

Predaceous Ants, Beach Replenishment, and Nest Placement by Sea Turtles

JAMES K. WETTERER,^{1,2} LAWRENCE D. WOOD,³ CHRIS JOHNSON,³ HOLLY KRAHE,⁴
AND STEPHANIE FITCHETT¹

Environ. Entomol. 36(5): 1084–1091 (2007)

ABSTRACT Ants known for attacking and killing hatchling birds and reptiles include the red imported fire ant (*Solenopsis invicta* Buren), tropical fire ant [*Solenopsis geminata* (Fabr.)], and little fire ant [*Wasmannia auropunctata* (Roger)]. We tested whether sea turtle nest placement influenced exposure to predaceous ants. In 2000 and 2001, we surveyed ants along a Florida beach where green turtles (*Chelonia mydas* L.), leatherbacks (*Dermochelys coriacea* Vandelli), and loggerheads (*Caretta caretta* L.) nest. Part of the beach was artificially replenished between our two surveys. As a result, mean beach width experienced by nesting turtles differed greatly between the two nesting seasons. We surveyed 1,548 sea turtle nests (2000: 909 nests; 2001: 639 nests) and found 22 ant species. *S. invicta* was by far the most common species (on 431 nests); *S. geminata* and *W. auropunctata* were uncommon (on 3 and 16 nests, respectively). In 2000, 62.5% of nests had ants present (35.9% with *S. invicta*), but in 2001, only 30.5% of the nests had ants present (16.4% with *S. invicta*). Turtle nests closer to dune vegetation had significantly greater exposure to ants. Differences in ant presence on turtle nests between years and among turtle species were closely related to differences in nest placement relative to dune vegetation. Beach replenishment significantly lowered exposure of nests to ants because on the wider beaches turtles nested farther from the dune vegetation. Selective pressures on nesting sea turtles are altered both by the presence of predaceous ants and the practice of beach replenishment.

KEY WORDS exotic species, Florida, red imported fire ant, *Solenopsis invicta*

Several predaceous ant species are known to attack and kill vertebrates. In North America, the most notorious of these is the red imported fire ant, *Solenopsis invicta* Buren, which arrived in Alabama by ship from South America in the early 20th century and has spread across the southeastern United States from Texas to North Carolina and Florida, causing tremendous ecological and economic damage (Tschinkel 1988, 1993, Allen et al. 1994, 2004). *S. invicta* most commonly invades and dominates open, disturbed habitats (Tschinkel 1988, Forsy et al. 2002, Wetterer and Moore 2005).

Solenopsis invicta seems to be a particularly great threat to the eggs and hatchlings of ground-nesting birds and reptiles (Ridleyhuber 1982, Sikes and Arnold 1986, Steigman 1993, Drees 1994, Allen et al. 1995, Dickinson 1995, Lockley 1995, Giuliano et al. 1996, Mueller et al. 1999, Aresco 2004). Cintra (1985) found that *S. invicta* commonly attacked and killed hatchling caiman [*Caiman yacare* (Daudin)]. Allen et al. (1997) found that hatchling American alligators [*Alligator*

mississippiensis (Daudin)] stung by fire ants showed decreased weight gain and increased mortality. Reagan et al. (2000) found that *S. invicta* in alligator nests had a significant negative impact on hatching success.

Most sea turtle nesting beaches in the southeastern United States are now infested to varying degrees with *S. invicta* (Allen et al. 2001). The great threat that *S. invicta* poses to hatching sea turtles is only now gaining recognition (Wilmers et al. 1996, Foote et al. 2000, Allen et al. 2001, Parris et al. 2002, Krahe et al. 2003, Krahe 2005). On islands in Key West Wildlife Refuge, FL, Wilmers et al. (1996) found a great increase in the proportion of sea turtle nests infested with *S. invicta* between 1990 and 1994, e.g., infestation rate at Main Beach in Marquesas Keys increased from 0% in 1990–1992, to 9% in 1993, and 50% in 1994. LeBuff (1990 in Moulis 1997) concluded that, for sea turtles on Sanibel Island, in southwest Florida, “fire ants were the most dangerous predators upon hatchlings.” Moulis (1997) found a significant decrease in emergence success in loggerhead sea turtle (*Caretta caretta* L.) nests infested with *S. invicta* compared with uninfested nests (40.6 versus 54.0%). Hatchling sea turtles are particularly vulnerable to attack by ants because hatchlings typically take from several hours to several days after pipping before they emerge from their nests. During this vulnerable time, ants may invade the nests and

¹ Wilkes Honors College, Florida Atlantic University, 5353 Parkside Dr., Jupiter, FL 33458.

² Corresponding author, e-mail: wetterer@fau.edu.

³ Marinelife Center, 14200 US Highway 1, Juno Beach, FL 33408.

⁴ Department of Biology, Florida Atlantic University, 777 Glades Rd., Boca Raton, FL 33431.

Table 1. Nest location and incidence of ants on sea turtle nests

Year	Sea turtle species	No. nests	Mean wrack (mean \pm SD)	Mean toe (mean \pm SD)	Percent ants present	Percent <i>S. invicta</i> present
2000	<i>Chelonia mydas</i>	290	16.4 \pm 6.7	5.8 \pm 7.3	74.8	37.2
	<i>Caretta caretta</i>	586	10.8 \pm 5.8	10.9 \pm 7.2	56.5	35.2
	<i>Dermochelys coriacea</i>	33	12.7 \pm 5.4	8.2 \pm 5.7	60.6	36.4
	Overall	909	12.6 \pm 6.8	9.2 \pm 7.3	62.5	35.9
2001	<i>Chelonia mydas</i>	18	19.1 \pm 7.8	4.9 \pm 9.0	94.4	50.0
	<i>Caretta caretta</i>	511	11.3 \pm 7.4	22.1 \pm 18.4	27.8	15.5
	<i>Dermochelys coriacea</i>	110	14.4 \pm 6.4	23.9 \pm 18.1	32.7	15.5
	Overall	639	12.0 \pm 7.4	22.0 \pm 18.4	30.5	16.4

Wrack, distance to most recent high tide line; toe, distance to dune vegetation line.

attack trapped hatchlings (Fowler 1979, Krahe et al. 2003, Krahe 2005). Ants also sting hatchlings as they exit the nest (Krahe et al. 2003, Krahe 2005). Hatchlings may die as a direct result of the ant stings, or as an indirect result, because of impairment caused by stings, particularly stings to their eyes (Krahe et al. 2003, Krahe 2005).

In addition to *S. invicta*, two other stinging ant species found on beaches in the southeastern United States are also known to attack vertebrates: the tropical fire ant, *Solenopsis geminata* (Fabr.), and the little fire ant, *Wasmannia auropunctata* (Roger). *S. geminata* is known to attack the hatchlings of birds and reptiles (Stoddard 1931, Emlen 1938, Travis 1941, Kroll et al. 1973, Mrazek 1974). *W. auropunctata* in the Solomon Islands attack hatchlings of the ground-nesting Melanesian scrubfowl (*Megapodius eremita* Hartl) and commonly sting the eyes of dogs, causing them eventually to become blind (Wetterer 1997).

In the summers of 2000 and 2001, we surveyed ants on an important sea turtle nesting beach in southeastern Florida to evaluate the potential threat of *S. invicta* and other predaceous ants to hatching sea turtles. Part of the study beach was artificially replenished with sand pumped from off-shore in the winter between our two surveys, allowing us to evaluate experimentally the influence of beach width on the incidence of ants on sea turtle nests.

Materials and Methods

We studied the distribution of ants at sea turtle nests along a 9.7-km stretch of beach in Jupiter and Juno Beach, Palm Beach County, FL. For long-term sea turtle research, the beach was divided into 11 zones marked with permanent stakes (Rusenko and Wood 1996, Wood 2004). Zone 1 began in the north at the seawall of the Jupiter Reef Club; zone 11 ended in the south at the northern border of John D. MacArthur Beach State Park. The level of public use of the beach differed markedly across zones. Zones 1–5 were freely accessible public beaches with roadside parking; Zones 6–8 were lined by condominiums and private homes with public access about every 300 m, zone 9 bordered a golf course with no public access, and zones 10 and 11 bordered on private properties with no public access. Three species of sea turtle nested on this beach: endangered green turtles (*Chelonia mydas*

L.) and leatherbacks (*Dermochelys coriacea* Vandelli) and threatened loggerheads (*Caretta caretta*). Nesting by *C. mydas* at this beach showed a 2-yr cycle of alternating high and low nesting years (Rusenko and Wood 1996, Wood 2004); 2000 was a high year and 2001 was a low year.

Beginning in 1990, every morning during sea turtle nesting season (March to October), workers from the Marinelife Center of Juno Beach have recorded all new sea turtle nests along this beach and marked a fraction of these nests with wooden stakes placed 0.3 m to the west ($\approx 10\%$ of *C. caretta* nests, 50% *C. mydas* nests during high nesting years or 100% in low nesting years, respectively, and all *D. coriacea* nests). Workers recorded information on nest locations using Differential GPS, as well their distance above the most recent high tide mark (wrack) and below the dune vegetation line (toe) (Rusenko and Wood 1996, Wood et al. 1999, Wood 2004). We calculated minimum beach width experienced by each nesting sea turtle as wrack plus toe.

We surveyed ants on marked nest sites using a folded index card with ≈ 1 g of water-packed canned tuna inside placed at the base of each marking stake between 2200 and 2330 hours. We returned after 2 h (± 15 min) and put each card in a separate zip-lock bag. After killing the collected ants in a freezer, we counted the number of ants in each bag and put them in vials of 95% ethanol for later identification. Stefan Cover at Harvard University's Museum of Comparative Zoology (MCZ) identified the ant specimens. Voucher specimens have been deposited at the MCZ.

Results

Between 5 June and 22 August 2000, we surveyed ants on 909 sea turtle nests, and between 20 June and 3 September 2001, we surveyed 639 nests (Table 1). In 2000, the mean beach width (\pm SD) experienced by nesting turtles in this study was 21.8 ± 7.1 m (Fig. 1). In 2001, the mean beach width was 34.0 ± 17.6 m; beach replenishment greatly increased beach width in most beach zones, more than doubling mean beach width in zones 3–6 (Fig. 1).

In both years, *C. mydas* nested significantly higher on the beach, nearer the dune vegetation, than did *C. caretta* and *D. coriacea* (Table 1; Bonferroni *t*-tests of *C. mydas* versus *C. caretta*: $P < 0.005$ for all compar-

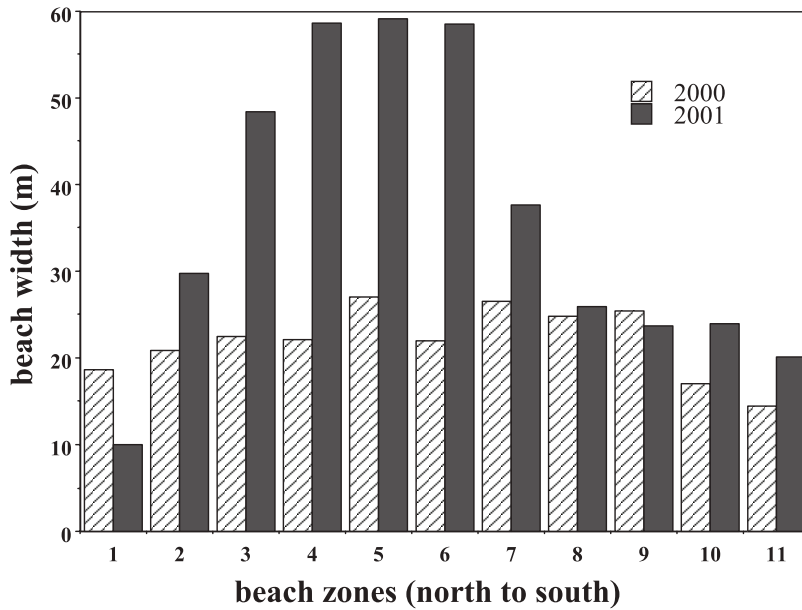


Fig. 1. Mean beach width in different beach zones (zones 1-11) experienced by nesting sea turtles in the 2000 and 2001 (before and after beach replenishment).

isons; for *C. mydas* versus *D. coriacea*: $P < 0.005$ for 2000 wrack, $P = 0.012$ for 2001 wrack, $P = 0.016$ for 2000 toe, $P < 0.005$ for 2001 toe). The differences were more pronounced in 2001, both because mean beach width was much greater and because, in 2001, all 18 *C. mydas* nested on narrow, southern portions of the beach that were relatively unaffected by the beach replenishment (one on a narrow part of zone 7 and the rest in zones 8-11).

We found a total of 22 ant species present on sea turtle nests. In both years, *S. invicta* was by far the most common species, and *S. geminata* and *W. auropunctata* were uncommon (Table 2). In 2000, 568 nests (62.5%) had at least one ant present (for baits with ants: range = 1-1,030 ants; median = 41 ants). In 2001, 195 nests (30.5%) had at least one ant present (for baits with ants: range = 1-871 ants; median = 31 ants). This difference is significant ($Z = 13.17$, $P < 0.001$). The percentage of nests with ants present varied greatly among beach zones and between years (Fig. 2). In both 2000 and 2001, there was a negative relationship between mean beach width in each of the 11 zones (W_b) and the percentage of turtle nests with ants (%A) present, although the relationship was stronger in 2001 when variation in beach width was much greater (2000 regression: %A = $1.0 - 0.017 W_b$, $R^2 = 0.38$, $P = 0.05$; 2001 regression: %A = $0.7 - 0.012 W_b$, $R^2 = 0.81$, $P < 0.01$). Beach zones that had greater increases in width between 2000 and 2001 showed greater decreases in the presence of ants on sea turtle nests (Fig. 2; $\Delta\%A = 0.71 - 0.012 \Delta W_b$, $R^2 = 0.81$, $P < 0.001$).

In 2001, the six zones with greatest beach width (zones 2-7) had ants present on only 11% of nests, whereas in the remaining zones (zones 1 and 8-11),

ants were present on 45% of nests, a significant difference ($Z = 10.4$, $P < 0.001$). In contrast, in 2000, before replenishment, the beach widths were similar in the two groups of zones (Fig. 1), and there was no significant difference in infestation between these zones: 63% of nests in zones 2-7 versus 62% of nests in zones 1 and 8-11 ($Z = -0.4$, $P = 0.68$).

Table 2. Ants collected at tuna baits on sea turtle nests in 2000 ($n = 909$) and 2001 ($n = 639$)

	No. nests	
	2000	2001
<i>Solenopsis invicta</i> ^{a,b}	326	105
<i>Paratrechina bourbonica</i> ^a	80	26
<i>Dorymyrmex bureni</i>	60	16
<i>Paratrechina longicornis</i> ^a	56	16
<i>Tapinoma melanocephalum</i> ^a	32	21
<i>Pheidole megacephala</i> ^a	20	6
<i>Camponotus floridanus</i>	11	11
<i>Tetramorium bicarinatum</i> ^a	10	8
<i>Wasmannia auropunctata</i> ^{ab}	12	4
<i>Pheidole floridana</i>	3	2
<i>Technomyrmex difficilis</i> ^a	3	0
<i>Solenopsis geminata</i> ^b	2	1
<i>Solenopsis globularia</i>	1	1
<i>Tetramorium caldarium</i> ^a	0	2
<i>Camponotus zonatus</i>	0	2
<i>Brachymyrmex depilis</i>	1	0
<i>Cardiocondyla emeryi</i> ^a	1	0
<i>Cardiocondyla venustula</i> ^a	1	0
<i>Forelius pruinosus</i>	1	0
<i>Pheidole dentata</i>	1	0
<i>Tetramorium simillimum</i> ^a	1	0
<i>Pheidole moerens</i> ^a	0	1

^a Not native to Florida (Deyrup et al. 2000).

^b Threat to sea turtles.

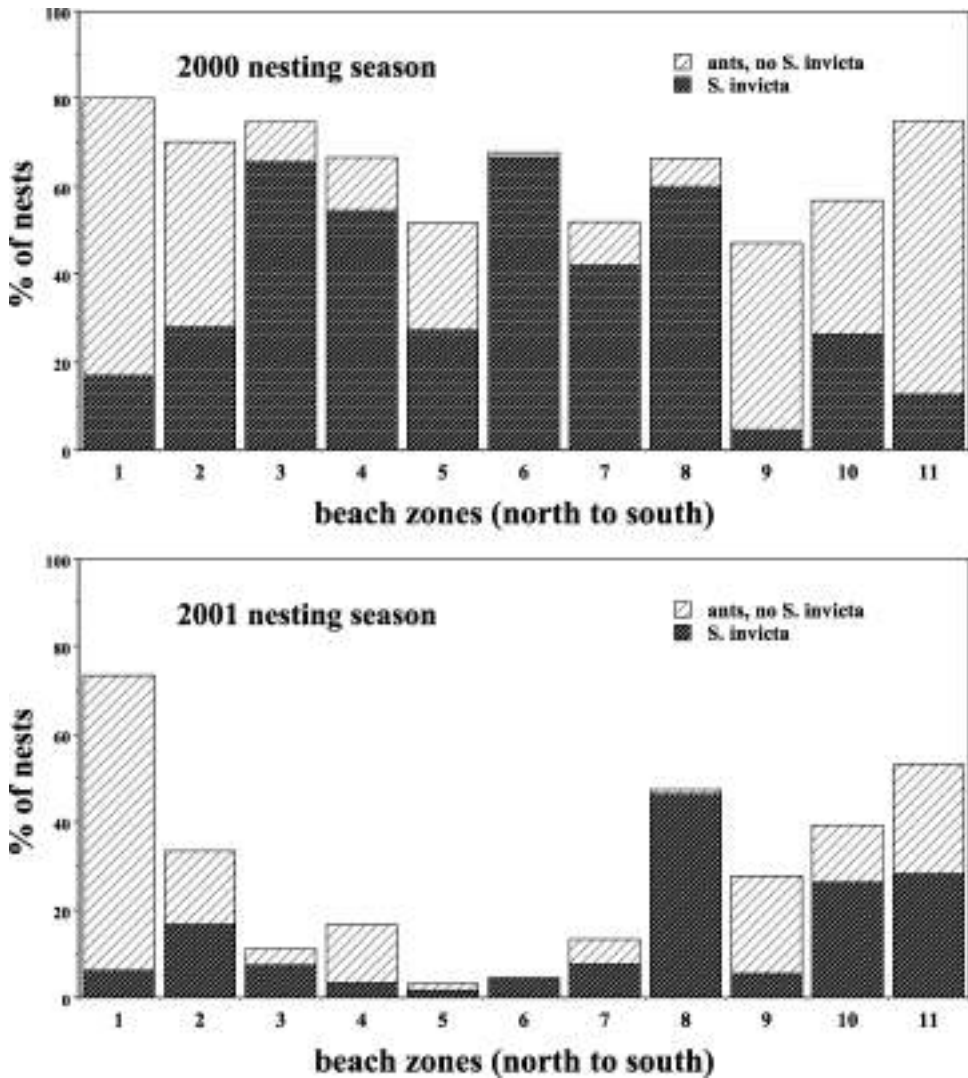


Fig. 2. Occurrence of ants on sea turtle nest in each beach zone (zones 1–11) in 2000 and 2001 (before and after beach replenishment).

In both years, ≈93% of nests within 2 m of the dune vegetation had ants present (Fig. 3). However, the percentage of nests with ants present significantly decreased with distance from the dune vegetation [Fig. 3; $\log(P_+/P_-) = 1.97 - 0.17D$, $P < 0.001$ for test of whether D slope = 0, where P_+ = probability that a nest has ants, P_- = probability that a nest has no ant, and D = distance from vegetation]. Controlling for toe, *C. mydas* nest were significantly more like to have ants present than were nests of the other two turtle species [$\log(P_+/P_-) = 1.80 - 0.17D + 0.51C$, $P < 0.001$ for test of whether D slope = 0; $P < 0.002$ for test of whether C slope = 0; where C indicates whether the turtle species in *C. mydas*]. The median number of ants on nests with ants present also decreased with distance from the dune vegetation (Table 3). Overall, *S. invicta* recruited to the baits in higher numbers than other ant species (Table 3).

Discussion

Where a sea turtle chooses to lay her eggs may greatly influence nesting success. For example, sea turtles that nest low on the beach, close to the ocean, have increased risk of nest failure because of beach erosion and drowning of eggs during major storms (Lewis 1998; L.D.W., unpublished data). Nesting higher on the beach, however, can increase the risk of nest destruction by raccoons (*Procyon lotor* L.; Horton 1990). We found that nesting higher on the beach also increases exposure to another important threat, attack by predaceous ants.

Sea turtle nests closer to the dune vegetation were much more likely to have ants present. This is because most ant species do not nest on open beaches. Instead, they nest in adjacent vegetated areas and make forays out onto the beach in search of food. As a result, green

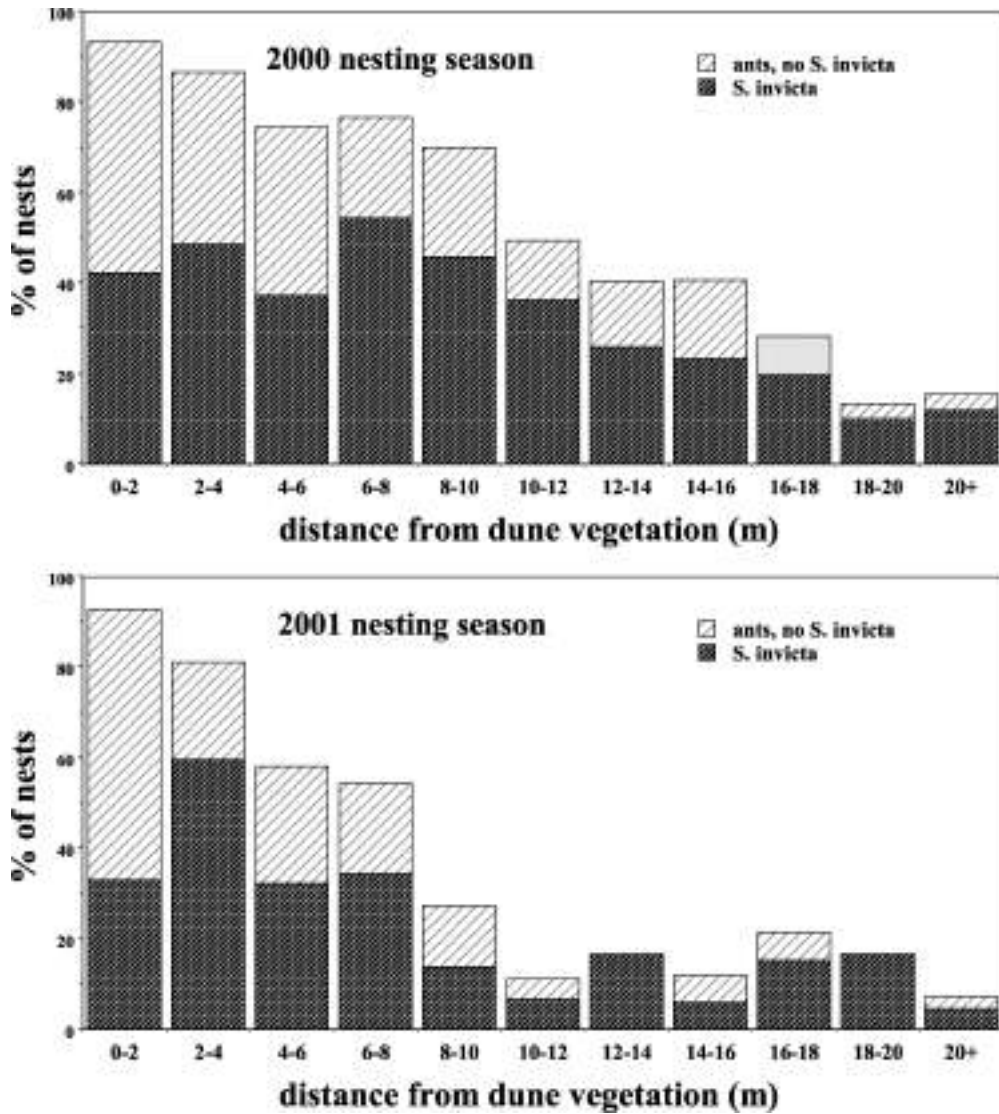


Fig. 3. Occurrence of ants on sea turtle nest in relation to distance from dune vegetation in 2000 and 2001 (before and after beach replenishment).

Table 3. Median no. ants present on sea turtle nests in relation to distance from dune vegetation (toe), at baits with ants, but no *S. invicta* present and at baits with *S. invicta* present (no. of nests in parentheses)

Toe (m)	2000		2001	
	No <i>S. invicta</i>	<i>S. invicta</i>	No <i>S. invicta</i>	<i>S. invicta</i>
1-2	51 (88)	206 (73)	24 (49)	142 (27)
2-4	40 (50)	144 (64)	4 (11)	85 (23)
4-6	26 (29)	57 (29)	16 (8)	88 (10)
6-8	34 (18)	75 (44)	7 (7)	18 (12)
8-10	6 (17)	51 (32)	5 (3)	51 (3)
10-12	8 (11)	18 (30)	5 (2)	17 (3)
12-14	5 (9)	19 (16)	0 (0)	40 (5)
14-16	3 (12)	25 (16)	1 (1)	1 (1)
16-18	16 (4)	33 (9)	2 (2)	7 (5)
18-20	55 (1)	1 (3)	0 (0)	20 (3)
20+	42 (3)	16 (10)	51 (7)	15 (13)
Overall	24 (242)	91 (326)	19 (90)	58 (105)

turtles (*C. mydas*), which nest higher on the beach than do leatherbacks (*D. coriacea*) and loggerheads (*C. caretta*), were more likely to have their nests infested with ants. In addition, sea turtle nests on narrow sections of the beach had higher infestation rates. Beach replenishment lowered the exposure of sea turtle eggs and hatchlings to ants because on the wider beaches turtles nested farther from the dune vegetation. The distribution of nests relative to the high tide mark remained similar from 2000 to 2001, but the distribution of nests relative to the dune vegetation greatly increased, a change closely mirrored by the change in beach width caused by the replenishment (Table 1; see Wood 2004 for further discussion).

We found that *S. invicta* was by far the most common ant on sea turtle nests on our study beach. Here,

as on other nesting beaches in the southeastern United States, *S. invicta* seems to be a serious threat to sea turtles, preying on eggs and hatchlings within the nest (Moulis 1997, Krahe et al. 2003, Krahe 2005, Wetterer and Wood 2005). These ants may be having their greatest impact on sea turtles by stinging hatchlings emerging from the nests. Although stung hatchlings may be recorded by researchers as having successfully emerged from the nest, even a single fire ant sting may seriously impair a hatchling and greatly increase the likelihood of subsequent mortality because of secondary infection, disorientation, and decreased ability to avoid other predators (Krahe et al. 2003, Krahe 2005). Risk of predation seems to be very high for hatchling sea turtles, particularly during their first few hours outside their nest. At our study site, common hatchling predators include ghost crabs (*Ocyropsis quadrata* Fabr.; L.D.W., personal observation) on the beach and tarpon (*Megalops atlanticus* Valenciennes) in the ocean. At this beach, Stewart and Wyneken (2004) found that 11 of 217 hatchling sea turtles were preyed on within their first 15 min in the ocean, primarily by tarpon.

The spread of *S. invicta* through the southeastern United States, and more recently through the West Indies (Davis et al. 2001, Wetterer and Snelling 2006), seems to pose an important threat to sea turtles that alters the balance of selective pressures acting on nest placement. Krahe (2005) found that even a single *S. invicta* sting greatly increases the likelihood of mortality for *C. caretta* hatchlings but has a much less pronounced effect on *C. mydas* hatchlings. This relative sensitivity of *C. caretta* to ant stings may affect the balance of selective pressures and offer an explanation for why *C. caretta* females nest lower on beaches than do *C. mydas* females (Krahe 2005).

Predaceous ants also threaten nesting sea turtles in other parts of the world. For example, Wetterer (2006) found that *S. geminata* was by far the most common ant at Tortuguero, Costa Rica, an important *C. mydas* nesting beach where Fowler (1979) and Mangel et al. (2001) noted ants in *C. mydas* nests. Fowler (1979) found that ants invaded 35 of 237 (14.8%) *C. mydas* nests where they fed on hatchlings and eggs, although Fowler (1979) "could not tell whether the ants killed developing eggs and hatchlings, or fed only on dead and weak individuals." Fowler (1979) noted that the ants "chew into eggs, particularly those in vegetated areas." Mangel et al. (2001) noted ants "depredating or killing eggs, pipped hatchlings, hatchlings in the nest and hatchlings in the vicinity of the nest." In Tongaland, South Africa, McAllister et al. (1965) observed driver ants (*Dorylus* sp.) invade a sea turtle nest by the thousands and destroy every egg, consuming the embryos, which were in late stages of development. At the same site, Hughes (1970a, b, 1971, 1975) repeatedly observed *Dorylus* sp. preying on sea turtle eggs. Hughes (1971) found that "observations of marked nests showed that a not inconsiderable number of wild nests succumb to the depredations of ants." At one hatchery with 10 *C. caretta* and 2 *D. coriacea* nests that were unprotected

by insecticide, ant predation caused 100% mortality (Hughes 1975). Chan and Liew (1999) reported that "red ants" infested 53% of hawksbill turtle nests (*Eretmochelys imbricata* L.) in Malaysia. Chen sent us ant specimens from this study and S. Cover identified them as three native Asian species, the driver ant *Dorylus orientalis* Westwood, plus *Lophomyrmex* sp. and *Pheidole* sp.

There is considerable controversy over how changes in the beach environment caused by artificial replenishment (e.g., changes in sand temperature, grain size, compaction, moisture) may impact coastal species, including sea turtle nesting adults, eggs, and hatchlings (Broadwell 1992, Parkinson et al. 1994, Crain 1995, Steinitz et al. 1998, Rumbold et al. 2001). Although some of these physical changes may influence ant distribution on the beach, we believe that the primary impact of beach replenishment on ants was mediated through changes in beach width. We found a lower occurrence of ants on sea turtle nests at night after beach replenishment, largely because, on wider beaches, sea turtle nests were on average further from the dune vegetation where the ants nest. In addition, we found a decline in the occurrence of ants at a given distance from the vegetation after beach replenishment (Fig. 3), possibly because, on wider beaches, there were fewer food resources from the ocean available within foraging distance of the dune vegetation, resulting in fewer ants out foraging on the beach.

Our study identified one distinct benefit of beach replenishment for sea turtles in Florida, i.e., reduced exposure to attacks by *S. invicta*. Raccoons, which are the major vertebrate predators on sea turtle nests in Florida, also preferentially attack on nests nearer to the dune vegetation (Horton 1990). Beach replenishment therefore may also reduce sea turtle nest predation by raccoons and perhaps other land-based nest predators, such as red foxes (*Vulpes vulpes*), cats (*Felis catus* L.), and dogs (*Canis domesticus* L.).

Although beach replenishment lowers the exposure of sea turtles to attack by predaceous ants, this expensive procedure could not be considered a cost-effective measure aimed solely at protecting sea turtles from ants. Future studies should examine whether certain types of vegetation adjacent to beaches encourage or discourage infestation by *S. invicta* and other predaceous ants. In addition, judicious efforts to control fire ant populations in the vegetation adjacent to nesting beaches during peak sea turtle nesting season, particularly on narrow beaches where the sea turtles are most vulnerable, may prove useful in helping conserve these threatened and endangered species worldwide.

Acknowledgments

We thank S. Cover for ant identification; A. Wetterer, M. Wetterer, and H. Smith for comments on this manuscript; E. H. Chan for sending ant specimens from Malaysia; Florida Atlantic University, the National Save the Sea Turtle Foundation, Environmental Defense, and National Science Foundation (DUE 0088211) for financial support.

References Cited

- Allen, C. R., S. Demarais, and R. S. Lutz. 1994. Red imported fire ant impact on wildlife—an overview. *Texas J. Sci.* 46: 51–59.
- Allen, C. R., R. S. Lutz, and S. Demarais. 1995. Red imported fire ant impacts on Northern Bobwhite populations. *Ecol. Appl.* 5: 632–638.
- Allen, C. R., K. G. Rice, D. P. Wojcik, and H. F. Percival. 1997. Effect of red imported fire ant envenomization on neonatal American alligators. *J. Herpetol.* 31: 318–321.
- Allen, C. R., E. A. Forsys, K. G. Rice, and D. P. Wojcik. 2001. Effects of fire ants on hatching sea turtles and the prevalence of fire ants on sea turtle nesting beaches in Florida. *Fla. Entomol.* 84: 250–253.
- Allen, C. R., D. M. Epperson, and A. S. Garmestani. 2004. Red imported fire ant impacts on wildlife: a decade of research. *Am. Midl. Natur.* 152: 88–103.
- Aresco, M. J. 2004. Reproductive ecology of *Pseudemys floridana* and *Trachemys scripta* (Testudines: Emydidae) in northwestern Florida. *J. Herpetol.* 38: 249–256.
- Broadwell, A. L. 1992. Effects of beach nourishment on the survival of loggerhead sea turtle nests. Proceedings of the 11th Annual Sea Turtle Symposium. NOAA Tech. Memorandum NMFS-SEFSC 302: 21–23.
- Chan, E.-H., and H.-C. Liew. 1999. Hawksbill turtles, *Eretmochelys imbricata*, nesting on Redang Island, Terengganu, Malaysia, from 1993 to 1997. *Chelon. Conserv. Biol.* 3: 326–329.
- Cintra, R. 1985. Nascimento de filhotes de *Caiman yacare* (Daudin, 1802) (Crocodylia: Alligatoridae) em condicoes semi-naturais no pantanal matogrossense. *Pap. Avuls. Zool. S. Paulo.* 36: 91–101.
- Crain, D. A. 1995. Effects of beach nourishment on sea turtles: review and research initiatives. *Restor. Ecol.* 3: 95–104.
- Davis, L. R., Jr., R. K. Vander Meer, and S. D. Porter. 2001. Red imported fire ants expand their range across the West Indies. *Fla. Entomol.* 84: 735–736.
- Deyrup, M., L. Davis, and S. Cover. 2000. Exotic ants in Florida. *Trans. Am. Entomol. Soc.* 126: 293–326.
- Dickinson, V. M. 1995. Red imported fire ant predation on Crested Caracara nestlings in south Texas. *Wilson Bull.* 107: 761–762.
- Drees, B. M. 1994. Red imported fire ant predation on nestlings of colonial waterbirds. *Southwest. Entomol.* 19: 355–359.
- Emlen, J. T. 1938. Fire ants attacking California quail chicks. *Condor* 40: 85–86.
- Foote, J. J., J. L. Floyd, T. L. Mueller, M. Salmon, and J. M. Spinkel. 2000. Changes in loggerhead nest predation patterns on west central Florida beaches. Proceedings of the 18th Annual Sea Turtle Symposium. NOAA Tech. Memorandum NMFS-SEFSC 436: 189–190.
- Forsys, E. A., C. R. Allen, and D. P. Wojcik. 2002. Influence of the proximity and amount of human development and roads on the occurrence of the red imported fire ant in the lower Florida Keys. *Biol. Conserv.* 108: 27–33.
- Fowler, L. E. 1979. Hatching success and nest predation in the green sea turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. *Ecology* 60: 946–955.
- Giuliano, W. M., C. R. Allen, R. S. Lutz, and S. Demarais. 1996. Effects of red imported fire ants on northern bobwhite chicks. *J. Wildl. Manag.* 60: 309–313.
- Horton, M. 1990. Factors affecting loggerhead sea turtle (*Caretta caretta*) production on Wabasso Beach, Florida. Proceedings of the 10th Annual Symposium on Sea Turtle Biology and Conservation, NOAA Tech. Memorandum NMFS-SEFSC 278: 3–6.
- Hughes, G. R. 1970a. Further studies on marine turtles in Tongaland III. *Lammergeyer* 12: 7–25.
- Hughes, G. R. 1970b. Further studies on marine turtles in Tongaland IV. *Lammergeyer* 12: 26–36.
- Hughes, G. R. 1971. The marine turtles of Tongaland V. *Lammergeyer* 13: 7–24.
- Hughes, G. R. 1975. Further studies on marine turtles in Tongaland 8. *Lammergeyer* 22: 9–18.
- Krahe, H. 2005. Impact of the red imported fire ant (*Solenopsis invicta*) on two species of sea turtle hatchlings. MS thesis, Florida Atlantic University, Boca Raton, FL.
- Krahe, H., J. K. Wetterer, and L. D. Wood. 2003. Impact of fire ant stings on sea turtle hatchling survival. Proceedings of the 22nd Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memorandum NMFS-SEFSC 503: 211–212.
- Kroll, J. C., K. A. Arnold, and R. F. Gotie. 1973. An observation of predation by native fire ants on nestling Barn Swallows. *Wilson Bull.* 85: 478–479.
- LeBuff, C. H. Jr. 1990. The loggerhead turtle in the eastern Gulf of Mexico. *Caretta Research Inc.*, Sanibel, FL.
- Lewis, T. E. 1998. Storm effects on sea turtle nests at St. Vincent National Wildlife Refuge, Florida, USA. Proceedings of the Seventeenth Annual Sea Turtle Symposium. NOAA Tech. Memorandum NMFS-SEFSC 415: 232.
- Lockley, T. C. 1995. Effect of imported fire ant predation on a population of the least tern—an endangered species. *Southwest. Entomol.* 20: 517–519.
- Mangel, J., S. Troëng, L. Segura, M. Stockmann, A. Ortega, C. Reyes, Z. Hudgson, A. Opazo, L. Fernández, R. Hernández, D. Hussy, M. Ramírez, S. de la Parra, M. Martínez, R. Hajar, and E. Rankin. 2001. Report on the 2000 Green Turtle Program at Tortuguero, Costa Rica. Caribbean Conservation Corporation and the Ministry of Environment and Energy, Costa Rica.
- McAllister, H. J., A. J. Bass, and H. J. Van Schoor. 1965. The marine turtles of Tongaland, Natal. *Lammergeyer* 3: 10–40.
- Moulis, R. A. 1997. Predation by the imported fire ant (*Solenopsis invicta*) on loggerhead sea turtle (*Caretta caretta*) nests on Wassaw National Wildlife Refuge, Georgia. *Chelon. Conserv. Biol.* 2: 433–436.
- Mrazek, R. W. 1974. The relationship of the fire ant (*Solenopsis geminata* [sic.] Fab) to nestlings of birds nesting on two spoil islands in the Laguna Madre. *Texas J. Sci.* 25: 140.
- Mueller, J. M., C. B. Dabbert, S. Demarais, and A. R. Forbes. 1999. Northern bobwhite chick mortality caused by red imported fire ants. *J. Wildl. Manag.* 63: 1291–1298.
- Parkinson, R. W., J. White, and M. Perez-Bedmar. 1994. Effects of beach nourishment on compaction, grain-size, moisture and temperature, Sebastian Inlet. Proceedings of the 14th Annual Sea Turtle Symposium. NOAA Tech. Memorandum NMFS-SEFSC 351: 112–114.
- Parris, L. B., M. M. Lamont, and R. R. Carthy. 2002. Increased incidence of red imported fire ant (Hymenoptera: Formicidae) presence in loggerhead sea turtle (Testudines: Cheloniidae) nests and observations of hatchling mortality. *Fla. Entomol.* 85: 514–517.
- Reagan, S. R., J. M. Ertel, and V. L. Wright. 2000. David and Goliath retold: fire ants and alligators. *J. Herpetol.* 34: 475–478.
- Ridlehuber, K. T. 1982. Fire ant predation on wood duck ducklings and pipped eggs. *Southwest. Nat.* 27: 222.
- Rumbold, D. G., P. W. Davis, and C. Perretta. 2001. Estimating the effect of beach nourishment on *Caretta caretta* (loggerhead sea turtle) nesting. *Restor. Ecol.* 9: 304–310.

- Rusenko, K. W., and L. D. Wood. 1996. Nesting surveys and nest survivabilities for sea turtles on Juno/Jupiter Beach, Florida during 1990–1994. Proceedings of the 15th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memorandum NMFS-SEFSC 387: 269.
- Sikes, P. J., and K. A. Arnold. 1986. Red imported fire ant (*Solenopsis invicta*) predation on cliff swallow (*Hirundo pyrrhonota*) nestlings in east central Texas. Southwest. Nat. 31: 105–106.
- Steigman, K. L. 1993. Nesting ecology of the Dickcissel (*Spiza americana*) on a tallgrass prairie relict in North Central Texas. PhD dissertation, University of North Texas, Denton, Texas.
- Steinitz, M. J., M. Salmon, and J. Wyneken. 1998. Beach renourishment and loggerhead turtle reproduction: a seven year study at Jupiter Island, Florida. J. Coast. Res. 14: 1000–1013.
- Stewart, K. R., and J. Wyneken. 2004. Predation risk to loggerhead hatchlings at a high-density nesting beach in Southeast Florida. Bull. Marine Sci. 74: 325–335.
- Stoddard, H. L. 1931. The bobwhite quail. Charles Scribner's Sons, New York.
- Travis, B. V. 1941. Notes on the biology of the fire ant *Solenopsis geminata* (F.) in Florida and Georgia. Fla. Entomol. 24: 15–22.
- Tschinkel, W. R. 1988. Distribution of fire ants *Solenopsis invicta* and *S. geminata* in north Florida in relation to habitat and disturbance. Ann. Entomol. Soc. Am. 81: 76–81.
- Tschinkel, W. R. 1993. The fire ant (*Solenopsis invicta*): still unvanquished, pp. 121–136. In B. N. McKnight (ed.), Biological pollution: the control and impact of invasive exotic species. Indiana Academy of Science, Indianapolis, IN.
- Wetterer, J. K. 1997. Alien ants of the Pacific islands. Aliens 6: 3–4.
- Wetterer, J. K. 2006. The tropical fire ant, *Solenopsis geminata*, on an important sea turtle nesting beach in Tortuguero National Park, Costa Rica. Proceedings of the 23rd Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memorandum NMFS-SEFSC 536: 281–283.
- Wetterer, J. K., and J. A. Moore. 2005. Red imported fire ants (Hymenoptera: Formicidae) at gopher tortoise (Testudines: Testudinidae) burrows. Fla. Entomol. 88: 349–354.
- Wetterer, J. K., and L. D. Wood. 2005. Distribution and impact of ants on a sea turtle nesting beach in Palm Beach County, Florida. Proceedings of the 21st Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memorandum NMFS-SEFSC 528: 351–353.
- Wetterer, J. K., and R. R. Snelling. 2006. The red imported fire ant, *Solenopsis invicta*, in the Virgin Islands (Hymenoptera: Formicidae). Fla. Entomol. 89: 431–434.
- Wilmers, T. J., E. S. Wilmers, M. Miller, and P. Wells. 1996. Imported fire ants (*Solenopsis invicta*): a growing menace to sea turtle nests in Key West National Wildlife Refuge. Proceedings of the 15th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memorandum NMFS-SEFSC 387: 341–343.
- Wood, L. D. 2004. Nest placement by three species of sea turtles in southeast Florida. MS, Florida Atlantic University, Boca Raton, FL.
- Wood, L. D., C. Johnson, and D. Carson. 1999. Differential Global Positioning System (GPS) as a tool for studying nesting distribution on a Florida sea turtle nesting beach. Proceedings of the 19th Annual Symposium on Sea Turtle Conservation and Biology. NOAA Tech. Memorandum NMFS-SEFSC 443: 192.

Received for publication 17 January 2007; accepted 26 April 2007.