Competitive interaction between two ant species facilitates egg hatching in yellow-spotted Amazon River turtles (*Podocnemis unifilis*)

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Abstract. Competition and facilitation are opposite sides of the species-interaction continuum. However, competitive interactions between species could result in facilitation for a third species. We evaluated the patterns of infestation and competitive exclusion between crazy-ants (*Nylanderia* sp.1) and fire-ants (*Solenopsis geminata*) and their effect on yellow-spotted Amazon River turtle (*Podocnemis unifilis*) nests in central Amazonia. We found that *Nylanderia* sp.1 colonizes *P. unifilis* nests at the start of their incubation period, whereas *S. geminata* was more abundant in nests during the final third of the incubation period. After colonization, the ant colonies remained in the nest through the breeding season. We did not observe differences in hatching success between nests with or without *Nylanderia* sp.1; however, in all nests colonized by *S. geminata* the entire *P. unifilis* clutch was lost. Our results suggest that during the incubation period, *P. unifilis* clutches benefit from *Nylanderia* sp.1 colonization, which prevents nest colonization by *S. geminata*. During the most defenseless stage in the life history of turtles, indirect facilitation by *Nylanderia* sp.1 appears to support the coexistence between prey, *P. unifilis* clutches, and their main predator, *S. geminata,* during the incubation period.

Keywords. Associative resource; Hatching success; Indirect facilitation; *Nylanderia;* Predator-prey; *Solenopsis geminata.*

INTRODUCTION

Resource competition influences not only competitive interactions between species, but also the growth of consumer population (Stachowicz, 2001; Allen et al., 2016). However, in some cases the niche occupied by a species in co-occurrence of interspecific interactions ends up being greater than that occupied when the same species lives alone (Bruno et al., 2003; Maestre et al., 2009; He et al., 2013). Such patterns occur when changes in population density of one species makes the local environment more favorable to another interacting species (Miller, 1994; Allen et al., 2016).

Among know interactions, predation is frequently reported as a key factor determining life history patterns (Vermeij, 1994). Adaptations to deal with high predation risk may include faster development at especially vulnerable life cycle stages or adaptations directly related to reduce mortality (Abrams, 2000; Creel et al., 2016). Given their major effects on fitness, traits that prevent predation should be under strong selection (Guin et al., 2016; Wang et al., 2016). However, predator-prey relations are embedded in broader assemblages, and to understand the consequences of the coupled evolution of a given predator and prey species pair, it is necessary to also consider the interactions with other species (Abrams, 2000; Xu et al., 2016).

In contrast, positive interactions between different species are also of particular interest due to their potential to create cascade effects within the assemblage involved. Such events may occur when one organism makes the local environment more favorable for another (Wang et al., 2016), as when benefits outweigh costs of this association (Bronstein, 2009). Species that are more resistant to predators can provide "associative refuges" for other species that are susceptible to these predators (Guin et al., 2016). Similarly, species susceptible to predators may function as an "associative resource" for species that compete with them (Abrams, 2000). Many species can also modify the local environment, facilitating the occurrence of other species and, as with other interactions, this facilitation may be attenuated by a variety of competitive mechanisms and the environment itself (Miller, 1994; Bruno et al., 2003; Allen et al., 2016).

Mechanisms that facilitate species co-occurrence are important but often neglected in their role of regulating populations (Bruno et al., 2003). Studies on facilitation have emerged from tests of the stress gradient hypothesis (Bertness and Callaway, 1994; Callaway and Walker, 1997), which predicts that the relative importance of positive interactions between species increases with increased environmental stress (Miriti, 2006; Nesnera, 2016). Probably, the "nurse species" are among the most known facilitat-

ing mechanism. "Nurse species" may provide protection against disturbances and facilitate population growth of the attend species (Bertness and Callaway, 1994; Brooker et al., 2008; Bronstein, 2009). However, nurse species are just one facet of the facilitation spectrum (Stachowicz, 2001). When interactions between multiple species occur simultaneously, one species may competitively suppress another, leading to indirect facilitation of a third species (Brooker et al., 2008). Competitive or facilitating mechanisms may be more relevant during different stages of the life cycle of the species involved. In many cases, incubation period and juvenile stage are the most vulnerable period for survival, especially in species with abiotically incubated egg stages, such as turtles (Weisrock and Janzen, 1999; Erickson and Baccaro, 2016; Erickson et al., 2020a, b).

Turtle populations are declining globally, which is mainly due to increases in adult mortality (Congdon and Gibbons, 1990; Heppell, 1998). In addition, vulnerability of turtle nests also explains the relatively low survival rate for some groups (Escalona and Fa, 1998; Erickson and Baccaro, 2016; Erickson et al., 2020b). Both biotic and abiotic nesting site characteristics have direct consequences on reproductive success, development, and survival during incubation (Weisrock and Janzen, 1999; Ferreira and Castro, 2010; Erickson et al., 2020a, b). Nests with longer incubation period may suffer higher mortality, either from water infiltration (Packard et al., 1987; Erickson et al., 2020b) or due to increased predation rates (Pignati et al., 2013; Erickson and Baccaro, 2016; Erickson et al., 2020b). Lizards, small and medium-sized mammals, and invertebrates are among the most frequent predators during turtle incubation and hatching periods (Blamires et al., 2003; Leighton et al., 2008; Longo et al., 2009; Erickson and Baccaro, 2016; Erickson et al., 2020b), while rats and birds are most common during hatchlings' emergence (Caut et al., 2008; Ferreira and Castro, 2010). Among invertebrates, ants are important predators during the incubation phase of freshwater turtles (Allen et al., 2004; Pignati et al., 2013; Erickson et al., 2020b). For example, *Solenopsis geminata* (Fabricius, 1804) was responsible for up to 65% of all natural (e.g., not human-based) clutch losses of yellow-spotted Amazon River turtles, *Podocnemis unifilis* Troschel, 1848 in central Amazonia (Erickson and Baccaro, 2016; Erickson et al., 2020b).

Ants account for about 25% of the animal biomass in tropical forests (Fittkau and Klinger, 1973; Wilson and Hölldobler, 2005). Because of their high local abundances, competition between ant species is common, with species competing for both resources and nesting sites (Fellers, 1987). These interactions usually result in competitive hierarchies between dominant, subdominant, and subordinate species (Albrecht and Gotelli, 2001; Arnan et al., 2011). Dominant species usually exclude other species from using some nutrient-rich resources, such as protein baits (Baccaro et al., 2012; Cerdá et al., 2013). However, several niche partition mechanisms that allow co-occurrence among species within such hierarchical systems have been described (Kaspari and Weiser, 2000; Albrecht and Gotelli, 2001; Gibb and Parr, 2010; Arnan et al., 2011).

In some cases, the less aggressive subordinate species locates and exploits food quickly, circumventing interference from aggressive and behaviorally dominant species (Fellers, 1987). In other regions, dominant species may facilitate the occurrence of subordinate species by neutralizing the effects of subdominant species (Arnan et al., 2011).

Solenopsis geminata is an abundant ant species in some turtle nesting areas. It has been reported as the major predator of *Podocnemis unifilis* nests in clayey soils in central Amazonia (Erickson and Baccaro, 2016; Erickson et al., 2020b). *Nylanderia* sp.1 is the second most abundant species in such areas and is typically specialized in quickly finding and exploiting resources (LaPolla et al., 2011). Both species colonize *P. unifilis* nests, probably attracted by biological material such as the maternal mucus deposited during egg-laying (Erickson and Baccaro, 2016). So far, however, predation on eggs and young turtles for the genus *Podocnemis* have been reported only by ants of the genus *Solenopsis* Westwood, 1840 (*S. geminata*: Erickson and Baccaro, 2016; Erickson et al., 2020b) and fire-ants (Westwood, 1840) (*S. saevissima:* Pignati et al., 2013). In the current study we investigated the infestation patterns of the two most locally abundant ant species: *S. geminata* and *Nylanderia* sp.1, and the influence of both species on *P. unifilis* egg hatching rates. In particular, we addressed the following questions: (1) Does colonization of *P. unifilis* nests by *S. geminata* and *Nylanderia* sp.1 occur more frequently soon after egg deposition or close to the time of hatchling-emergence? (2) Is there evidence that *S. geminata* and *Nylanderia* sp.1 are competing for *P. unifilis* nests? And (3) what is the effect of the presence of both ant species on *P. unifilis* nests?

MATERIALS AND METHODS

Study area

The nesting area was located in the Itapuru sector of the Sustainable Development Reserve Piagaçu-Purus (04°26′30″S, 62°17′42.7″W). There were several clay banks along streams and lakes connected to the Purus River. The area has abundant grass cover (Erickson and Baccaro, 2016; Erickson et al., 2020b), with variable declivity and extension along canals and lakes connected to the Purus River. We monitored *Podocnemis unifilis* nests from mid-September through to early December (dry season) in 2013 and 2014, which is when the rivers are at their lowest levels (Bittencourt and Amadio, 2007), the soil is exposed, and female turtles begin to nest (Fig. 1A).

Sampling design

During both years, we surveyed 30 nests of *Podocnemis unifilis* via active search from the tracks left on the substrate and individually marked with a numbered stake. We protected nests with plastic-screen fences and moni-

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tored them weekly throughout the incubation period until hatching and emergence of hatchlings. The fences protected nests from larger predators only, keeping free access to small invertebrates. We sampled ants using three pitfall traps (plastic cups of 500 ml with 9 cm diameter) arranged around each focal *P. unifilis* nest (Fig. 2). Approximately 20 m from each nest, we installed a second set of three pitfalls using the same spatial design, hereafter referred as control plots. We ensured that the area adjacent to controls had no other turtle nest and were the same distance from water (Fig. 2). Pitfalls were filled with 70% alcohol and left open for 48 h. Two data-collection sampling periods were carried out each year for each of the 30 nests: 1) start of the incubation period; 2) near hatchling-emergence period. Overall, we sampled 30 nests (15 nests per year) and the control plots (15 control plots per year).

Figure 1. (A) Nesting area of *Podocnemis unifilis* in clayey soil. **(B)** Emergence of *P. unifilis* hatchlings. **(C)** Nest of *P. unifilis* predated by *Solenopsis geminata.* **(D)** Turtle embryo killed by *S. geminata.*
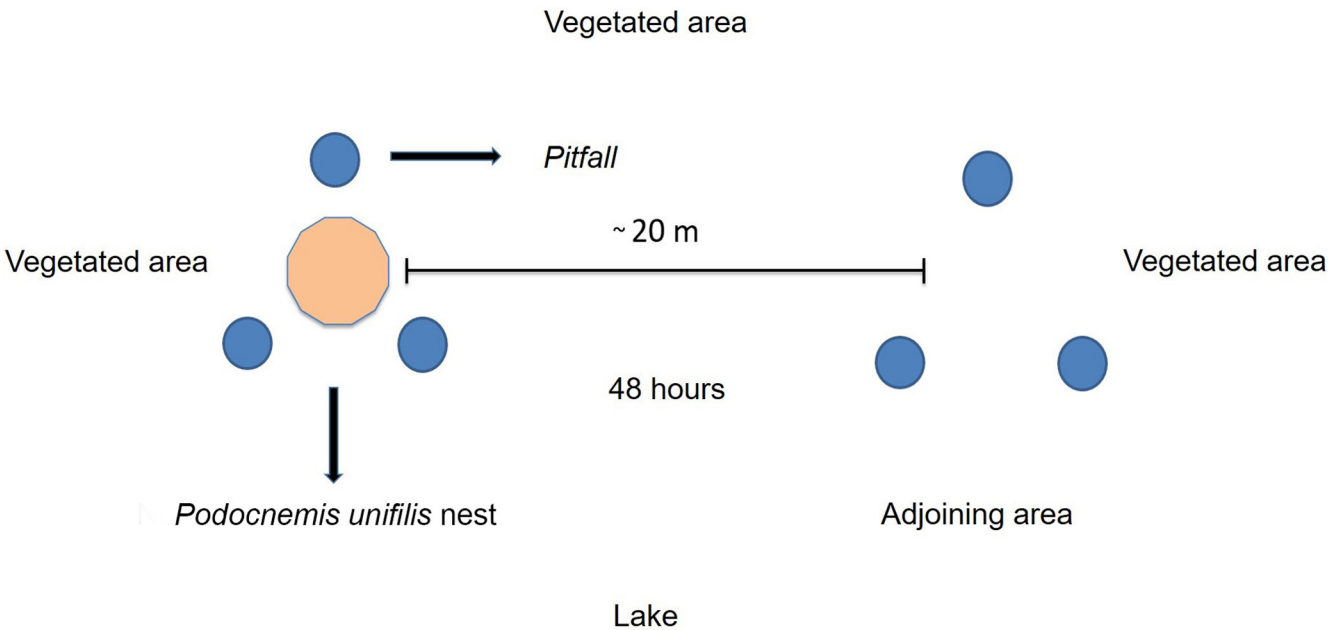

Figure 2. Design used to sample ants at the beginning and end of the *Podocnemis unifilis* incubation period and area adjacent to each monitored nest.

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At the end of incubation period, we counted the proportions of *P. unifilis* hatchlings that emerged from each nest. We also noted the presence of ant nests inside the turtle nest. We adopted this sampling design to estimate when the ants located the nest without disturbing the clutch.

We identified all ants to species or morphospecies and counted the number of individuals per species. Because ants are colonial organisms, we used a 7-point abundance scale (adapted from Andersen, 1997): 1, 1 ant; 2, 2–5 ants; 3, 6–10 ants; 4, 11–20 ants; 5, 21–50 ants; 6, 50–500 ants and 7, > 500 ants. Voucher specimens were deposited in the Entomological Collection of the Zoological Paulo Bührnheim, Universidade Federal do Amazonas.

Statistical analysis

We used paired *t*-tests to investigate when the two dominant ant species colonized turtle nests. The 7-point abundance scale of *Solenopsis geminata* and *Nylanderia* sp.1 found in *Podocnemis unifilis* nests and the nearby area (control) were compared at the beginning and at the end of the turtle-nesting season.

We tested for non-random patterns of species co-occurrence to evaluate whether deterministic assembly rules, such as those resulting from competition, could be occurring at the sites (Gotelli, 2000). The species pool included all ant species, including the two numerically dominant species, *Solenopsis geminata* and *Nylanderia* sp.1. A presence-absence matrix was produced, where each row was a different species, and each column was a different *Podocnemis unifilis* nest. We created two such matrices, one for each year of monitoring. The C-score, which measures the tendency of a species to segregate in space, was used to quantify co-occurrence (Stone and Roberts, 1990).

For each presence-absence matrix, 5,000 random matrices were produced using a fixed algorithm that retains the row and column sums of the original matrix (Gotelli, 2000). Null model analyses were conducted using the *oecosimu* function from the Vegan package (Oksanen et al., 2016), which calculated the C-score values for each randomly permuted matrix, and then determined the probability of encountering the observed matrix by comparing it with the simulated values. We repeated the same procedure, using an occurrence matrix without *S. geminata* and another occurrence matrix without *Nylanderia* sp.1 to better understand the role of each species in the assembly structure.

We compared the mean percentage of eggs hatched between nests occupied by *Solenopsis geminata,* by *Nylanderia* sp.1, and nests that were not occupied by ants at the end of the nesting season. Given the nature of this data (percentages) we used an arcsine transformation before running an ANOVA test, to improve normality of residuals. Statistical analyses were carried out in R 3.3.2 (R Core Team, 2018).

RESULTS

A total of 4,945 ants were collected in *Podocnemis unifilis* nests, and 2,396 ants were sampled in the area adjacent to nests (control plots) during the four sampling periods in 2013 and 2014. We collected a total of 14 ant species, 8 species within nests and 12 in the control plots. These belonged to five subfamilies and 10 genera, with seven genera sampled in the *P. unifilis* nesting area, and eight genera sampled in the area immediately adjacent to the nests. During the experiment, *Nylanderia* sp.1 and *Solenopsis geminata* were by far the most abundant species (Fig. 3).
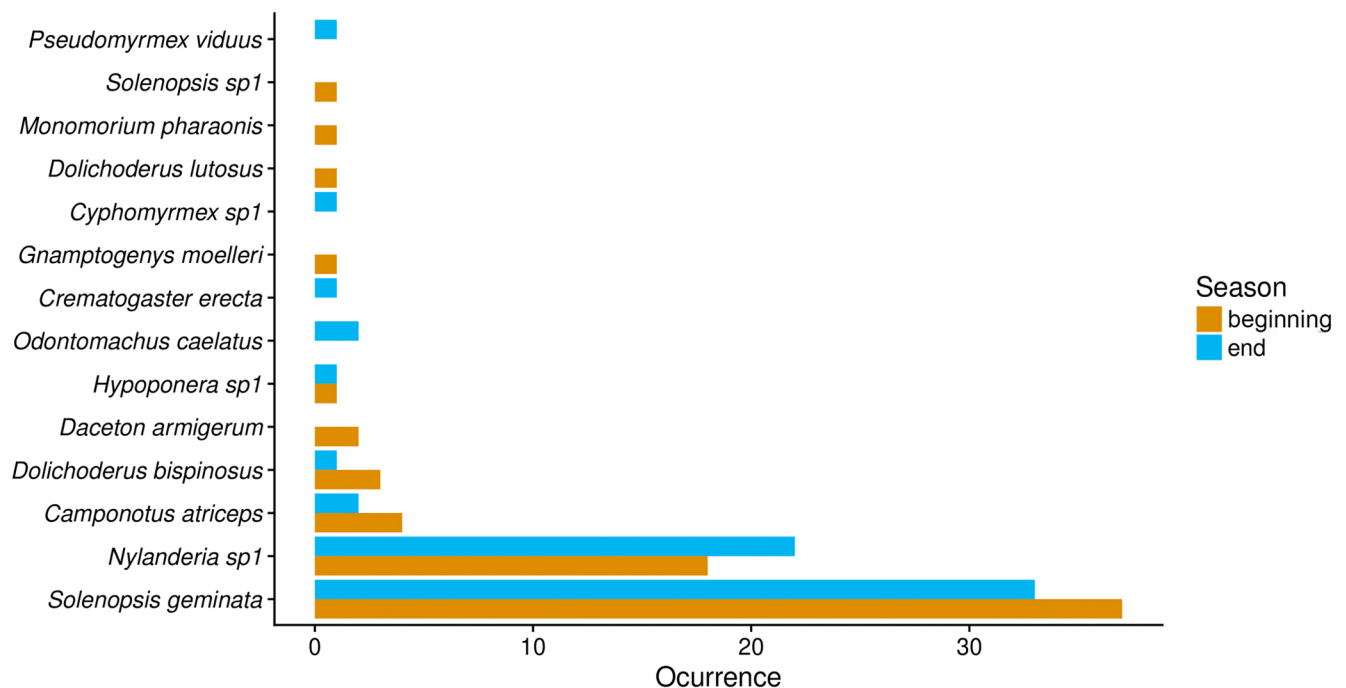

Figure 3. Occurrence (abundance scale) of ants in the nests of *Podocnemis unifilis* and in the area adjacent to the nest, between the beginning and end of the incubation period.
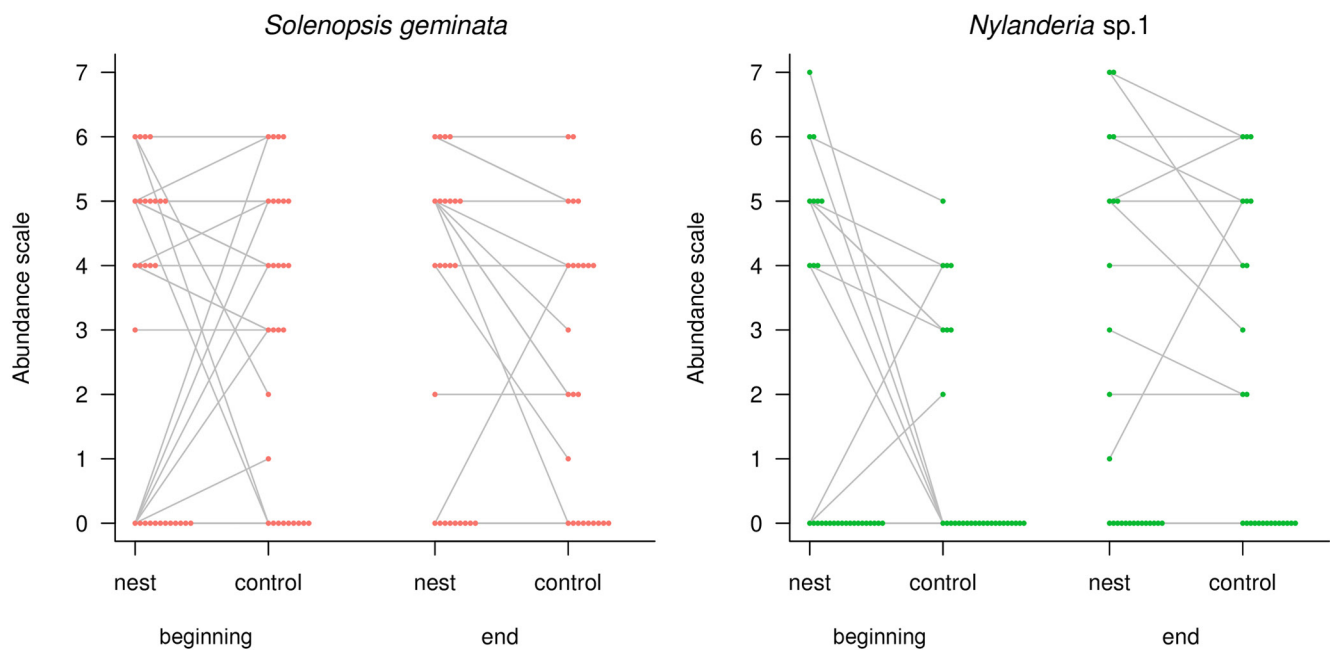
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Figure 4. Distribution of the ants *Solenopsis geminata* and *Nylanderia* sp.1 between the beginning and end of *Podocnemis unifilis* incubation period. **(A)** The ant *S. geminata* is more frequent at the end of the incubation period. **(B)** The beginning of the incubation period is characterized by the highest abundance of *Nylanderia* sp.1 in the nests of *P. unifilis.*
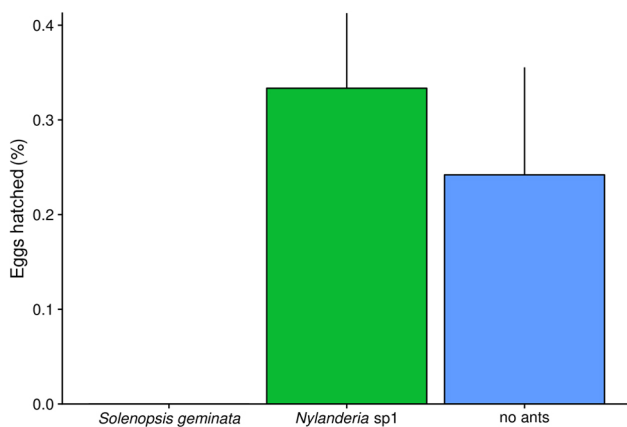

Figure 5. Proportion of *Podocnemis unifilis* eggs that hatched in the presence of *Solenopsis geminata* and *Nylanderia* sp.1 and in the absence of the two species of ants.

Solenopsis geminata was more abundant in *Podocnemis unifilis* nests during the final third of development (Fig. 4A). At the beginning of the incubation period, abundance of *S. geminata* in *P. unifilis* nests was similar to control plots ($t = -0.379$, $P = 0.646$). However, at the end of the incubation period the abundance of *S. geminata* around the nest was twice as much as that of control plots ($t = 1.754$, $P = 0.046$). The abundance of *Nylanderia* sp.1 in *P. unifilis* nests was significantly greater at the start of the incubation period than in control plots ($t = 1.918$, $P = 0.032$; Fig. 4B).

The observed C-score was higher than the randomized C-score for each year of monitoring, suggesting that the occurrence of ants in the nests of *Podocnemis unifilis* could be structured by competition. However, observed C-score is similar to randomized when *Solenopsis geminata* or *Nylanderia* sp.1 were removed (Table 1). For *P. unifilis* hatching success, we found that survival of hatchlings was similar for nests with and without *Nylanderia* sp.1 (Fig. 1B, Fig. 5), which presented similar abundance between nest and control plots at the end of the hatching incubation period ($t = 0.514$, $P = 0.305$). However, in nests containing *S. geminata,* all hatchlings died (ANOVA: $F = 9.953$, $P < 0.001$; Fig. 1C–D, Fig. 5).

DISCUSSION

Our data suggest that *Solenopsis geminata* and *Nylanderia* sp.1 compete for the colonization of *Podocnemis unifilis* nests. *Nylanderia* sp.1 appears to find and colonize nests faster, being more abundant at the beginning of the breeding season, soon after eggs are laid by females. In most cases, ants remain in the nests throughout the incubation period until emergence. In contrast, *S. geminata* was more common in nests during the final third of the incubation period that had not been colonized by *Nylanderia* sp.1. Hatching rate of nests colonized by *Nyl-*

Table 1. Observed and randomized C-scores for each year of monitoring, suggesting patterns of ant species co-occurrence in the yellow-spotted Amazon River turtle (*Podocnemis unifilis*) nests. Statistically significant P values for observed C-scores greater than expected are indicated by an asterisk (*).

Years	All species		*Solenopsis geminata* excluded		*Nylanderia* sp.1 excluded	
	C-score observed	C-score expected	C-score observed	C-score expected	C-score observed	C-score expected
2013	234*	219.27	114	116.79	105	103.32
2014	323*	291.84	67	67.386	95	97.809

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anderia sp.1 was similar to that of nests without the presence of ants, and the hatching rate in nests colonized by *S. geminata* was zero. Consequently, our results indicate that, once established in a nest, *Nylanderia* sp.1 can act as a facilitator for hatchlings of *P. unifilis,* buffering them against predation by *S. geminata.*

Facilitating interactions can have a relevant role in species sorting in local assemblages. Typically, if a species suffers high predation at the early life cycle stages it generally has two options: either produce many poorly protected offspring that pass rapidly through such vulnerable stages (Abrams and Rowe, 1996), or reduce exposure by prolonging early stages, but with some form of individual protection (Abrams, 2000). After hatching, juveniles show incomplete closure of the central plastron openings and spend an additional 10–15 d in the nest (Erickson et al., 2020b). During this time, they subsist on the remaining yolk of the eggs, which has yet to be fully absorbed. Once this occurs, the animals ascend, emerge from the nest, and head toward aquatic environments. This behavior allows time for additional *ex-ovum* growth, and it may therefore reduce the chances of predation by other aquatic organisms that use olfactory and visual mechanisms, especially crabs (Santos et al., 2016), fishes (Britson and Gutzke, 1993), giant water bugs (Ohba, 2011), and waterfowl (Tomillo et al., 2010). The additional period inside the nest also promotes mass emergence, which reduces the risks of predation as animals move to the water, by control of synchronization. Studies investigating mass emergence of other *Podocnemis* species (e.g., *P. expansa* [Schweigger, 1812]) have shown potential for fine tune control of mass-emergence. This occurs by the use of acoustic signals between adult females and hatchlings still inside the nests (Ferrara et al., 2012, 2014).

In contrast, staying in the nest too long may prove disadvantageous because hatchlings can become easy prey for other predators (Erickson et al., 2020b), such as aggressive *Solenopsis* species (Pignati et al., 2013; Erickson and Baccaro, 2016). In general, when prey cannot hide or escape, they can develop a defensive strategy (Townsend et al., 2006). For the most part, such defenses rarely involve physical fighting, since few prey species can effectively confront their predators (Townsend et al., 2006; Alcock, 2011). Additionally, many seemingly defenseless organisms produce strong or painful chemical secretions to deter predators (Townsend et al., 2006; Alcock, 2011). None of these alternatives are available to hatchling turtles since they are unable to defend themselves against a voracious colony of *S. geminata* when inside the egg or newly hatched. The permanence of the hatchlings in the nest could be linked to predation risk reduction; however, staying too long may instead increase the risk of predation (Allen et al., 2004; Erickson and Baccaro, 2016; Erickson et al., 2020b), depending on the type of predator involved in the interaction. Such explanations are not mutually exclusive and probably operate simultaneously.

While it is important to know that *Solenopsis geminata* is potentially the main predator of *Podocnemis unifilis* in areas with dense vegetation cover and clay-rich soil (Erickson and Baccaro, 2016; Erickson et al., 2020b), it is also important to consider other interspecific relationships. Our data suggest that interactions such as indirect facilitation between species might have a relevant role in species sorting in local assemblages. Neighboring species with similar requirements could have negative impacts on each other (Bruno et al., 2003), with each species competing for space and available resources. This competition can be relaxed in predator-prey systems because most predators feed on several species of prey, and most prey are consumed by several predators (Escalona and Fa, 1998; Blamires et al., 2003; Longo et al., 2009; Ferreira and Castro, 2010; Erickson and Baccaro, 2016; Silva et al., 2016). Our data suggest that competitive interactions between these two ants species might be mediated by resource competition and that *Nylanderia* sp.1 might prevent the colonization of *P. unifilis* nests by *S. geminata.*

The combined results of our research indicate that the pattern of infestation exhibited by both ant species is indicative of niche shrinkage. The niche concept implicitly assumes that neighboring species could have negative impacts on each other (Bruno et al., 2003), with each species competing for space and available resources. Under such circumstances, indirect facilitation can support the coexistence of species, reducing the potential for species exclusion (Laird and Schamp, 2006). Our study corroborates this hypothesis. When colonizing a nest, *Nylanderia* sp.1 seems to facilitate the hatching and emergence of *Podocnemis unifilis* hatchlings by simply keeping colonies of *Solenopsis geminata* away. The two species of ants seem to compete for the same resource (*P. unifilis* nests) but are probably attracted to them by different means. *Nylanderia* sp.1 seems to be attracted to the mucous deposited by the female turtles (Erickson and Baccaro, 2016) or is more efficient at locating newly laid nests, which explains why they have a higher colonization rate at the first third of the nesting process, whereas nest occupation by *S. geminata* is more random, resulting in a cumulative probability distribution throughout the nesting season (more *P. unifilis* nests are colonized at the end of the breeding season). Resource competition, particularly consumer-resource (ants/eggs and hatchlings) relations, is therefore an important factor in the local organization of the species assemblages in our study.

Much of the diversity of behavioral strategies to obtain food and avoid being eaten results from natural selection acting on organisms seeking resources and escaping predation (Abrams, 2000; Allen et al., 2016). In the case of turtle hatchlings, they are unable to put such strategies directly into practice, and little is known about possible interspecific relationships with other species. It is important to note that the most easily detected processes are not always those with the greatest impacts (Brooker et al., 2008), and the vulnerability of turtle nesting to predation is a commonly cited, but little studied process (Erickson and Baccaro, 2016). Little is known about possible interspecific relationships of turtles with other species, and despite the inherent difficulties of studying such interactions in turtles, a focus on nesting ecology will bring a new

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perspective to already known ecological interactions. For decades, efforts have been made to conserve and protect turtle nesting areas, yet the vast majority of these studies focused on areas characterized by sandy soils (Erickson et al., 2020a, b). This bias may mask a few important, but hitherto unknown processes such as colonization and resource competition by some ant species that may have profound consequences on turtle hatchlings' survival. We suggest that facilitation may support the coexistence between turtle clutches and some ant species during incubation, which is the most defenseless stage in the life history of turtles. Relevant for wildlife conservation, we provide in our study new insights that challenge current views about interspecific interactions that facilitate the coexistence between preys and predators.

ACKNOWLEDGMENTS

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