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Presence of Red Fire Ants (*Solenopsis invicta* Buren) in Broad-Snouted Caiman (*Caiman latirostris*) Nests

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ABSTRACT.—**The presence of *Solenopsis invicta* in *Caiman latirostris* nests is suspected to be a possible cause of death in caiman hatchlings, but this has not been documented within the native distribution of this ant. In crocodilian ranching programs, wild eggs are collected from the field, and delays between collection and transportation to incubators are usually minimized in the hope of maximizing embryo survival. We analyzed nests harvested during five consecutive nesting seasons of *C. latirostris* to determine the phenology of *S. invicta* colonization of caiman nests. The percentages of colonized caiman nests for each season were calculated. Densities of *S. invicta* mounds built on bare ground were assessed to determine potential relationships between density and the proportion of caiman nests colonized by the end of nesting season. We also evaluated whether *S. invicta* preferred certain habitats to establish their mounds. We found no relationship between *S. invicta* mound densities and the percentage of *C. latirostris* nests with Red Fire Ants. The presence of *S. invicta* mounds among years was similar between different habitats at the beginning of each season. We found that *S. invicta* can colonize *C. latirostris* nests during the breeding period and that colonization of nests is higher than 50% in seasons where rainfall was 200 mm at the beginning of the season (December and January). In contrast, during years in which rainfall was below 200 mm, caiman nest colonization was reduced.**

Ants (Formicidae) are an important component of practically all terrestrial ecosystems (Wilson, 1990). They frequently represent a large fraction of the animal biomass in ecological systems, especially in deserts, savannas, and tropical forests, and may be functionally irreplaceable (Petal, 1978; Farji-Brener and Illes, 2000). Recent measurements suggest that ants and termites, make up about one-third of the animal biomass of the Amazonian rain forest, and a hectare of soil may contain in excess of eight million ants and one million termites. These two insects, along with bees and wasps, make up more than 75% of the total insect biomass of the world (Hölldobler and Wilson, 1990). Ants often interact strongly with other species (Lomascolo and Farji-Brener, 2001), and there are a broad array of strongly co-evolved mutualisms between plants and ants (Zettler et al., 2001). Globally, Formicidae comprise a relatively large portion of introduced or invasive species (>150 species; McGlynn, 1999). The Red Fire Ant, *Solenopsis invicta*, is considered the most destructive invasive nonnative ant species in the southeastern United States, negatively impacting invertebrates and vertebrates (Porter and Savignano, 1990; Allen et al., 1994; Wojcik, 1994). These ants have a high ability to colonize and adapt to new environments and are competitively superior to native species because they are capable of monopolizing all resources and locations (Moloney and Vanderwoude, 2002). This ant has been studied in different countries, and it has been cited recently in reports related to the breeding ecology of crocodiles (Allen et al., 1997; Reagan et al., 2000). However, there is little information concerning the impact of *S. invicta* on caiman species in Argentina or any other South American country where both Red Fire Ants and caimans are native (but see Cintra, 1985).

The reproductive cycle of the Red Fire Ant is longer than many other ant species (Tschinkel, 1993). Colonies have extremely high fecundity, fast growth, and early maturation. Queens can reproduce for five to seven years and can lay up to 5,000 eggs/day (Tschinkel, 1987, 1993). One of the characteristics that identify colonies of *S. invicta* is the mound, which is constructed with soil. This structure is a cone-shaped dome, which has a hard outer layer, resistant to rain (Tschinkel, 1988). There are usually no external openings on the mound, but there are underground tunnels, approximately 25–50 mm below the surface, that radiate from the mound (Tschinkel, 2006). Even if the mounds are important for colony health, they are not absolutely essential for the survival of the colony. *Solenopsis invicta* makes mounds in a wide variety of microhabitats (e.g., rotten logs, walls of buildings, on sidewalks and roads, in cars, dry cow manure; Lockley, 1995; Green et al., 1999). In North America, this ant also uses alligator nests to establish new colonies, and it has been reported that more than 20% of alligator nests have been colonized in Louisiana (Reagan et al., 2000).

Solenopsis invicta can affect crocodilian hatchling survival (McIlhenny, 1934; Joanen, 1969; Dietz and Hines, 1980; Taylor, 1984). These ants pose a particularly great threat to eggs and hatchlings of ground-nesting birds and reptiles (Wojcik et al., 2001). Cintra (1985) found that *S. invicta* commonly attack and kill Yacare Caiman (*Caiman yacare*) hatchlings and were observed in Broad-Snouted Caiman nests (Parachú Marcó and Piña, 2008).

The native range of *C. latirostris* includes parts of Argentina, Bolivia, Brazil, Paraguay, and Uruguay, and this species has a broad latitudinal distribution in South America, from 5°S to 32°S (Verdade et al., 2010), coinciding with the *S. invicta* distribution (Folgarait et al., 2006). The Broad-Snouted Caiman prefers shallow, heavily vegetated aquatic environments that are often difficult for most predators to access (Larriera and Imhof, 2006).

Flora and fauna sustainable use, based on economic benefits as stimuli for in situ conservation, has become the most realistic action for natural ecosystem conservation (Piña, 2001). The ”Yacare Project” has operated in Santa Fe, Argentina, since 1990 and became commercial in 1999. The project harvests *C. latirostris* eggs from natural populations to produce animals to be grown in captivity (Larriera et al., 2004). This technique is referred to as ranching and is an example of the sustainable use

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FIG. 1. Location of *Solenopsis invicta* mounds (full squares) and the egg harvest sites (empty circles) of *"Proyecto Yacare"* in the Santa Fe Province (30°37′S; 60°47′W), Argentina. (1) Los Saladillos; (2) Cacique Araicaiquin; (3) El Estero Ranch; (4) Cañada Ombú; (5) Intiyaco; (6) Fortín Olmos; (7) El Lucero; (8) El Fisco Natural Reserve.

of wildlife (Ross, 1999). Crocodile ranching programs offset the expected high loss during embryonic development and the early perinatal period of wild crocodilians by incubating and hatching eggs in captivity.

Relative humidity, air temperature, and mound temperatures are abiotic parameters that influence populations of Red Fire Ants (Pranschke and Hooper-Bui, 2003). However, ants generally are subject to stress from desiccation in all habitats (Xu et al., 2009). Even in tropical forests, ants are likely to be displaced from part of their mound sites during the dry season (Hölldobler and Wilson, 1990). Some reptile eggs are able to condense water inside nests, especially in high moisture environments. Upon exposure of eggshells to high relative humidities of 90–100%, wetting of the calcareous surface was observed and small water droplets formed (Huang, 2008). Thus, we hypothesized that Broad-Snouted Caiman nests represent an optimal site for development and growth of *S. invicta* colonies in drought years.

There is a lack of data on the impacts of *S. invicta* on its native habitat. However, the potential of this ant to affect reproduction in *C. latirostris* in Argentina, and its impact as an invasive species in other countries, make information about this ant essential for designing conservation efforts both in its native and invasive range. Understanding the role of *S. invicta* in its native range may also increase the use, management, and preservation of this native species of crocodile.

In this study, we evaluated the percentage of harvested *C. latirostris* nests colonized by *S. invicta* in wild populations in the province of Santa Fe. We also estimated ant colony establishment to determine whether *S. invicta* had preferences among habitats or seasons. In addition, we have attempted to determine whether rainfall amounts (an abiotic variable) influenced *S. invicta* colonization on caiman nests.

MATERIALS AND METHODS

Our study site included the areas of harvest for *Proyecto Yacaré* (Laboratorio de Zoología Aplicada: Anexo Vertebrados, FHUC–UNL/MASPyMA) throughout the northeastern portion of the Santa Fe Province (30°37′S, 60°47′W), Argentina (Fig. 1).

We considered all *C. latirostris* nests harvested during five nesting seasons (2004–09). We examined 757 caiman nests (45 nests in 2004/05 season; 289 nests in 2005/06; 158 nests in 2006/07; 192 nests in 2007/08; and 73 nests in 2008/09) between December and March. Caiman use three nesting habitats in this region: floating vegetation, savanna, and forest (Montini et al., 2006). Floating vegetation is characterized by heavily vegetated bodies of water, and in this habitat, caiman nests are mostly built with grass, which typically float on the surface as the water level varies. Savanna consists of area with low slopes that flood in periods of heavy rain. Caiman nests are built with grass, which are frequently found on levees near the water bodies. In forests, which are located on higher plateaus, nests are generally built with mud, small stumps, and some grass and are found up to 2,000 m from water. The habitat (floating vegetation, savanna, or forest) and the presence of Red Fire Ants were recorded for each nest.

Data were analyzed by linear regression to determine whether *S. invicta* colonization occurred at a particular time during caiman reproductive season. Thus, we considered the percentage of nests colonized on each trip during the sampling period to determine whether there was an increase of colonization by ants over the season. Egg-laying in Santa Fe occurs from late December to mid-January (Larriera et al., 2004). We considered a nesting period of 100 days in each season, taking 1 December as "day 0" because no caiman nest before that date. Data were analyzed using a Chi-square test to compare the final proportion of colonization between reproductive seasons, considering all *C. latirostris* nests harvested after day 60 from the start of the nesting period. The final proportion of colonization (caiman nests colonized by ants / all nest found) was calculated after 60 days of start of breeding season.

We estimated the number of *S. invicta* mounds per 400 m^2 built on bare ground to determine whether the density of mounds varied among seasons. We also evaluated location of the nests that might indicate habitat preferences of the ants. Study sites were selected based on the known presence of nesting sites (Fig. 1): Los Saladillos (30°43′S, 60°17′W) and Cacique Araicaiquín (El Cacique Ranch; 30°38′S, 60°17′W) during the 2005/06 season. In the following seasons (2006/07, 2007/08, and 2008/09), we added the third study site: El Estero Ranch (30°03′S, 59°57′W). To estimate the number of *S. invicta* mounds at each habitat, we used three quadrats of 400 m^2 each (20 × 20 m), located randomly in the three habitats. Each quadrat was divided into 16 sections of 25 m^2 (5 × 5 m). We selected four quadrats, and we searched for the presence of *S. invicta* mounds. We performed a Kruskal-Wallis test to determine whether there were differences in density of *S. invicta* mounds built on bare ground among seasons and among habitats. In the 2005/06 nesting season, we sampled only at the beginning of the caiman reproductive period (15–24 December). During the following seasons (2006/07 to 2008/09), we surveyed *S. invicta* mounds in each habitat and study site at two different time periods (one at the beginning of the caiman nesting season [15–24 December] and the other at the end [15–22 March]) because ants have a summer breeding period (Allen et al., 1994). In this way, we aimed to assess whether the density of *S. invicta* mounds increased during summer. Then, we used regression analysis to determine whether densities of *S. invicta*

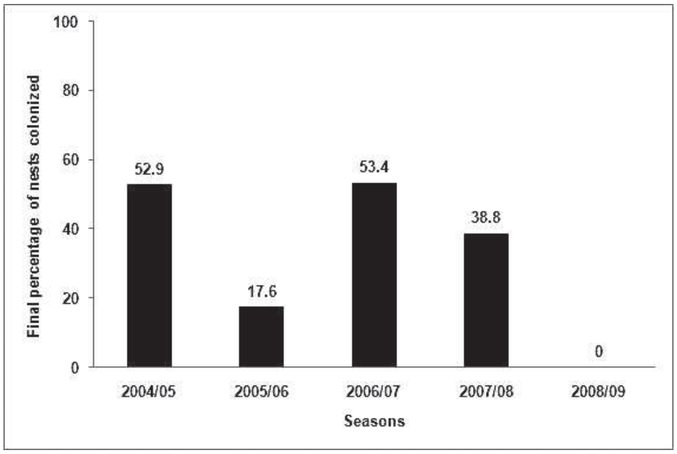

FIG. 2. Final percentage of *Caiman latirostris* nests colonized by Red Fire Ants in each season.

mounds built on bare ground influenced the proportion of caiman nests colonized at the end of each season.

We also assessed whether rainfall was related to colonization by ants of caiman nests by using regression analysis to examine the proportion of colonized nests in each season compared with the amount of rainfall registered at the beginning of the reproductive period (December and January). We also performed a regression test to evaluate whether rainfall amounts at the start of the caiman reproductive period (December) could affect the density of *S. invicta* mounds built on bare ground among seasons.

RESULTS

Nest colonization by ants was found to occur at any time during the caiman reproductive season. Colonization increased throughout the entire reproductive period in three nesting seasons studied (2004/05: $R^2 = 0.72$, $P = 0.016$; 2006/07: $R^2 = 0.61$, $P = 0.001$; 2007/08: $R^2 = 0.29$, $P = 0.017$). We found no significant change in ant colonization over the entire nesting season during 2005/06 ($P = 0.556$) or 2008/09 ($P = 0.163$). However, for those nesting seasons, we found an increase in colonization until day 45 (2005/06: $R^2 = 0.72$, $P = 0.002$; 2008/09: $R^2 = 0.55$, $P = 0.036$).

The final proportion of caiman nests colonized differed between seasons ($\chi^2 = 11.66$, df = 4, $P = 0.020$). We found a high rate of ant colonization in three seasons, and in 2008/09, infestation of nests by the end of the incubation period was reduced to zero. The mean colonization for all seasons was 32.5 ± 23.3% (range 0–53.4%; Fig. 2). The proportion of caiman nests colonized by ants did not differ between habitats in most of seasons ($P > 0.061$; Table 1), however during the 2007/08 season, the colonization was higher in the forest habitat ($\chi^2 = 8.47$, df = 2, $P = 0.014$).

TABLE 1. Percentage of *Caiman latirostris* nests colonized (after 60 days of the start of harvest) by habitat type.[1]

Season/habitat	Floating vegetation	Savanna	Forest
2004/05	25 (1/3)	77.78 (7/2)	25 (1/3)
2005/06	20 (4/16)	18 (2/9)	0 (0/3)
2006/07	65.5 (19/10)	22.2 (2/7)	40 (2/3)
2007/08	38.4 (10/16)	23.8 (5/16)	85.71 (6/1)
2008/09	0 (0/3)	0 (0/4)	–

[1] Parentheses show the number of *Caiman latirostris* nests with and without ants.

TABLE 2. Density of *Solenopsis invicta* mounds/400m^2 by season and percentage of *Caiman latirostris* nests colonized by red fire ants.

Season	*Solenopsis invicta* Mounds/400 m^2 ± SD[1]	Percentage of *Caiman latirostris* nests colonized by red fire ants
2005/06	0.67 ± 0.76	17.6
2006/07	0.87 ± 0.98	53.4
2007/08	0.37 ± 0.67	38.8
2008/09	0.46 ± 0.63	38.3

[1] Standard deviation.

The density of ant mounds differed between seasons (H = 7.17, $P = 0.026$). The 2007/08 season had fewer, and the 2006/07 season exhibited the highest total density of Red Fire Ants (mounds/400 m^2, including all habitats and places; Table 2). The density of ant mounds during 15–24 December was similar between habitats and study sites in all seasons (2005/06: H = 0.95, $P = 0.9511$, 2006/07: H = 6.68, $P = 0.490$, 2007/08: H = 3.26, $P = 0.718$, 2008/09: H = 4.30, $P = 0.308$). At the end of the nesting seasons, ant mound densities in Cacique Araicaiquín habitats were lower than on Los Saladillos's forest (H = 13.38, $P = 0.038$) for 2008/09 season.

Seasonal densities of *S. invicta* mounds and percentage of *C. latirostris* nests colonized were not related ($P = 0.720$). However, the amount of rainfall at the start of the breeding period (December and January) was related to the percentage of colonization by Red Fire Ants. Ant colonization ($R^2 = 0.980$) increased with higher rainfall and stabilized after rainfall reached approximately 200 mm (Fig. 3). Nevertheless, mound densities built on bare ground were not affected by December rainfall ($P > 0.380$).

DISCUSSION

The increase of caiman nests colonized by ants during three nesting seasons suggests that the risk of ant colonization does not occur during a particular time during caiman reproductive season. However, during the other two reproductive seasons, we observed that colonization increased until only halfway through the nesting season and decreased toward the end. One possible explanation for these results may be rainfall at the beginning of the reproductive period (December and January).

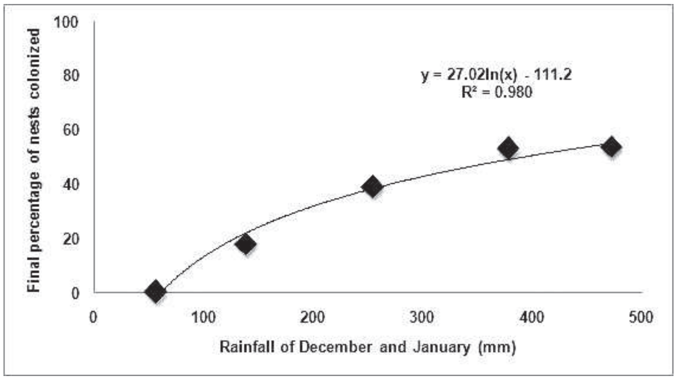

FIG. 3. Logarithmic regression between the percentage of Red Fire Ant colonization in caiman nests (measured at the end of the harvest period) and the amount of rainfall (mm) of December and January in each season.

The two nesting seasons that had the lowest amounts of rainfall at the beginning of the season possibly influenced the colonization of caiman nests by ants (Fig. 3). On the other hand, the highest colonization observed (53.4%) occurred during the wettest months of December and January (472.9 mm). Microhabitats that have requirements (humidity and temperature) for the establishment and development of ant colonies, such as caiman nests, are apparently used more extensively by *S. invicta* during wettest seasons, similar to what was reported in nests of *A. mississippiensis* (Reagan et al., 2000; Allen et al., 2001). As a consequence, fire ants inside nests could reduce caiman hatchling success. Previous observations found that Red Fire Ants readily penetrate other reptile eggs (Diffie et al., 2010) but did not enter *C. latirostris* eggs (Parachú Marcó et al., 2005). However, during the incubation period, the outer shell of most alligator eggs begins to crack because of swelling, and degradation begins as early as two weeks before hatching (Joanen, 1969), allowing Red Fire Ants prolonged access to egg contents. Cracked eggs are protected only by the inner egg membrane, a soft covering that is readily breached by *S. invicta*. Embryos and albumin of alligator eggs are an attractive food source for *S. invicta*, as demonstrated by Allen et al. (1997) in experiments with nonviable eggs. Furthermore, fire ants attack anything that creates a disturbance inside nests. For example, when female caiman try to maintain the nest, or if the clutch is in the final period of incubation and hatching occurs, ants can attack the hatchlings causing death (Parachú Marcó et al., 2005; Platt et al., 2008).

In southwestern coastal Louisiana (North America), we know that up to 20% of alligator nests can contain *S. invicta* colonies (Reagan et al., 2000). In northern Argentina, we found that Red Fire Ants can colonize over 50% (average among season 32.5 ± 23.3%) of nests by the end of incubation. As has been reported for alligators (Allen et al., 1997), we speculate that a large percentage of the population of caiman in the wild may suffer the effects of ant stings, consequently affecting their survival. Therefore, knowing the incidence of Red Fire Ants in *C. latirostris* nests is important when estimating recruitment rates for this reptile. The wetter months of December and January showed a higher colonization rate and, consequently, should have a greater loss of hatchlings. Therefore, egg harvest should take place at least two weeks prior to caiman hatching to preclude ants from penetrating the inner egg membrane after the outer eggshells begin to crack. Our results suggest that harvesting on the last part of the incubation period could increase hatchling mortality caused directly by ants or indirectly because the female may reduce nest attendance. Other studies have mentioned that early harvest should be considered to prevent hatchling losses from increased exposure to predation, flooding, and low temperatures (Hutton and Webb, 1992; Larriera, 1995).

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