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Abstract.—Flooding and predation are the two major causes for the decline in hatching rate and hatchling survival in crocodilian species. Recently, *Solenopsis invicta* (Red Fire Ant) has been recognized as a formidable invasive species, causing changes in wild populations of reptiles. Because of the elevated densities of Red Fire Ants present in *Caiman latirostris* (Broad-Snouted Caiman) nests during the breeding season, experiments in captivity and in the wild were performed to verify if the presence of *S. invicta* affects nest success or care of eggs and the hatching-assistance behavior of *C. latirostris* females. Hatchling survival from eggs incubated in a lab setting in the presence of Red Fire Ants decreased by approximately 10% compared to nests without ants. In a second experiment performed in the wild, the presence of Red Fire Ant resulted in a 43% reduction in nest success including direct (14.5%) and indirect (28.5%) effects. Our study confirmed that Red Fire Ants negatively affect *C. latirostris* nest success, directly because Red Fire Ants attack and cause the hatchling's death after pipping and indirectly by preventing females from caring for eggs, providing hatching assistance, and maintaining nests.

Resumen.—Las inundaciones y la depredación son las dos principales causas de la disminución en la tasa de eclosión y supervivencia de las crías en especies de cocodrilos. Recientemente, *Solenopsis invicta* (Hormiga Colorada) ha sido reconocida como una formidable especie invasora, provocando cambios en las poblaciones silvestres de reptiles. Debido a las altas densidades de Hormigas Coloradas presentes en los nidos de *Caiman latirostris* (yacaré overo) durante la época reproductiva, se realizaron experimentos en cautiverio y en la naturaleza para comprobar si la presencia de *S. invicta* afecta el éxito de eclosión, el cuidado de los huevos y el comportamiento de asistencia durante la eclosión por parte de las hembras de *C. latirostris*. La supervivencia de neonatos de los huevos incubados en condiciones de laboratorio en presencia de Hormigas Coloradas disminuyó aproximadamente un 10% comparado con los nidos sin presencia de hormigas. En un segundo experimento realizado en la naturaleza la presencia de Hormigas Coloradas produjo una reducción del 43% en el éxito de eclosión, incluyendo los efectos directos (28,5%) e indirectos (14,5%). Nuestro estudio confirmó que las Hormigas Coloradas afectan negativamente la tasa de eclosión de *C. latirostris*, directamente cuando las Hormigas Coloradas atacan causando la muerte de las crías producto de sus picaduras, e indirectamente mediante el impedimento del cuidado de los huevos, la asistencia durante la eclosión, y el mantenimiento de los nidos por parte de las hembras.

Several studies have investigated the causes of hatching success reduction in different species of crocodilians (Joanen and McNease, 1980; Larriera, 1994; Tschinkel, 2006; Platt et al., 2008). Predation (Larriera and Piña, 2000), floods, or droughts are important factors that can reduce hatching success (Larriera, 1994). Rains during the nesting season can cause water-level changes and lead to a complete loss of the eggs of the Broad-Snouted Caiman (*Caiman latirostris*; Larriera, 1994). In Brazil, Crawshaw and Shaller (1980) found that 77% of *Caiman yacare* (Yacare Caiman) nests are destroyed by predation and flooding. Nest flooding and egg predation may cause 13% mortality of eggs in some populations of *Crocodylus acutus* (American Crocodile; Mazzotti et al., 1988). Hunt and Ogden (1991) suggest that females might be less able to defend alligator (*Alligator mississippiensis* [American Alligator]) nests during dry years. Several authors mention the "Coatí" (*Nasua nasua*), the fox (*Cerdocyon thous* [Crab-eating Fox]), and the big cats (*Puma concolor* [Puma], *Leopardus pardalis* [Ocelot], and *Panthera onca* [Jaguar]) as possible predators of crocodilian eggs (Crawshaw and Schaller, 1980; Larriera and Piña, 2000; Da Silveira et al., 2010). Activity of maternal *C. acutus* near the nest can reduce predation and can be related to higher hatching success (Casas-

Andreu, 2003), but this activity does not guarantee the nest will not experience predation (Joanen, 1969; Lance, 1989; Simoncini, unpubl. data).

Studies in the United States have shown that the invasive Red Fire Ant (*Solenopsis invicta*) is an important predator to be considered when evaluating nesting success of several species of wildlife, especially those that are ground-nesters (Holway et al., 2002; Diffie et al., 2010). High densities of Red Fire Ants can reduce nesting sites of Wood Duck (*Aix sponsa*) in some areas (Ridlehuber, 1982) and alter the behavioral patterns of the lizard *Sceloporus undulatus* (Eastern Fence Lizard; Freidenfelds et al., 2011). It has also been demonstrated that Red Fire Ants attack turtle hatchlings (*Terrapene carolina triunguis* [Three-toed Box Turtle]), causing loss of body mass (Montgomery, 1996). When *S. invicta* establish colonies within an area, it has been reported that populations of native ant species (Gao et al. 2011), oviparous snakes (Tuberville et al., 2000), turtles (Buhlmann and Coffman, 2001), small mammals (Ferris et al., 1998), and birds (Kopachena et al., 2000) are reduced. In some cases, species have been completely eliminated by Red Fire Ants (Porter and Savignano, 1990; Smith et al., 2004). All these cases were reported in places where *S. invicta* has been introduced but not in the native range of the species.

Experimentally, *S. invicta* have affected *A. mississippiensis* hatching success by killing neonates inside the nest and indirectly affecting the well being of surviving hatchlings by reducing weight gain (Allen et al., 1997). In crocodiles, female protection or assistance involves protection of the nest from predators, maintenance of nest temperature and humidity,

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assistance at hatching time and, in some cases, reforming nests to maintain shape (Zug et al., 2001). However, it has been observed in *A. mississippiensis* nests colonized by Red Fire Ants that female attendance activities were reduced because ants responded to the female, disturbing the nest by attacking her (Reagan et al., 2000).

The interaction between ants and crocodilians begins when ants build their mounds on recently modified places (Tschinkel, 1988), such as caiman nests, which are ideal for establishing ant colonies (Parachú Marcó et al., 2012). The presence of *S. invicta* in *C. latirostris* nests has been reported in their native areas (Parachú Marcó and Piña, 2008). Colonization by ants could include more than 50% of *C. latirostris* nests (Parachú Marcó et al., 2012). While calcareous egg coverage of some reptiles, such as crocodilians, can protect embryos from Red Fire Ants (Diffie et al., 2010), ants will also attack hatchling crocodilians inside the nest after they pip (i.e., break through the eggshell), producing injuries that sometimes lead to death (Platt et al., 2008). Because of the elevated densities of Red Fire Ants present in *C. latirostris* nests during the breeding season (Parachú Marcó et al., 2012), we conducted experiments in captivity and in the wild to verify if the presence of *S. invicta* affects *C. latirostris* nest success. Nest success includes two different components: hatching rate, which refers to caimans that were able to complete embryonic development and emerge live from eggs, and hatchling survival, defined as the number of animals that emerged from the nest alive in relation to the number of eggs that hatched. Previous studies showed that *S. invicta* reduces nest attendance and hatchling care in *A. mississippiensis* females (Allen et al., 1997; Reagan et al., 2000). This has been hypothesized for *C. latirostris* (Parachú Marcó et al., 2012) but not tested. Therefore, we observed wild nests with the aim of assessing the behavior (care and assistance) of the *C. latirostris* female with the presence of Red Fire Ants.

Our objectives were to evaluate the effects of Red Fire Ants on *C. latirostris* hatchling survival using a designed field study and a lab setting experiment. An additional objective was to verify if the presence of *S. invicta* affects nest success or care of eggs and the hatching assistance behavior of *C. latirostris* females in the wild.

Materials and Methods

Experimental Phase in Captivity.—We constructed 26 artificial nests (8 during each of the 2004–05 and 2006–07 seasons and 10 during 2005–06) with natural nest material and grass, similar to those used by females in the wild, in the facilities of the Proyecto Yacare, Santa Fe, Argentina. Each artificial nest was located in a 2-m^2 enclosure to prevent hatchlings from escaping and/or mixing with nearby nests. The nesting area had a grass zone and a container with water. We established wild ant colonies in half of the artificial caiman nests 2–3 wk prior to the introduction of caiman eggs. Ant colonies were fed with sucrose during the first week to discourage dispersal.

We selected 13 wild clutches (four in 2004–05, five in 2005–06, and four in 2006–07), and the eggs of every clutch were divided equally into two groups that were placed into nests with and without ants. Every artificial nest received 15 to 19 eggs from a single clutch. Nests were monitored periodically until hatching. We recorded the number of caimans that hatched but died before leaving the nest because of ant attacks, and we used this number to calculate hatchling survival. A non-parametric analysis test (Kruskal-Wallis) was performed because of a lack

of homogeneity of variances and to evaluate the effect of the Red Fire Ant presence (as a grouping variable) on hatchling survival.

Wild Nests.—During the 2007–08 season, a study was carried out in the wild to see if the effects of Red Fire Ants on wild nests were consistent with effects on artificial nests. Initially, clutches from natural habitats were collected and transported to an incubator to allow embryos to develop under controlled conditions of humidity and temperature. This reduced the vulnerability of the eggs to environmental extremes and enabled us to perform a better evaluation of the effects of the Red Fire Ants on nest success. We selected 10 wild nests built by *C. latirostris* females within a floating vegetation habitat, five of which were colonized by Red Fire Ants and five that had no Red Fire Ants. We used nests on floating vegetation to reduce the chances of predation because predation has not been reported for that habitat in this species (Larriera and Piña, 2000). In the middle of the incubation period (early February), we selected five clutches from the incubator that were harvested in the same floating vegetation habitat. From each of the five clutches we selected 24 eggs (total: 120 eggs); each group of 24 eggs was split into two groups of 12 eggs to be placed in the wild caiman nests, one group in a nest colonized by *S. invicta* and the other in a nest without ants. Thus, we had clutches in nests with ($n = 5$) and without ($n = 5$) Red Fire Ants. Before adding the 12 eggs in these 10 natural nests, we removed the existing clutch of eggs. After introduction of the experimental eggs, nests were inspected after approximately 20 and 50 days.

To minimize traces that could attract predators or alter the natural incubation environment (Campos, 1993), we made only two visits. During these visits, we recorded Red Fire Ant presence, without nest opening, and observed female activity (care and assistance). To minimize interference with treatments, nests were not opened until hatching was observed or until we saw evidence of the female assisting in the hatching process.

On every visit nests were categorized as: hatched or unhatched (based on eggshells and/or membrane presence), with or without Red Fire Ants, and with or without female care or assistance. The hatching rate of a nest was determined by the presence of eggshells or hatchlings. If eggshells were not found but we observed signs of female assistance such as fresh tracks, feces on the nest or opening characteristics of the nest by the female (described in Larriera and Piña, 2000), we considered the nest successfully hatched. Female *C. latirostris* are thought to transport hatchlings to water, and they sometimes carry the eggshells with them, as seen in other species of crocodilians (Hunt and Watanabe, 1982; Platt et al., 2008). The hatching rate was calculated as the proportion of total eggshells (large pieces and membranes) found divided by the total eggs left in the nest. If a nest was opened by a caiman female, a 100% hatching rate was assigned to that nest, unless we were able to find unhatched eggs inside or around the nest. Hatchling survival was evaluated as described in the captivity experiment. We considered a nest to have female activity if we detected fresh tracks, no green vegetation around the nest, and the presence of caiman feces on the nest.

Results

Experiment in Captivity.—For all years combined, hatchling survival was approximately 10% less in the presence of Red Fire Ants (mean $= 0.88 \pm 0.20$ SD, $n = 13$ nests) compared to without ants (mean $= 1.00 \pm 0$ SD, $n = 13$ nests), ($H = 4$, $P = 0.0068$).

TABLE 1. Female care (Y = yes , N = no), nest success (%), and female assistance (Y,N) of wild *C. latirostris* nests in Argentina with (W/A) or without (N/A) *Solenopsis invicta* presence. 1° and 2° = hatching during first and second visit, respectively.

Nest by clutch	Treatments at the beginning	Visit after hatching	Female care	Nest success	Female assistance
(1) A	W/A	W/A	N	100 (1°)	N
(2) A	N/A	N/A	Y	100 (2°)	Y
(3) B	W/A	N/A	Y	—[a]	—
(4) B	N/A	W/A	N	100 (1°)	N
(5) C	W/A	W/A	N	0 (2°)	N
(6) C	N/A	W/A	Y	100 (2°)	Y
(7) D	W/A	W/A	N	0[b] (2°)	N
(8) D	N/A	W/A	N	0[c] (2°)	—
(9) E	W/A	N/A	Y	100 (2°)	Y
(10) E	N/A	W/A	N	100 (1°)	N

[a] Hatchlings with problems during development.
[b] Unhatched animals (9 dead inside of eggs, and 3 nonviable eggs).
[c] Nest depredated by a *Conepatus chinga*.

Experiment in the Wild: 2007–08 Breeding Season.—During the first visit we observed signs of hatching in three of the 10 nests colonized by *S. invicta* (Table 1). We observed small holes in the nests that were presumably made by hatchlings as they emerged, and empty eggshells in the nests, but no evidence of female assistance. At the second visit, made 30 days after the first, we found four of seven remaining nests colonized by *S. invicta*. Of the four colonized nests, one nest was assumed to have a 100% nest success; it showed signs of assistance by maternal caiman (fresh tracks, evidence of nest opening). A second clutch showed evidence of *S. invicta* attack; we observed broken caiman eggs with hatchlings inside and many *S. invicta* eating them. All hatchlings were found dead inside the second nest. The third nest was opened near the egg chamber and nest material was dispersed, suggesting predation by a Molina's Hog-nosed Skunk (*Conepatus chinga*). The remaining nest had no signs of hatch so we opened it, finding nine fully formed dead caimans inside the eggs, three unviable eggs, and an active Red Fire Ant colony.

Of the three nests without *S. invicta* we observed a 100% nest success of two nests (12 hatchlings each) with evidence of female assistance. The third nest showed evidence of female care but, when we opened the nest, all the hatchlings inside the eggs had abnormalities. We excluded this nest from the analysis of nest success and assistance.

Female care (as measured by nest maintenance such as vegetation removal, fresh tracks, and nest repair) was reduced by the presence of Red Fire Ants in caiman nests. All the nests without ants had evidence of frequent visitation by the female (3/3); however, only one of the seven nests (14%) colonized by ants showed evidence of female care. Nest opening by the female during hatching improved hatching success of eggs. Sixty percent of nests without female assistance (3/5) had hatchability compared to 100% (3/3) of nests that received female assistance during hatching.

We observed 57% nest success in nests colonized by ants, whereas nests without Red Fire Ants had a 100% nest success (Table 1). This suggests that in the wild *C. latirostris* nest success could be reduced by 43%, corresponding to a 28.5% hatching rate (indirect effect: ants preventing nest care and assistance by caiman female and consequent death of embryos), and 14.5% hatchling survival (direct effect: ants killing the hatchlings) in nests with *S. invicta*.

DISCUSSION

Results from artificial nests in captivity showed that if a clutch reaches the final period of development, and pipping occurs, fire ants can attack and kill the hatchlings, reducing *C. latirostris* hatchling survival by 10%. Conversely, nests colonized by ants in the wild showed a 43% decrease in nest success (considering 28.5% decrease in hatching rate and 14.5% decrease in hatchling survival). Nests without Red Fire Ants showed 100% hatchling survival in the captive experiment and a 100% hatching rate and 100% hatchling survival in wild nests. A reduced hatchling survival was also observed in *A. mississippiensis* nests infected with Red Fire Ants (Allen et al., 1997). Not all the nests, either in captivity or in the wild, were affected negatively by the presence of Red Fire Ants, perhaps because Red Fire Ant colonies can exhibit different levels of aggressiveness (Vander Meer and Alonso, 2002).

In our field study, 86% of *C. latirostris* nests colonized with *S. invicta* showed no signs of female activity at the nest. In contrast, all nests that were not colonized by ants showed care and maintenance by the female caiman. Based on this observation, we speculate that female activity of *C. latirostris* during the egg incubation period is affected by the presence of *S. invicta*. Reagan et al. (2000) reported a decline of 24% in attendance of nests by females because of the presence of *S. invicta* (from 85% with no ants to 61% in nests with Red Fire Ants), as these ants interfere with female alligators' ability or willingness to release hatchlings when the hatchlings vocalize. This result was contrary to our expectations because we hypothesized that female care by *C. latirostris* would be less affected by Red Fire Ants than would be care by alligators because the caimans have had a longer period to co-evolve with ants.

Other researchers suggest that a reduction in hatching rate is not directly related to the *S. invicta* presence during the pre-hatching time (Reagan et al., 2000) because ants only come in contact with hatchlings after they hatch. However, the presence of Red Fire Ants has also been associated with reduced parental care during the incubation period and even with preventing the assistance of female *Crocodylus moreletii* (Morelet's Crocodile) when hatchlings vocalize (Platt et al., 2008). We estimate an indirect effect of an approximately 28% decrease in hatching rate of *C. latirostris* eggs because of the presence of Red Fire Ants in wild nests. In one nest, we found nine hatchlings dead inside the eggs without any breaks on shells. Thus, we assume that the nest was unsuccessful because of the absence of female assistance during hatching time caused by the Red Fire Ant presence. This could be related to the process at the end of development, when reptile embryos extract calcium carbonate of the eggshell to form bone, the shell thickness decreases, and its flexibility increases (Claessen, 1979). This degradation causes weakening of the shell and facilitates hatchling exit (Ferguson, 1981). However, some eggs have a high amount of calcium, thus presenting a very hard shell that, without the assistance of the female, makes it difficult for hatchlings to emerge. Therefore, our work identifies an indirect effect on hatching rate associated with Red Fire Ant presence. We do not believe our presence at the nest has modified female behavior because disturbed nests are often repaired by females (between 54% to 90%; Hunt and Odgen, 1991, Larriera and Piña, 2000).

Reagan et al. (2000) reported that the absence of female assistance during hatching negatively affected nest success of *A. mississippiensis*, resulting in a 26% lower hatch rate in ant-colonized nests. Correspondingly, in this study we observed some evidence of an effect on nest success, specifically in

decreased female assistance, with only 50% of the nests without female assistance hatching. However, all clutches with female assistance hatched and hatchlings left their nests successfully. We observed some evidence that the presence of Red Fire Ants in caiman nests could reduce female assistance in hatching because only one nest out of seven was opened by the female as compared to both nests (2/2) without ants that were opened by the females. It is assumed that female assistance of colonized nests by Red Fire Ants could optimize nest success by opening the nest and transporting hatchlings to water; a behavior described in several species of crocodilians (Ferguson, 1985). Female assistance behavior would therefore reduce the contact time of the hatchlings with Red Fire Ants, thus potentially increasing the overall hatchability of a clutch (Parachú Marcó et al., 2013).

In summary, we suspect that Red Fire Ants colonize Broad-Snouted Caiman nests because they not only provide a suitable habitat of warm and humid conditions for the development of ant eggs and larvae, but nests may also provide food (Allen et al., 1997; Vinson et al., 1997). These small predators attack during hatching, killing hatchlings within the nest, and losses associated with Red Fire Ants could be up to 43% in the wild. Parachú Marcó et al. (2012) reported that Red Fire Ants can colonize over 50% of the nests by the end of the incubation season in the northern part of Argentina. Considering this, and the consequences of attacks in the nest, we estimate that the loss of *C. latirostris* hatchlings because of *S. invicta* could reach up to 21% (50% colonization rate × 43% nest success reduction) in a breeding season. We provide evidence that Red Fire Ants negatively affect nest success of *C. latirostris* nests, indirectly by preventing female care and maintenance of the nest, opening and assisting hatchlings during hatching, and by killing hatchlings directly when they hatch.

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