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RED IMPORTED FIRE ANTS (HYMENOPTERA: FORMICIDAE) AT GOPHER TORTOISE (TESTUDINES: TESTUDINIDAE) BURROWS

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ABSTRACT

The gopher tortoise, Gopherus polyphemus Daudin, is endemic to the southeastern US, where its populations are declining primarily due to habitat destruction. Tortoises are preyed upon by many species, including the red imported fire ant, Solenopsis invicta Buren, a destructive exotic species now common throughout the tortoises' entire range. We surveyed ants using tuna bait at 154 G. polyphemus burrows in a greenway reserve established to protect the tortoises in a residential area of southeast Florida. We found S. invicta present, typically recruiting to the bait in very high numbers, on the aprons of 33% of the tortoise burrows. Solenopsis invicta occurred significantly more often at burrows within 30 m of the greenway's outer edge than at burrows in more interior parts of the greenway (57% versus 16%). Among the interior burrows, S. invicta occurred significantly more often at burrows directly on two narrow strips of disturbed habitat, along an old fence line and an old pipeline, than at burrows not on these two strips (46% versus 12%). The greenway interior appears to offer tortoises and other species some refuge from S. invicta. However, the long thin design typical of greenways, the inclusion of walking paths through the greenways, and the policies of prescribed burning and reduction mowing used to maintain open habitat for the tortoises all may increase the tortoises' exposure to S. invicta. Solenopsis invicta is also a grave threat to other native species in these reserves, including the many animals that obligately live inside gopher tortoise burrows.

Key Words: edge effect, exotic species, Florida, Gopherus, greenway, Solenopsis invicta.

Resumen

La especia tortuga gopher, Gopherus polyphemus Daudin, es endémica al sudeste de los EE.UU., donde sus poblaciones disminuyen principalmente debido a la destrucción de habitat. Las tortugas son atacadas por muchas especies, inclusive la hormiga roja de fuego importada, la Solenopsis invicta Buren, una especie exótica destructiva ahora común a toda la región geográfica de las tortugas. Estudiamos las hormigas que atraemos con cebo de atún en 154 madrigueras de la G. polyphemus en una reserva ecológica que se estableció para proteger las tortugas en un área residencial del sudeste de la Florida. Encontramos a la S. invicta presente, alistanda típicamente al cebo en números muy altos, en los delantales de 33% de las madrigueras de las tortugas. La presencia de la S. invicta ocurrió apreciablemente más a menudo en madrigueras dentro de un parámetro de 30 m de la orilla exterior de la reserva que en las madrigueras en partes más interiores de la reserva (57% contra 16%). Entre las madrigueras interiores, la S. invicta ocurrió apreciablemente más a menudo en madrigueras directamente en dos tiras estrechas del habitat perturbado, por una línea vieja de la cerca y una tubería vieja, que en las madrigueras que no en estaban en estas dos tiras (46% contra 12%). El interior de la reserva ecológica aparece ofrecer las tortugas y otras animales algún refugio de S. invicta. El largo y estrecho diseño típico de las reservas ecológicas, la inclusión de senderos caminantes en las reservas ecológicas, y por la costumbre de incendios prescritos y la reducción por cortes utilizados para mantener el habitat abierto para las tortugas, todo ello puede aumentar la exposición de las tortugas a la S. invicta. La S. invicta es también una amenaza grave a otras especies nativas en estas reservas, inclusive los muchos animales que se ven obligados a vivir en las madrigueras de las tortugas.

Translation provided by the authors.

Gopher tortoises, *Gopherus polyphemus* Daudin, are endemic to the coastal plains of the southeastern United States (Diemer 1992) and populations are declining through most of their range, primarily due to habitat destruction (Diemer 1986). The tortoises' decline has been particularly great in southeastern Florida, where most of the tortoise's preferred upland habitat has been converted to, for example, citrus orchards, housing developments, and phosphate mines (Diemer 1992). The gopher tortoise is now protected in Florida as a "species of special concern" (Diemer 1992; Florida Game & Fresh Water Fish Commission 1994). Gopher tortoises prefer habitats with sandy soils for burrows, herbaceous plants for food, and open sunny spots for nesting and basking (Diemer 1992). Fire is a normal element in gopher tortoise habitat, and when natural fires are suppressed, habitats may become overgrown. To maintain the open spaces necessary for herbaceous vegetation and tortoise nesting and basking sites, land managers often use prescribed burning or reduction mowing (Wade & Lunsford 1989; Main & Tanner 1999).

Female tortoises lay clutches of 3-15 eggs, usually in the sand apron in front of their burrow or in another nearby sunny spot (typically 16-67 cm from the burrow entrance; Butler and Hull 1996). Many predators attack gopher tortoise nests, including raccoons, foxes, skunks, armadillos, and snakes (Douglass & Winegarner 1977; Diemer 1992). Nest predation is often very high (Alford 1980). Landers et al. (1980) found that mammalian predators destroyed most gopher tortoise nests (87% within the first few weeks after laying) and the few surviving hatchlings were often attacked and killed by the red imported fire ant, Solenopsis invicta Buren. Epperson & Heise (2003) found that S. invicta predation accounted for 27% of posthatching mortality of gopher tortoise hatchlings.

Solenopsis invicta is probably the most destructive exotic ant species in the southeastern US, negatively impacting both invertebrates and vertebrates (Wojcik 1994; Porter & Savignano 1990). This invasive species arrived in Alabama by ship from South America and has spread across the southeast US from Texas to North Carolina, now occupying the entire range of the gopher tortoise.

Solenopsis invicta is a well-known predator on bird hatchlings, particularly ground-nesting species (e.g., see Ridlehuber 1982; Sikes & Arnold 1986; Steigman 1993; Drees 1994; Lockley 1995; Powell 1995; Dickinson 1995; Giuliano et al 1996; Mueller et al. 1999; Kopachena et al. 2000; H. Smith, pers. comm.). Solenopsis invicta also attacks reptile hatchlings. Cintra (1985) found that S. invicta commonly attacked and killed hatchling caiman (*Caiman yacare* (Daudin)). Love (1997) noted records of S. invicta attacking captive tortoises and hatching turtles and alligators. 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. Solenopsis invicta also appears to be an important threat to hatching sea turtles (Wilmers et al. 1996; Moulis 1996; Allen et al. 1998, 2001; Krahe et al. 2003; Wetterer & Wood 2005).

Solenopsis invicta appears to be an important threat to some adult reptiles as well, and is considered important in the decline of numerous rep-

tile species in the southeastern US (Mount 1981). Montgomery (1996) observed six cases of S. invicta attacking adult three-toed box turtles (Terrapene carolina triunguis (Agassiz)) in Texas, with only one of the turtles surviving due to human intervention. "It seems that the box turtle's defensive reaction is to withdraw the plastron, which cannot keep the ants out completely even when tightly closed. This reaction also renders the turtle immobile, which enables the ants to swarm over it, seeking out small openings between the plastron and the carapace. The turtle must eventually relax the plastron, which allows more ants to gain further access to its body." Montgomery (1996) concluded, "it would be difficult to estimate just how much effect the ants alone are having. But my observations lead me to believe that fire ants pose a serious threat to three-toed box turtles.

In addition to *S. invicta*, two other ant species found in the gopher tortoises' range also are known to attack vertebrates and may pose a threat to gopher tortoises: Solenopsis geminata (Fab.) and Wasmannia auropunctata (Roger). Although not generally as virulent as its congener S. invicta, S. geminata is also known to attack the hatchlings of birds and reptiles (e.g., Stoddard 1931; Travis 1941; Mrazek 1974). Where W. auropunctata occurs at high densities, it also can have a great impact on vertebrates. For example, in Gabon, W. auropunctata has been implicated in blinding house cats (Felis catus L.) and native wildlife, including elephants (Loxodonta africana (Blumenbach)) (Wetterer et al. 1999). In the Solomon Islands, locals reported that W. auropunctata commonly stings the eyes of dogs that eventually become blind, and attacks hatchlings of the ground-nesting Melanesian Scrubfowl (Megapodius eremita Hartlaub) (Wetterer 1997).

The present study was motivated, in part, by the discovery in a local greenway reserve of a Florida box turtle (*Terrapene carolina bauri* Taylor) being attacked by *S. invicta* (M. Floyd, pers. comm.). To evaluate the potential threat of *S. invicta* to gopher tortoises in the reserve, we surveyed ants at gopher tortoise burrows in the greenway.

MATERIALS AND METHODS

Study Area

Our study site was one section ("Range VIa") of a greenway reserve set up through the Abacoa residential development in Jupiter, Florida (26.90°N, 80.11°W), to preserve gopher tortoise habitat. The entire Abacoa greenway system encompasses roughly 10% of the development's land area. Our study segment included a 9.16-ha wooded range and an adjacent sunken water retention basin (Fig. 1). A path encircles the range

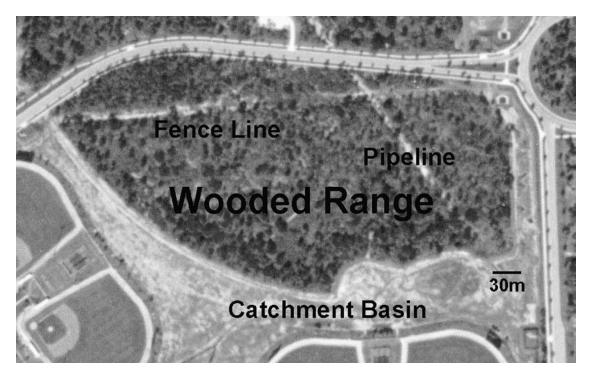


Figure 1. Aerial photograph of "Range VIa" in the Abacoa greenway, Jupiter, Florida, a wooded range bounded in the north by Frederick Small Road and on other sides by a sunken water catchment basin. An old fence line and a recent pipeline cross the northern and eastern parts of the range. The black bar equals approximately 30 m.

and two linear areas of disturbance cross through the northern and eastern portions of the range; one is an old (>6 years-old) cleared cattle fence line (fence removed) and the other is a recently (<3 years-old) dug pipeline (Fig. 1). A chain-link fence, separating the reserve from Frederick Small Road, bounds the north side of the range. The range is bounded on the other three sides by the water catchment basin with channels for directing and holding rainwater runoff from storms. Except for the channels, the basin is dry through most of the year. A chain-link fence separates the catchment basin from Central Road to the east and several baseball fields to the south and west.

The relatively undisturbed portions of the range consist of typical flatwood scrub (Myers and Ewel 1990) with a sparse canopy of mature slash pines (*Pinus elliottii* Engelman), an understory of saw palmetto (*Serenoa repens* (Bartram)) thickets and scrubby oaks (*Quercus spp.*), and open spaces dominated by wiregrass (*Aristida beyrichiana* Trin. & Rupr.), with lesser amounts of runner oak (*Quercus minima* Small) and deer moss lichens (*Cladina spp.* and *Cladonia spp.*). The old fence line is dominated by bunches of wiregrass and chalky bluestem (*Andropogon virginicus* L.) with small stands of young slash pine saplings and gallberry (*Ilex glabra* (L.)). The pipeline area is largely open sand with low grasses and herbs

growing in patches. The path around the outer edge of the wooded range is primarily covered with bahiagrass (*Paspalum notatum* Flueggé) that is mowed about every two to three weeks.

We surveyed ants at gopher tortoise burrows on 26 February, 14 March, and 16 April 2002 $(\text{sampling} \sim 1/3 \text{ of the burrows on each day}) using$ a folded index card with ~1 g of canned waterpacked tuna inside placed within 0.2 m of the burrow entrance between 1300 and 1500 h. We surveyed ants using tuna bait to assess ant species present at the burrows that recruit heavily to rich animal protein resources. We returned 2 h (±10 min) later and collected the cards, putting each in a separate zip-lock bag. We found that two h was enough time to allow significant recruitment, but not complete bait removal. After killing the collected ants in a freezer, we counted them, then preserved them in alcohol for identification. Stefan Cover (Museum of Comparative Zoology) and Mark Deyrup (Archbold Biological Station) identified the ants.

As of 16 April 2002, there were 85 marked gopher tortoises and 164 marked burrows within our study site. This density of 9.3 tortoises/ha is extremely high, e.g., it is more than three times higher than the highest mean density (2.7/ha) at Kennedy Space Center in east-central Florida (Breininger et al. 1994). This high density is due, in part, to people releasing gopher tortoises found elsewhere into the greenway (Diemer 1986).

From a map of burrow locations in the study area, we calculated the distance to the nearest edge of the wooded range for each burrow. We classified burrows less than 30 m from the perimeter of the wooded range as "edge" burrows; all others we classified as "interior" burrows.

RESULTS

We surveyed ants at 154 of the 164 marked gopher tortoise burrows; we excluded ten burrows because other animals removed the bait cards. All surveyed burrows had at least one ant present (range = 1-637 ants; median = 62 ants). We found 19 ant species (1-3 species per bait; Table 1); the most common was *S. invicta*, which occurred at 51 burrows (33%; Table 1). The only other ant found that may pose a threat to tortoises was the little fire ant, *Wasmannia auropunctata*, which occurred at four burrows (3%). *Solenopsis invicta* tended to recruit more workers to baits they occupied (median = 160 ants) than did other ant species (median = 40 ants).

We found *S. invicta* significantly more often at edge burrows (36/63 = 57%) than at interior burrows $(15/91 = 16\%; \chi^2 = 27.8; P < 0.001)$. In contrast, we found one or more species of native ant significantly less often at edge burrows (23/63 = 37%) than at interior burrows $(62/91 = 68\%; \chi^2 =$

15.0; P < 0.001). We found one or more species of exotic ant other than *S. invicta* equally often at edge burrows (8/63 = 13%) as at interior burrows (18/91 = 20%; χ^2 = 1.3; ns). We found only one species significantly less often at edge burrows than at interior burrows, the native *Crematogaster atkinsoni* Wheeler (χ^2 = 6.4; P < 0.05); several ant species showed a strong trend in this direction, but we lacked sufficient sample size to demonstrate statistical significance.

Among the 91 interior burrows, we found *S. invicta* significantly more often at burrows directly on the narrow disturbed strips along the old fence line and pipeline (6/13 = 46%) than at interior burrows not on these strips (9/78 = 12%; χ^2 = 9.7; *P* < 0.005). Sample size for edge burrow on and off these disturbed strips was too small for statistical comparison.

DISCUSSION

We found *S. invicta* present at most gopher tortoise burrows around the outer perimeter of the greenway reserve, but at few burrows in the interior portions of the greenway. Conversely, native ants were significantly less common on the outer perimeter than in the interior of the greenway. We also found that *S. invicta* was present more often at burrows on two disturbed strips through the interior of the greenway than at burrows in other parts of the greenway interior. These corridors of

Exotic ant species	Occurrence at burrows	
	# edge	# interior
‡Solenopsis invicta Buren	36	15
Pheidole moerens Wheeler	3	10
Technomyrmex albipes (Smith)	1	4
‡Wasmannia auropunctata (Roger)	1	3
Brachymyrmex obscurior Forel	1	1
Cardiocondyla emeryi Forel	1	1
Tapinoma melanocephalum (Fabr.)	1	1
Paratrechina longicornis (Latr.)	0	1
Native ant species		
Pheidole floridana Emery	13	32
Crematogaster atkinsoni Wheeler	4	21
Crematogaster ashmeadi Mayr	0	6
Forelius pruinosus (Roger)	3	3
Pheidole dentata Mayr	3	3
Dorymyrmex bureni (Trager)	3	2
Pheidole morrisii Forel	2	2
Aphaenogaster miamiana Wheeler	1	1
Temnothorax pergandei (Emery)	1	1
Aphaenogaster flemingi Smith	1	0
Dorymyrmex bossutus (Trager)	0	1

TABLE 1. ANTS ON TUNA BAITS AT TORTOISE BURROWS ON THE GREENWAY EDGE (n = 63) and the greenway interior (n = 91). \ddagger = Potential threat to gopher tortoises.

disturbance thus allowed *S. invicta* more access to the interior of the greenway. Footpaths through greenway areas may have a similar influence. The greenway interior appears to offer tortoises and other species some refuge from *S. invicta*.

Our findings have conservation and development policy implications. For example, the long, thin design of many segments of the greenway may increase the exposure of gopher tortoises and other native species to S. *invicta* predation by increasing the spatial extent of edges (Saunders et al. 1991). Our study site was one of the wider segments in the Abacoa greenway. Narrower portions of the greenway may not have as much intact interior fauna. The division of the Abacoa greenway into sections separated by roads further increases the amount of edge. Because S. in*victa* prefers disturbed habitats (Tschinkel 1988; Stiles & Jones 1998), prescribed burning and reduction mowing, which land managers use to maintain open habitat for the gopher tortoises, could lead to increased S. invicta infestation and allow these ants to penetrate interior sites.

Stings of S. invicta may have serious detrimental effects on both adult and hatchling gopher tortoises. Gopher tortoise hatchlings sometimes remain in their nest one or more days after hatching (Butler & Hull 1996), during which time they may be particularly at risk to S. invicta attack. Hatching sea turtles, which typically take from several hours to several days after pipping before they emerge from their nests, are similarly vulnerable to ant attack. During this time, ants invade the nests and attack trapped hatchlings, particularly their sensitive eyes (Krahe et al. 2003). Because even a single fire ant sting may seriously impair a hatchling, ants may be having a tremendous impact on sea turtle hatchlings that are stung while emerging, through increases in subsequent mortality, e.g., increased vulnerability to other predators (Krahe et al. 2003).

Solenopsis invicta also poses a threat to other animals that use gopher tortoise burrows for shelter, including some species that are known only from gopher tortoise burrows, e.g., several species of beetle (including Copris gopheri Hubbard, Onthophagus polyphemi Hubbard, and Aphodius troglodytes Hubbard), a robberfly (Machimus polyphemi Bullington & Beck), the gopher frog (Rana capito LeConte), and the Florida mouse (Podomys floridanus (Chapman)) (Lago 1991; Lips 1991; Witz et al. 1991; Diemer 1992; Humphrey 1992; Deyrup & Franz 1995). Many of these animals are likely to be poorly defended against attacks by this exotic ant.

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