shorter than in both ants and tall-form plots (Fig. 2). Comparing vertically-explicit vegetation densities and the maximum high tide revealed additional differences among marsh plots. The average maximum (SE) high water level for Odum's Marsh and Dean Creek plots was 0.51 ± 0.03 m. Short plots contained less vegetation above the maximum high tide level than both plots containing ants and tall plots (Fig. 3). Although tall plots had more total vegetation above the maximum high tide, plots containing ants had more brown leaf vegetation that remained above tidal advances (Fig. 3).

Ants occurred most often where there was abundant brown leaf vegetation above the high water level. Logistic regression models indicated ant presence was negatively related to green leaf density at 0.21–0.40 m, and positively related to brown leaf density between 0.61 and 1.20 m (Table 2). Densities of brown leaves at 0.61–0.80 m, 0.81–1.00 m, and 1.01–1.20 m were all significantly (*P* < 0.1) related to ant presence. The combined brown leaf density between 0.61 and 1.20 m was also significantly related to ant presence (*P* = 0.03; Fig. 4). The logistic regression model predicts that marsh locations with more than 1.5 brown leaves occurring between 0.61 and 1.20 m above the soil surface have a <50% probability of containing ants (Fig. 4).
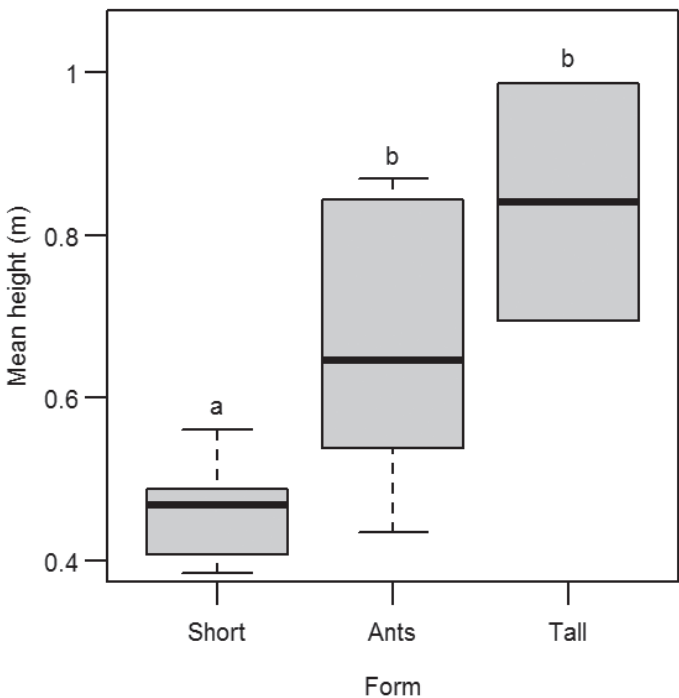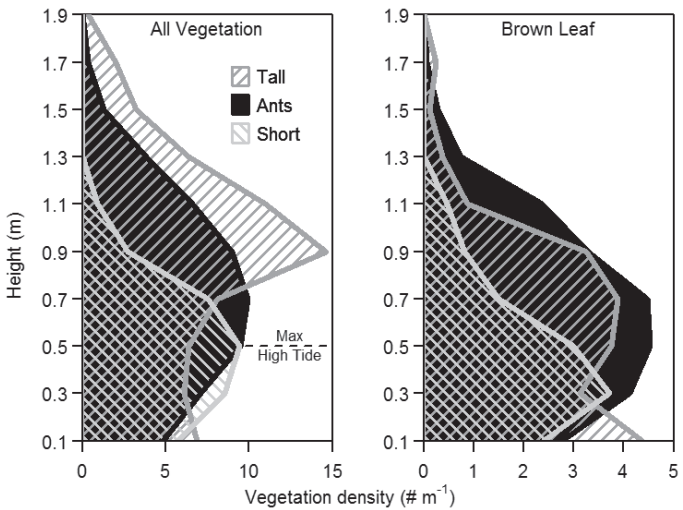

Fig. 3. Height-specific vegetation density for marsh plots with and without ants in Dean Creek and Odum's Marsh. Vegetation density is the number of vegetation features (i.e., stems and leaves) per vertical meter above an average point on the marsh surface. Integrating vertically produces the average number of vegetation features above a single point. All plots containing *Crematogaster pilosa* were grouped (ants); plots not containing ants were classified by the maximum vegetation height of *Spartina alterniflora* (i.e., tall or short). Vegetation density distributions are the means for tall (*n* = 2), ants (*n* = 8), and short (*n* = 7) plots.

Discussion

Crematogaster pilosa ants were abundant and easy to locate in new locations of the *S. alterniflora* salt marsh. Colonies were found frequently in intermediate-height *S. alterniflora* near depositional banks, which occur on the inside bends of tidal creeks. Ants were present in marsh patches with high densities of brown leaf (i.e., dying) vegetation above the high water line. In contrast to green vegetation that predominantly grows vertically, brown vegetation was often orientated horizontally, likely increasing the connectivity of the grass canopy and allowing the areal expanse of *C. pilosa*. As the connectivity of the salt marsh increases, so does the total area in which ants can gather essential resources (e.g., food, nesting structure), which allows a terrestrial ant species to flourish in this disruptive intertidal environment.

Crematogaster pilosa colonized the salt marsh where abundant vegetation occurred above the maximum high tide. Likely, these locations have a highly connected canopy among neighboring *S. alterniflora* plants. Dense brown vegetation above the high water level was the best predictor of ant presence within this study (Table 2). Habitat with abundant dying leaves was easy to identify visually, appearing as brown thatch in the otherwise green marsh. The thatch may have been particularly apparent because we sampled in autumn when the biomass of *S. alterniflora* is greatest (Gallagher et al. 1980) and the leaves had begun to discolor. In general, the standing stock of dead biomass is 2 to 3 times greater near creek banks compared with the high marsh (Gallagher et al. 1980). The thatch was copious in patches of intermediate-height *S. alterniflora* presumably because the upper part of the plant remains above the high water mark and is not transported into tidal creeks. Thatch may not accumulate in the marsh immediately bordering creek channels, as strong currents likely dislodge it. Thatch connections among neighboring plants may be critical for the survival of salt marsh *C. pilosa* colonies by increasing the area in which they can gather resources.

Crematogaster pilosa expanse toward tidal channels may be limited by disturbance. Even though there is abundant tall vegetation

Fig. 2. Mean vegetation heights for marsh plots containing ants (*n* = 8) and plots not containing ants classified by their dominant vegetation type: short (*n* = 7) and tall (*n* = 2). All plots were from Dean Creek and Odum's Marsh. Mean heights are the weighted average of all vegetation counts within plots. Letters above whiskers signify significant difference using Tukey's HSD with *P* < 0.05.

Table 2. Significance values (*P*) from single logistic models. Ant presence was regressed against vegetation density for each height-type categorical variable. All generalized linear models were fit using the generalized linear model function in R (R Core Team 2015).

Height (m)	Green leaf	Brown leaf	Green stem	Brown stem	All vegetation
0–0.20	0.145	0.911	0.159	0.503	0.311
0.21–0.40	**0.065**†	0.513	0.667	0.555	0.467
0.41–0.60	0.974	0.104	0.216	0.472	0.227
0.61–0.80	0.615	**0.045***	0.532	0.635	0.118
0.81–1.00	0.343	**0.065***	0.370	0.493	0.170
1.01–1.20	0.359	**0.040***	0.311	—	0.159
1.21–1.40	0.342	0.110	0.201	—	0.231
1.41–1.60	0.706	0.317	0.764	—	0.596
1.61–1.80	0.870	0.916	0.454	—	0.823
>1.80	0.929	—	0.994	—	0.577

Bold indicates significant at *P* < 0.1; *: positively correlated; †: negatively correlated; -: no data.

near creeks, the influence of water currents likely disrupts this habitat, making it less suitable for ant colonization. We occasionally observed *C. pilosa* in patches of tall *S. alterniflora*, suggesting it has sufficient dry nesting material. However, we did not observe *C. pilosa* regularly in this habitat, perhaps because of the lack of thatch (see previous paragraph). Additionally, ants may be restricted from tall *S. alterniflora* because it only grows immediately next to creek channels, which are disturbed frequently. We observed strong currents bending and submerging *S. alterniflora* growing along creek channels. Only *C. pilosa* nests above the high water level have been found (Childress & Koning 2013), and if nests were situated adjacent to tidal creeks, they would become inundated during tidal surges. Additional disturbances, such as wrack deposits (Reidenbaugh & Banta 1983), may disrupt *C. pilosa* nesting along the tidal creek. The instability of low-marsh *S. alterniflora* has also been suggested to drive interspecific variation in dispersal of the *Prokelisia* (Hemiptera: Delphacidae) planthopper (Denno et

al. 1996). Although tall *S. alterniflora* is an attractive habitat as it may provide more resources than shorter upland plants, it comes with increased risk for inhabitants. Investigations into the roles of tidal disturbance and vegetation stability on *C. pilosa* will likely provide better constraint of the lower bounds of *C. pilosa* habitat within salt marshes.

Crematogaster pilosa did not establish colonies in patches of short *S. alterniflora*. Plots in the higher marsh had lower densities of vegetation and thatch above the high water level (Fig. 3). *Crematogaster pilosa* nests have only been found above the high water level (Childress & Koning 2013), and without sufficient dry vegetation, ant colonization is unlikely. Additionally, marsh patches lacking a dense canopy would have limited connections among plants and a small resource base available for ant colonies. Although we did not find ants in short *S. alterniflora*, it is plausible that ants could persist there if supplemental material or debris accumulated in these locations. Other parts of the Atlantic or Gulf Coasts with substantial thatch deposits in *S. alterniflora* growing upland may harbor *C. pilosa* or other terrestrial organisms that cannot survive submersion. Childress & Koning (2013) observed ants colonizing wooden posts; we observed similar results as ants colonized hollow bamboo sticks within 3 d of installation. Future researchers could likely elicit colonization and alter ant abundance by supplementing the marsh with suitable nesting habitat in order to further assess the ecological importance of *C. pilosa* in salt marshes. We suggest that dry nesting material is limiting ant dispersal, restricting *C. pilosa* from the high *S. alterniflora* marsh.

Ants were observed frequently along the banks of Lighthouse Creek (Fig. 1B) suggesting that their required habitat is widespread across the marsh. Although we did not directly investigate dispersal mechanisms or food resources, *C. pilosa* likely has the potential to colonize the entire salt marsh but will establish only in areas with adequate resources and habitat. Most ants, including other *Crematogaster* species, have winged reproductive castes allowing the species to populate new environments (e.g., Türke et al. 2010). We found ants on islets within tidal creeks, indicating they have a dispersal strategy allowing them to colonize areas not connected to current populations. Although it is unlikely for individual colonies to migrate large distances, they may seasonally expand into adjacent marsh patches. It is conceivable that during other times of the year, *C. pilosa* may relocate nests in response to changes in destructive pressures, species interactions, or food resources. *Crematogaster pilosa* must rely solely on food and nesting resources within the *S. alterniflora* salt marsh. The ants responded to the baited traps and had a preference for honey over peanut butter, signaling that *C. pilosa* may be carbohydrate limited in the marsh in autumn. These results contrast a study on Argentine ants (*Linepithema humile* [Mayr]; Hymenoptera: Formicidae), in which ants exhibited protein limitation in a southern California saltwater marsh (Moore et al. 2013). However,
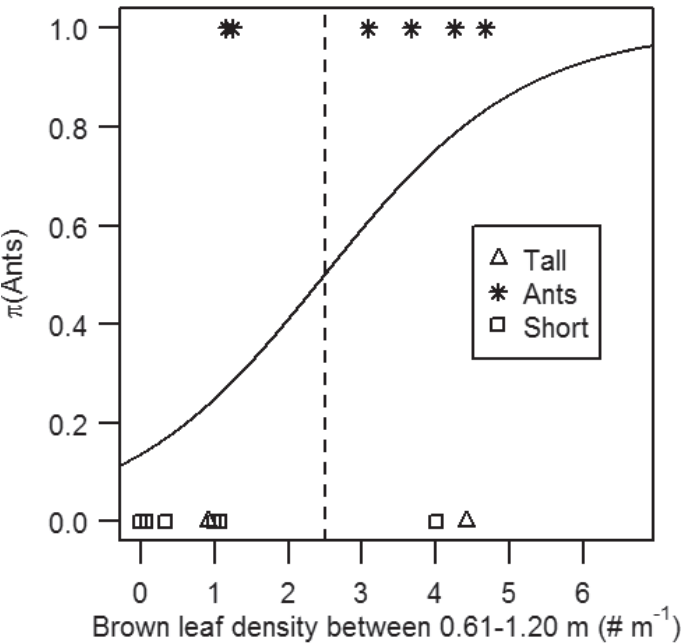

Fig. 4. Logistic regression model (*P* = 0.03) of the probability of *Crematogaster pilosa* as a function of brown leaf density between 0.61 and 1.20 m. Stars indicate plots containing ants, and open symbols indicate plots not containing ants. Vertical dashed line represents a 50% probability of ants and occurs at a brown leaf density of 2.5 m^{-1}, which equals 1.5 brown leaves between 0.61 and 1.20 m above the marsh surface.

these ants did not forage exclusively in intertidal areas. Other Argentine fire ants (*Solenopsis richteri* Forel; Hymenoptera: Formicidae) also feed in intertidal areas but nest in adjacent terrestrial habitats rarely exposed to tidal flooding (Palomo et al. 2003). Although the exact food resources exploited by *C. pilosa* are unknown, patches of *S. alterniflora* supported ant populations of up to 2,261 individuals per m^2 (Table 1).

Whereas our study focused on physical mechanisms controlling *C. pilosa*, other factors likely contribute to this species' distribution. Over 100 species of invertebrates inhabit the salt marsh (Preiffer & Wiegert 1981), some of which likely compete with and prey upon *C. pilosa*. Intertidal snails (*Littoraria irrorata* [Say]; Littorinimorpha: Littorinidae) have been shown to restrict other snails from sections of the salt marsh through interspecies competition and habitat alteration (Lee & Silliman 2006). Although we observed only low densities of *L. irrorata* inhabiting areas with ant activity, perhaps this or another species limits *C. pilosa*. Additionally, several species of predaceous arachnids are found in the salt marsh, which Foster & Treherne (1976) suggested are particularly important predators of salt marsh insects. Likely, predatory spiders would prefer the same dry and connected habitat as *C. pilosa*, which may impose an additional control on ant establishment. Alternatively, *C. pilosa* may be restricted to areas of the marsh also inhabited by stem-boring insects. In intertidal mangroves of Australia, a species of *Crematogaster* nests in the holes tunneled by weevils (Nielsen 2011). *Crematogaster pilosa* may be associated with a stem-boring organism that unintentionally grants access to nesting sites within damaged *S. alterniflora*. Further, these stem-borers may directly or indirectly provide food for *C. pilosa*. Future investigations looking at the community structure in parallel with *C. pilosa* may discover alternative controls on its distribution within salt marshes.

Although *C. pilosa* may be the only known ant species in *S. alterniflora* salt marshes, ants have been observed in other intertidal environments. An Australian *Crematogaster* species inhabits mangrove trees above the high water level (Nielsen 2011). Similar to *C. pilosa*, it distributes its brood among multiple cavities and remains in the canopy above the tide. Perhaps the most "marine"-like ants known are *Polyrhachis sokolova* Forel (Hymenoptera: Formicidae) (native to Australia; Nielsen 1997) and 2 species of *Iridomyrmex* (Hymenoptera: Formicidae) (native to Mexico; Yensen et al. 1980) that nest in intertidal mudflats. Individuals of these species place loose soil particles near nest entrances that collapse when inundated, plugging the hole and trapping air inside the nesting cavity. Very few ant species have been observed in intertidal environments. In all accounts, nests have been positioned or armored to avoid flooding. Perhaps eggs or larvae are very sensitive to inundation or salinity, which may be the ultimate driver restricting colonial insects from intertidal environments. If adapted, *C. pilosa* and other ant species are rewarded with exclusive access to a highly attractive resource.

The advancing tide, and the subsequent vegetation structure it creates, appears to define the *C. pilosa* niche within salt marshes. *Spartina alterniflora* salt marshes are an attractive resource for consumers, but organisms face harsh environmental conditions. Within intertidal zones, terrestrial organisms are at the edge of their ecological niches. The narrow but ubiquitous band of intermediate-height *S. alterniflora* in transition zones along tidal creeks provides both the needed horizontal structure and dry vegetation allowing a terrestrial ant to colonize this seemingly atypical environment.

Acknowledgments

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