

Ecosystem Ecology

Presence of Native and Non-native Ants Linked to Lower Emergence Success of Loggerhead Sea Turtle Nests: Implications for Management

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Abstract

Ants have been suggested as one of many population pressures sea turtles face potentially affecting nesting-beach survival of eggs and hatchlings. However, little is known about the extent to which ants act as incidental or primary mortality factors. Most research has focused on New World fire ants (genus *Solenopsis*), with confirmed records of other ant species interactions with sea turtle nests in situ being rare. Our study documented the ant species associated with loggerhead sea turtle *Caretta caretta* (Linnaeus) (Testudines: Cheloniidae) nests in Georgia and determined if ant presence was linked to lower hatching or emergence success. Samples ($n = 116$) collected from sea turtle nests on eight islands contained 14 ant species including *Solenopsis invicta* Buren (Hymenoptera: Formicidae), the red imported fire ant, which was the most common ant species encountered. Ant presence was not correlated with lower hatching success, but when other known disturbances were removed, correlated with significantly lower nest emergence success ($P < 0.0001$). Logistic modeling suggests that proximity of sea turtle nests to the primary dune significantly increases risk of ant predation on hatchling sea turtles. Population managers can reduce this risk by maintaining a 1-m buffer shoreward between dune vegetation and relocated sea turtle nests. Our results suggest that ants may exert a density-dependent pressure on nesting sea turtle populations and call for additional investigations to determine if managing native and invasive ants augments other efforts to improve hatchling survival.

Key words: fire ants, sea turtles, emergence success

Sea turtles face a wide range of natural and anthropogenic threats between egg laying and hatchling emergence. Among the many well-documented pressures like mammalian predators and tidal inundation of eggs, a potential emerging concern is an increased frequency of encounters with beach-dwelling ants (Allen et al. 2001; Wetterer et al. 2007, 2016; Wetterer and Lombard 2010). Most research on the potential interactions between sea turtle nests and ants has focused on new world fire ants of the genus *Solenopsis*, especially the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), yet published documentation of in situ interactions with sea turtle hatchlings for any ant species is rare at best. *Solenopsis invicta*'s range extends throughout the southeastern United States (Callcott and Collins 1996) and its spread to the

Caribbean (Wetterer 2013) has increased overlap with habitats where sea turtles nest.

Since little is known about interactions between sea turtles and ants, reviewing what has been shown for other reptiles can help us understand potential risks. Reptile nests and hatchlings in general are vulnerable to fire ants. The presence of red imported fire ant depresses both nestling and hatchling survival for Gopher tortoises *Gopherus polyphemus*, where although red imported fire ant cannot penetrate eggs they predate up to 50% of pipping hatchlings (Dziadzio et al. 2016). Red imported fire ant have been found in broad-snouted Caiman *Caiman latirostris* nests (Marco et al. 2012), where they may lower hatchling survival (Marco et al. 2013) and both directly and indirectly depress nest success (Marco et al. 2015).

Buhlmann and Coffman (2001) found that *S. invicta* can kill imperfectly shaped freshwater turtle eggs as well as hatchlings that attempt delayed emergence. It seems plausible that sea turtles undergo similar depressed hatchling survival and emergence success associated with ants.

While insects are a known pressure, documentation of insects preying on sea turtle eggs and hatchlings is sparse. Allen et al. (2001) demonstrated that red imported fire ant are present on sea turtle nesting grounds in Florida and will predate freshwater turtle eggs. Nests of green *Chelonia mydas* and loggerhead *Caretta caretta* (Linnaeus) (Testudines: Cheloniidae) sea turtles have reported eggs damaged by tenebrionids and dipterans (Aymak et al. 2017). Ants were documented to reduce Hawksbill *Eretmochelys imbricata* hatching success, especially in nests close to vegetation (da Silva et al. 2016), but were only identified to family. Additional studies found loggerhead nests are more likely to be infested by insects and acarids when closer to vegetation (Ozdemir et al. 2004). Collectively, this information points to a risk of ants depredating or scavenging sea turtle nests especially close to dune vegetation, but not which ant species pose a risk.

Where evidence of direct predation is not present, stinging ants still have the potential to cause deleterious effects. Red imported fire ant, in a lab setting, have been shown to induce loggerhead egg mortality via envenomation (Diffie et al. 2010). Gopher tortoises *G. polyphemus* and broad-snouted caiman *C. latirostris* pipped hatchlings are predated by red imported fire ant before emerging from the nest (Marco et al. 2012, 2013, 2015; Dziadzio et al. 2016). Krahe (2005) found that loggerhead hatchlings showing signs of ant stings had decreased survival and vigor over their first 10 d post-emergence. Sea turtle hatchlings, which remain in the nest chamber for hours to days before emerging from the sand, are likely similarly vulnerable to ant predation after hatching but before emergence.

Increasingly, two species of fire ants have been proposed as potential risks to sea turtle nests. The tropical fire ant *Solenopsis geminata* was reported present at sea turtle hatcheries in El Salvador (Wetterer et al. 2016) and both *S. invicta* and *S. geminata* were found on turtle nesting beaches in St. Croix, U.S. Virgin Islands (Wetterer and Lombard 2010). Red imported fire ant were first documented in loggerhead nests at Cape San Blas, FL, in 1995 with hatchling mortality documented 2 yr later (Parris et al. 2002). Researchers in Florida documented 22 ant species collected from tuna baits placed on marked sea turtle nests in Florida, with *S. invicta* being the most commonly collected species (Wetterer et al. 2007). Further, they found that 93% of baits at nests within 2 m of the dune vegetation had ants present (Wetterer et al. 2007).

Taken altogether, previous laboratory studies, beach surveys, and bait trials have shown that ants pose demonstrable risk to nesting sea turtles; however, studies combining identification of the ants within sea turtle nests and linkages between the found ants and reduced sea turtle success are lacking. The potential deleterious interactions between ants and sea turtle nests and hatchlings led us to investigate the occurrences and community composition of ants in sea turtle nests in Georgia. Georgia has some of the most protected and well-kept barrier islands along the Atlantic coast of the United States, where nests of loggerhead sea turtles incubate from May through October. Both native and non-native ants inhabit Georgia's barrier islands, but their impact on sea turtle nests is poorly understood. The objectives of our study were to 1) document which ant species were found in sea turtle nests along the Georgia Coast, 2) determine if the presence of ants was linked to lower hatching success and/or emergence success of sea turtle nests, and 3) provide recommendations to lower the risk of ant-induced hatchling mortality.

Methods

Study Site and Sea Turtle Data

Georgia's Atlantic coastline includes 14 major barrier islands (Fig. 1), all of which support nesting loggerhead sea turtles between May through October. Sea turtle activity along the coast is monitored by the Georgia Sea Turtle Cooperative (GSTC), a group of government and nongovernment organizations. Collaborators from the GSTC conduct daily beach monitoring patrols during the nesting seasons to locate and monitor sea turtle nests throughout incubation and document nest disturbances. Nests on most islands are relocated away from tidal areas if necessary (e.g., on Wassaw Island 91 nests, or 35.4% of nests in 2017) and protected with predator-exclusion screens. Five days after hatchling emergence or after 70 d without hatchling emergence, nest contents are excavated to determine clutch size (number of eggs), hatching success (number of eggs that hatched/clutch size), and emergence success (number of hatchlings that exited the nest chamber/clutch size). When known risks to secondary hatchling emergence exist (e.g., ants, developing storm, etc.), nests are excavated early and the time interval between observed emergence and excavation is recorded for all excavated nests.

Ant Collection and Identification

Ants were collected from sea turtle nests on eight of the islands during the nesting seasons in 2016 and 2017 (Fig. 1). GSTC members were provided with ant collection kits and asked to collect ant samples whenever ants were encountered following nest disturbances (e.g., raccoons or coyotes depredating a nest) or while excavating emerged nests. While GSTC members were monitoring sea turtle

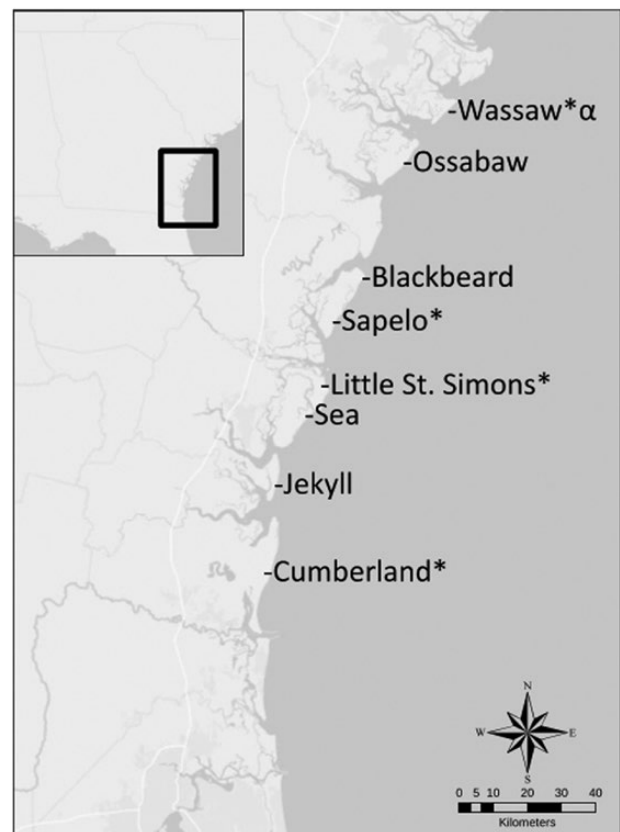


Fig. 1. The eight barrier islands of the Georgia Coast where ants were collected. Island names with a * provided success data. α indicates which island provided data for generalized linear modeling.

nests, ants visible on/within a sea turtle nest/egg/hatchling were scooped into a specimen cup.

Ants collected by GSTC members were frozen until retrieved by the first author for identification. Samples were identified to species using a combination of published and online keys (Pacheco et al. 2013, Deyrup 2016, <https://mississippientomologicalmuseum.org.msstate.edu/Researchtaxapages/Formicidaepages/Identification.Keys.htm>) as well as the ant collection at the University of Georgia Museum of Natural History. Voucher specimens have been retained at the University of Georgia.

Statistical Analyses

Four islands' (Cumberland, Little St. Simons, Sapelo, and Wassaw; Fig. 1) sea turtle monitoring projects provided nest disturbance and success data from the 2016 and 2017 sea turtle nesting seasons. All records of nests with known disturbances or causes of reduced success other than ants including predation by mammals and ghost crabs, root growth in the egg chamber, tidal overwash, storm damage, or flooding that resulted in the loss of five or more eggs were removed to create a 'disturbance-free' data set. Loggerheads have an average clutch size of 119 eggs (Frazer and Richardson 1985) and by selecting five or more eggs lost as the disturbance cutoff we removed all other disturbances resulting in more than 5% clutch loss.

Shapiro–Wilk tests (Shapiro and Wilk 1965) were used to assess data normality and the Brown–Forsythe test (Brown and Forsythe 1974) was used for determining homogeneity of variance using R's *car* package (Fox and Weisberg 2019). When data were not ideal for standard normality and homoscedasticity assumptions, nonparametric tests without those underlying assumptions were used. However, ANOVA/ANCOVA models were used when considering more than two factors as they are considered robust to violations of the normality assumption when sample size is greater than 50 (Pituch and Stevens 2016). The disturbance-free data were analyzed using the Brunner–Dette–Munk (hereafter BDM) test (Brunner et al. 1997) via the *BDM.2way* function of the *asbio* package (Aho 2020) to determine if hatching success differed in the presence or absence of ants with the island where each sample was collected treated as a blocking term. Negative binomial regressions performed with the *glm.nb* function of the *MASS* package (Ripley et al. 2013) were used to investigate the relationship between emergence success and ant presence after controlling for hatching success.

To reduce unknown error from multiple islands and better meet homogeneity of variance assumptions, data from a single island were selected for further modeling. While most projects within the GSTC patrol beaches each morning to inventory sea turtle nests along with their other duties, the Caretta Research Project has a field team which patrols the beaches throughout the night during the nesting season to document sea turtle nesting activity along with day time monitoring and data collection. The data set collected on Wassaw Island was thus considered the most rigorous documentation of direct ant/turtle nest interactions and used for statistical model fitting. Generalized linear models (Table 1) were used to determine the extent to which the presence or absence of ants affects emergence success. As nest success is influenced by both hatching success (Miller 1985) and beach position (Hays and Speakman 1993) and loggerhead hatchlings can (infrequently) exhibit up to seven night emergence durations (Glen et al. 2005), modeling terms accounting for nest-hatching success, distance to the dune edge, and the days between observed hatchling emergence and excavation were included. Models were calculated using the *glm.nb* function to model a negative binomial distribution with a log link function. Akaike's

Table 1. Comparison of models evaluating emergence success

Model	Hatching success (H)	Ant presence (A)	Days till excavation (D)	Distance to dune edge (E)	A * D	A * E	D * E	AIC	ΔAIC
H + A + D + E + (A * D) + (A * E) + (D * E)	0.020, <i>P</i> < 0.0001	0.476, <i>P</i> < 0.0001	0.081, <i>P</i> < 0.0001	-0.007, <i>P</i> = 0.421	0.006, <i>P</i> = 0.377	-0.084, <i>P</i> < 0.001	0.0004, <i>P</i> = 0.713	2,817.9	0
H + A + D + E + (A * E) + (D * E)	0.020, <i>P</i> < 0.0001	0.151, <i>P</i> < 0.0001	0.027, <i>P</i> = 0.0003	-0.0213, <i>P</i> = 0.0104	n/a	0.012, <i>P</i> = 0.084	0.002, <i>P</i> = 0.0605	2,832.1	14.2
H + A + D + E + (D * E)	0.020, <i>P</i> < 0.0001	0.117, <i>P</i> < 0.0001	0.030, <i>P</i> = 0.0027	-0.011, <i>P</i> = 0.0590	n/a	n/a	0.002, <i>P</i> = 0.0400	2,833.2	15.3
H + A + D + E + (A * E)	0.020, <i>P</i> < 0.0001	0.166, <i>P</i> < 0.0001	0.017, <i>P</i> = 0.0530	-0.012, <i>P</i> = 0.076	n/a	0.013, <i>P</i> = 0.056	n/a	2,833.7	15.8
H + A + D + E	0.020, <i>P</i> < 0.0001	0.130, <i>P</i> < 0.0001	0.019, <i>P</i> = 0.026	0.0007, <i>P</i> = 0.573	n/a	n/a	n/a	2,835.5	17.6
H + A + D + (A * D)	0.020, <i>P</i> < 0.0001	0.459, <i>P</i> < 0.0001	0.085, <i>P</i> < 0.0001	n/a	-0.085, <i>P</i> < 0.0001	n/a	n/a	3,156.4	338.5
H + A + D + (H * D) + (A * D)	0.017, <i>P</i> < 0.0001	0.461, <i>P</i> < 0.0001	0.038, <i>P</i> = 0.440	n/a	-0.086, <i>P</i> < 0.0001	n/a	n/a	3,157.4	339.5
H + A + D + (H * A) + (A * D)	0.019, <i>P</i> < 0.0001	0.701, <i>P</i> = 0.0002	0.035, <i>P</i> = 0.4824	n/a	4.353, <i>P</i> = 0.0002	n/a	n/a	3,157.5	339.6
H + A + D	0.020, <i>P</i> < 0.0001	0.121, <i>P</i> = 0.0015	0.022, <i>P</i> = 0.0152	n/a	n/a	n/a	n/a	3,171.6	353.7
H + D	0.020, <i>P</i> < 0.0001	n/a	0.028, <i>P</i> < 0.0001	n/a	n/a	n/a	n/a	3,179.6	361.7
A + D	n/a	0.182, <i>P</i> = 0.023	0.010, <i>P</i> = 0.616	n/a	n/a	n/a	n/a	3,622.5	804.6
H + A	0.032, <i>P</i> < 0.0001	0.111, <i>P</i> < 0.0001	n/a	n/a	n/a	n/a	n/a	4,740	1,922.1

Covariates include hatching success (H), ant presence/absence (A), and days until excavation (D), and distance to dune edge (E). Columns 2, 3, and 4 report the coefficient estimates and *P* value of A, D, and E respectively for each model. Columns 5, 6 and 7 indicate the coefficient estimates and *P* values of interactions. Columns 8 and 9 report each model's Akaike's Information Criterion (AIC) and the difference in AIC values between each model and the uppermost model which best fit to our data.

Information Criterion (AIC) was calculated for each resulting model to determine which model best fit our data. All analyses were performed in R version 4.0.3

To estimate the likelihood of ant presence, a predictive logistic model with emergence success, days until excavation, and nest distance to the dune edge as predictor variables was calculated through the *glm* function designating ‘binomial’ as the family and ‘logit’ as the link function. Hatching success was not included as it is correlated with emergence success (Pearson’s test, $P < 0.001$). The predictive model was k -fold cross-validated ($k = 10$) using R’s *caret* package (Kuhn 2008). The resulting model was used to predict the probability of an ant encounter along the gradient of distance to the dune edge when holding the emergence success and days until excavation constant at their respective means.

Our funding source had no involvement in the study design or analysis and interpretation of data.

Results

In total, 116 ant samples (a sample = ants collected from a single nest) representing 14 species were collected. Five samples contained more than one ant species. *Solenopsis invicta* was the most commonly encountered species on five islands (Blackbeard, Cumberland, Jekyll, Little St. Simons, and Wassaw) (Fig. 2). *Dorymyrmex bureni* (Trager) was the most commonly encountered species on Sapelo, and *D. reginicula* (Trager) was the most commonly encountered species on Sea Island, while *D. bureni*, *S. invicta*, and *Forelius pruinosus* (Roger) were each equally common encounters on Ossabaw Island (Fig. 2). All species encountered, except *S. invicta*, are native to the southeastern United States.

Combining the data from all eight islands showed *S. invicta* was encountered (40.5%, $n = 49$) two times more often than the next most common species *D. bureni* (20.7%, $n = 25$), followed by *F. pruinosus* (10.7%, $n = 13$), and *Pheidole morrissi* Forel (9.9%, $n = 12$). The remaining 10 species (*Brachymyrmex depilis* Emery, *Camponotus floridanus* (Buckley), *Dorymyrmex bossutus* (Trager), *Dorymyrmex reginicula*, *Pheidole bilimeki* Mayr, *Pogonomyrmex*

badius (Latreill), *S. geminata* (Fabricius), *Solenopsis globularia* (Smith), *Solenopsis molesta* Emery, and *Solenopsis pergandei* Forel) were each encountered <6 times (<5%) over the two seasons (Fig. 3).

Solenopsis invicta collections accounted for over 49% of the samples from three islands; Jekyll (70%, $n = 10$), Little St. Simons (90%, $n = 6$), and Cumberland (50%, $n = 16$), and represented the most abundant species collected on Wassaw (43%, $n = 47$). The proportion of *S. invicta* on Sea ($n = 6$), Sapelo ($n = 15$), and Ossabaw ($n = 20$) islands represented <20% of those island’s encounters over the 2 yr.

On the four islands that provided sea turtle nest success data, after removing observations from nests with known disturbances there were 1,500 nests in 2016 and 752 nests in 2017 for a total of 2,252 nests, hereafter referred to as the full ant data set. Eighty-five of these nests (3.7%) reported ant activity. Shapiro–Wilk tests on the full ant data set found neither hatching success ($W = 0.8120$, $P < 0.0001$) nor emergence success ($W = 0.8367$, $P < 0.0001$) were normally distributed. A BDM test on the response of hatching success to ant presence, blocking for Island, found no significant difference ($F = 0.6086$, $df = 1$, 35.648; $P = 0.440$). ANCOVA found significantly different emergence success between sea turtle nests with or without ants ($F = 46.946$, $df = 1$, 2249; $P < 0.0001$) after blocking for Island ($F = 24.887$, $df = 1$, 2245; $P < 0.0001$) and year ($F = 5.6974$, $df = 1$, 2245; $P = 0.017$) when controlling for hatching success as a covariate ($F = 18,937.6472$, $df = 1$, 2245; $P < 0.0001$). Negative binomial regression analyses of emergence success for nests with and without ants diverge significantly once hatching success exceeded 71% (Fig. 4) with nests with ants present exhibiting lower modeled emergence success. Multiple ant species were encountered in nests regardless of the hatching success or emergence success; however, most encounters of *Pheidole* spp. and *S. invicta* occurred in nests where hatching success was greater than 50% (Fig. 5).

The subset of sea turtle nests with ants was tested to examine differences in emergence success between species. No significant difference was found via ANCOVA (blocking for island and year with hatching success as the covariate) in emergence success between ant species ($F = 1.0078$, $df = 10$, 69; $P = 0.4459$). Ants were also categorized into stinging, nonstinging, and not collected to test if a broader

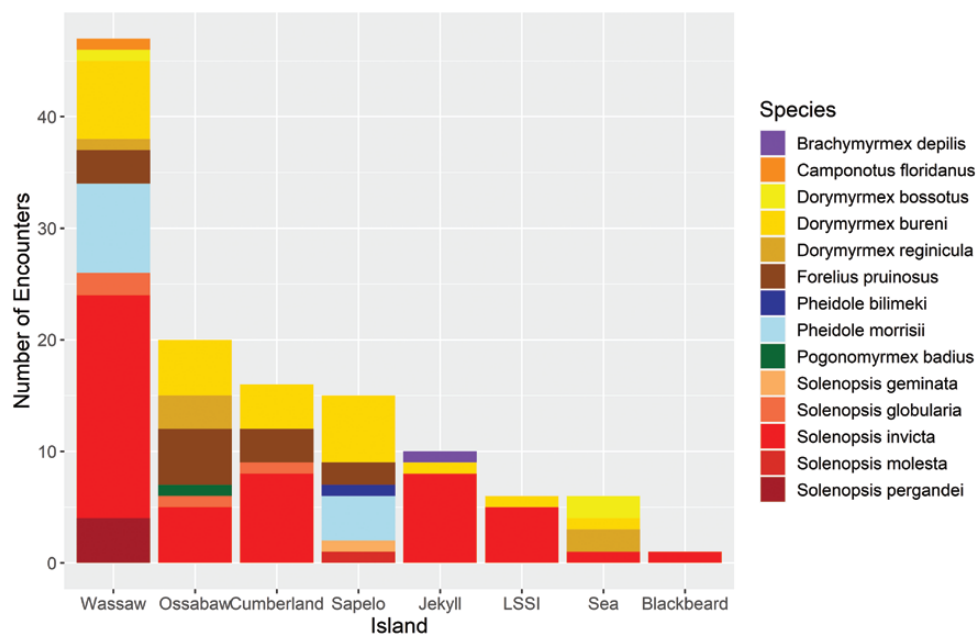


Fig. 2. Ant species assemblage and frequency of encounters collected from loggerhead sea turtle nests on eight Georgia islands in 2016–2017.

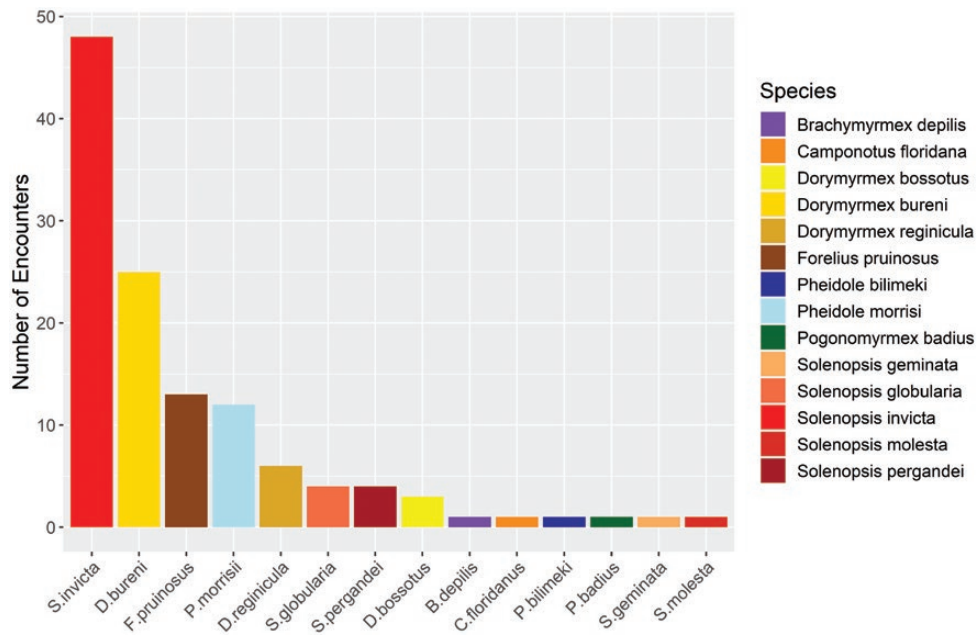


Fig. 3. Species composition and total encounters of each ant species collected from loggerhead sea turtle nests in Georgia (eight islands combined).

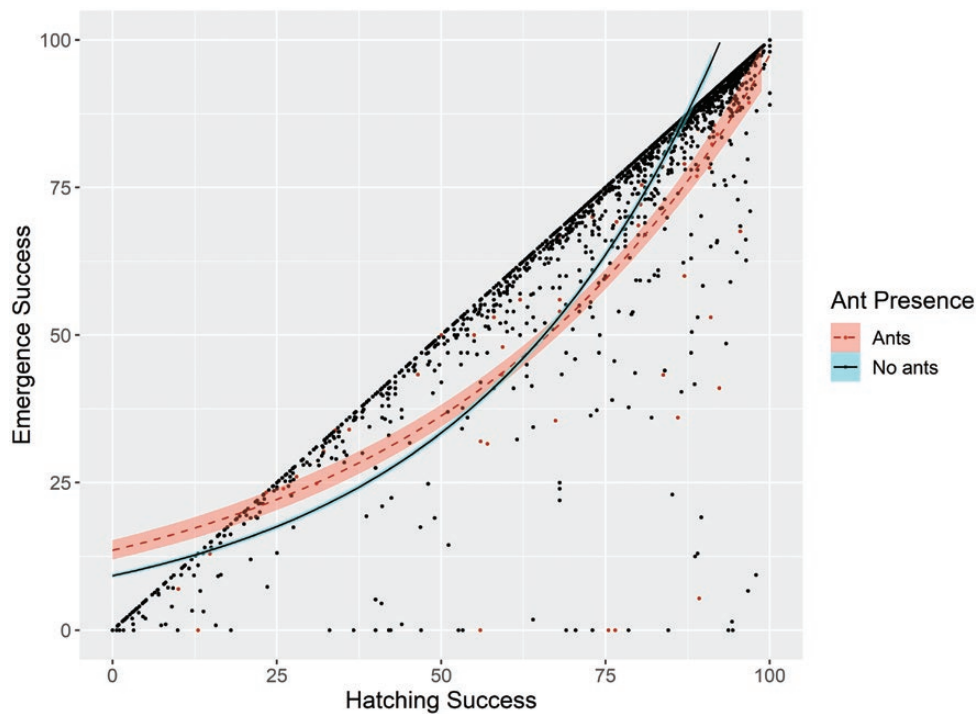


Fig. 4. Negative binomial regression analysis modeling the relationship of sea turtle hatching and emergence success in the presence (dashed red line) or absence (solid black line) of ants. Regression lines differ significantly once hatching success exceeds 71% for sea turtle nests with ant presence trending toward lower emergence success. Regression lines are plotted with 95% confidence intervals shown by their shaded areas. Each point is a sea turtle nest from the disturbance-free data set.

pattern of stinging versus nonstinging emerged. However, analysis via ANCOVA (blocking for island and year with hatching success as covariate) also found no significant difference in emergence success ($F = 0.6358$, $df = 2, 77$; $P = 0.53228$).

The distribution of sea turtle nests along the beach/dune profile shows most ant-impacted nests clustered near the primary dune vegetation edge (Fig. 6).

For modeling emergence success the model selected as the best fit (Table 1, AIC = 2,817.9) found significant positive effects for hatching success ($P < 0.0001$), presence or absence of ants ($P < 0.0001$), and days until excavation ($P < 0.0001$) as well as a significant interaction between ant presence and distance to the dune edge ($P < 0.001$). Simpler models excluding ant presence were a poorer fit to our data (Table 1).

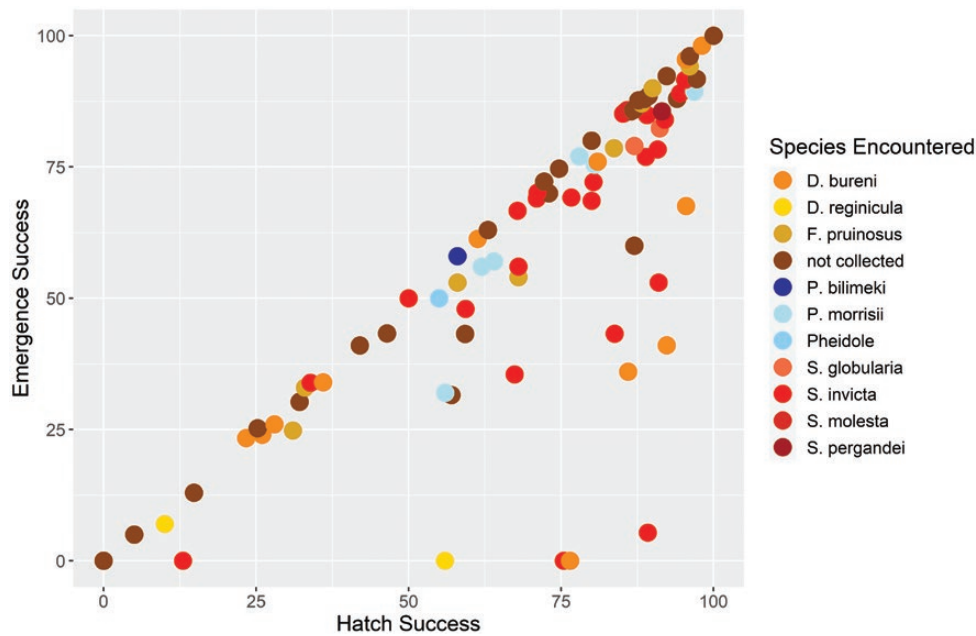


Fig. 5. Ant species encountered in sea turtle nests during 2016 and 2017 nesting seasons on Cumberland, Little St. Simons, Sapelo, and Wassaw islands. The percentage of eggs that hatched are along the x-axis and the percentage of eggs where hatchlings emerged from the nest cavity are on the y-axis. All known disturbances other than ants have been removed. Each dot represents a single nesting event ($n = 85$) where ants were collected or noted. Cases where ants were documented as present at the nest, but not collected are also reported.

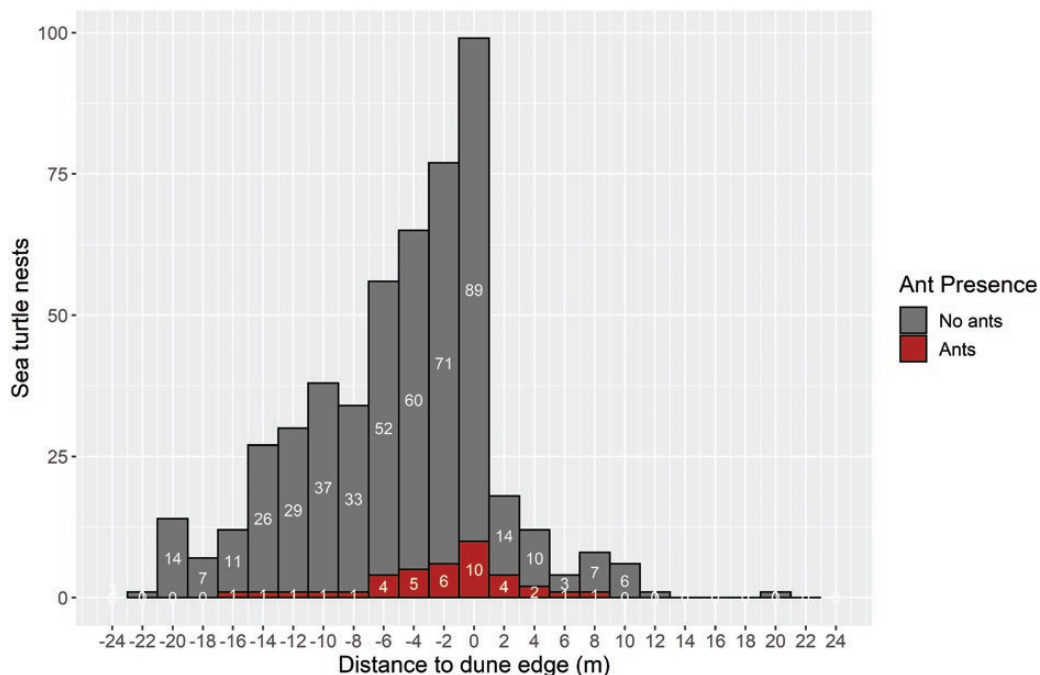


Fig. 6. Location of sea turtle nests on Wassaw 2016–2017 as a histogram by distance in meters to the primary dune vegetation edge at 0 m. Each bar is a count of the sea turtle nests every 2 m with nests where ants were encountered stacked underneath. The counts are displayed on each bar and counts of nests without ants are stacked on top of the counts of nests with ants. 53% of observed ant encounters occurred at 1 m from the dune or further inland.

The logistic model predicting the probability of an ant encounter found the distance to dune edge ($P = 0.0230$), emergence success ($P = 0.0056$), and days until excavation ($P < 0.0001$) to all be significant factors, but the interaction of distance to dune edge and days until excavation was not significant ($P = 0.6910$) and not included in the final model. The model accuracy was 91.81% and sensitivity was 15.15%. A curve constructed from the final predictive model with emergence success and days until excavation held constant at

their mean values of 58.24856 and 4.587629, respectively, indicates that at 1-m shoreward from the dune vegetation edge, there is a 12% probability of ant presence (Fig. 7).

Discussion

The collection of multiple native species in sea turtle nests (Figs. 2–4) demonstrates that both invasive red imported fire ant and

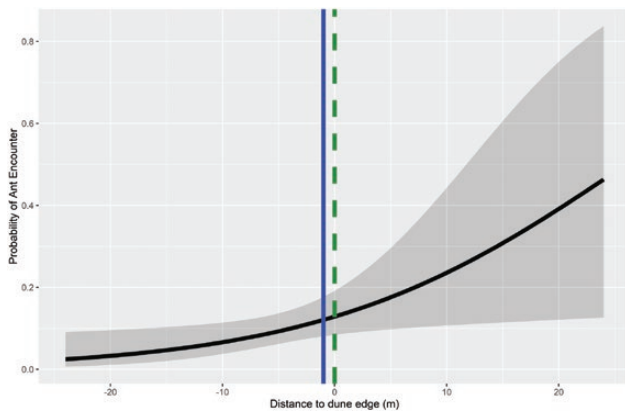


Fig. 7. Predictive logistic linear model (Probability of Encounter = Distance to dune Edge + Emergence success + Days until excavation) of the probability of encountering ants at a loggerhead sea turtle nest as a function of distance (in meters) to the primary dune edge with negative distances being shoreward of the dune edge and positive distances being inland of the dune edge. Nestling emergence success and days between emergence and nest excavation were held constant at their means. The hashed green line indicates the vegetated edge of the primary dune (distance = 0), and 95% confidence intervals of the probability prediction indicated by the shading. The solid blue line indicates the location of the suggested nest relocation buffer, where placing relocated sea turtle nests will result in a low risk of ant predation with only 12.1% probability of encounter. The model accuracy was 91.81% and sensitivity was 15.15%, with the low sensitivity meaning it is likely probabilities are somewhat higher than modeled.

opportunistic native ant species will use sea turtle nests as resources. The six most commonly encountered species in surveys of Cumberland, Sapelo, and Little St. Simons (Braman and Forschler 2018) accounted for 88% of ants encountered at sea turtle nests, indicating that species collected in this study mirror the community composition trends for encountering dune nesting ants and implying the major components of the dune nesting ant community will all forage at sea turtle nests. Despite the focus on *Solenopsis* species in the bulk of published literature discussing ants and sea turtles, 57% of our observed ant encounters at sea turtle nests were other species. Our data emphasize the need to also consider native ant species as potentially exerting pressure on beach nesting animal populations.

Proximity to the dune vegetation edge seems to be an important factor for predicting risk of encounters with ants, given the distribution of sea turtle nests relative to the primary dune vegetation edge (Fig. 6) and our predictive model (Fig. 7). This coincides with other studies reporting a risk of insects in sea turtle nests when near vegetation (Ozdemir et al. 2004) as well as Wetterer et al.'s (2007) study on ants and sea turtle nests. Sea turtle project managers often relocate at-risk sea turtle nests for a variety of reasons, including risk of flooding or predation. We propose allowing for a 1-m buffer shoreward between nests and the vegetated dune edge. On Wassaw, 53% of ant encounters were observed inland of 1 m (Fig. 6) and a 1-m risk boundary narrows the 2-m risk zone previously proposed by Wetterer et al. (2007), enabling nests on narrower beaches to be moved further from high tides while still reducing ant predation risk. Sea turtle project managers can use 1 m as an easy rule of thumb to minimize risk of ant encounters.

The main method of protecting sea turtle nests from ants is to surround nests prior to hatching with a granular ant bait containing the active ingredient hydramethylnon (Amdro) ant bait. However, recent work suggests that bait treatment increases visits to nests by

insects, crabs, and vertebrate predators (Smith et al. 2020) indicating that the current suggested practice may increase the risk of hatchling predation. An easy to implement, safer protocol for preventing deleterious ant encounters of hatchlings like a buffer zone is thus needed.

Further, given the multiple ant species our research found at sea turtle nests (Figs. 2 and 3), coastal managers applying nontarget bait treatments at sea turtle nests meant to kill alleged red imported fire ant incursions may in fact negatively impact the broader native ant community through poisoning of nontarget ant species. Doing so may have the unintended effect of harming the native ecosystem ant diversity, thereby fostering favorable conditions for establishment of more disruptive species like red imported fire ant. Consequently, future intervention aimed at ant management should be mindful that invasive fire ants are not necessarily the only possible ant species at nests. Our results identifying native ants found within sea turtle nests suggest that reducing native ant populations with pesticides could create an opportunity for red imported fire ant to colonize newly vacated dunes after treatment. Therefore, pesticidal interventions aimed at red imported fire ant may be a counterproductive approach to protecting turtle nests.

While hatching success appears to not be affected by the presence of ants, the emergence success does trend differently in the presence or absence of ants (Fig. 4), with lower emergence success in the presence of ants. This trend, combined with the multiple native ant species found in sea turtle nests (Figs. 2 and 5), implies that both invasive and native ants may be affecting sea turtle emergence success. It is worth noting that multiple species of ants were encountered at nests regardless of the relative hatching and emergence success but that the majority of encounters with *Pheidole* spp. and *Solenopsis* spp. occurred at nests where hatching success rates were greater than 50% (Fig. 4). It is possible that stingless species like the *Dorymyrmex* spp. which were found in nests across the success range may be performing more of a scavenging role while the strong mandibled *Pheidole* spp. and stinging *Solenopsis* spp. found in the nests with higher hatching but depressed emergence success are perhaps more directly interfering with hatchling emergence, but our data cannot directly point to a single species. Consequently, our data are not able to answer the question of which ants are directly affecting sea turtle hatchlings versus merely attracted to nests where hatchlings are already having difficulty emerging. The discrepancy between the 85 nests affected by ants in the ANCOVA data set and the 116 samples collected by collaborators stems from having success data for four out of the eight islands that collected ants and the inherently fractious nature of our data set. Because of such limitations, we cannot make claims as to whether each ant species observed in our study was scavenging or the cause of mortality. Due to the potential benefit to sea turtle recovery efforts if ants can be shown to be a preventable population pressure on sea turtles, however, the question of whether and to what extent ants in sea turtle nest are actually suppressing emergence should be investigated further.

One concern regarding our results is the common management practice of excavating hatched sea turtle nests earlier in areas where ants are a known risk. This practice can reduce the measured emergence success as loggerheads can exhibit up to a week-long emergence (Glen et al. 2005) and consequently often hatchlings are given 5 d to emerge before excavation. However, our linear modeling took both days until excavation and the presence or absence of ants into account and found the models containing both were the best fit for explaining our data (Table 1). The significant interaction (with a negative coefficient) of these two terms in some of our models is likely a result of standard management practice of excavating nests early where ants are a known risk. Our model containing

an additional ant presence term best fit the data which implies that while days between initial hatchling emergence and excavation matter, the presence of ants also significantly affects hatchling emergence and merits further investigation.

It is possible that ants foraging in sea turtle nests are mostly opportunistic encounters. However, as sea turtle populations recover and rookeries become more densely covered with sea turtle nests, the likelihood of encounters with ants could also increase and create increased population pressure for sea turtles. Currently, the reported incidence of ant encounters in sea turtle nests is small (85 out of 2,252, or 3.77% of our data set) relative to more notorious disturbances like raccoons and feral hogs on islands. However, any island where more than 100 sea turtle nests were deposited in both 2016 and 2017 reported ant activity, indicating a potential density-dependent relationship between sea turtle nests and ant activity. As sea turtle populations begin to recover in the Northwest Atlantic Ocean, it is possible that instances of ant predation will also increase in frequency. The relationship between ants and sea turtle nests should continue to be monitored as it presents a rare opportunity to get ahead of a population pressure to a species of conservation interest before the pressure fully emerges.

Conclusion

Both native ant species and *S. invicta* were documented in sea turtle nests on islands along the Georgia Coast. While the presence of ants did not have an effect on nest-hatching success rates, sea turtle nests where ants were encountered had a lower emergence success rate. Stakeholders managing nesting sea turtle populations can potentially reduce ant depredation risk by allowing for a 1-m buffer shoreward between the sea turtle nest and the dune vegetation edge when sea turtle nests are relocated. Further research into the interactions between ants and sea turtle nests is warranted to determine which ant species reduce emergence success of sea turtle hatchlings. Such information could help conservation efforts for sea turtles preempt any challenge ants may produce to recovery efforts before those challenges fully manifest.

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