

Effects of Predatory Fish on Survival and Behavior of Larval Gopher Frogs (*Rana capito*) and Southern Leopard Frogs (*Rana sphenocephala*)

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ABSTRACT.—Southern Leopard Frogs, *Rana sphenocephala*, are habitat generalists occurring in virtually all freshwater habitats within their geographic range, whereas Gopher Frogs, *Rana capito*, typically breed in ponds that do not normally contain fish. To evaluate the potential for predation by fish to influence the distribution of these species, we conducted a randomized factorial experiment. We examined the survival rate and behavior of tadpoles when exposed to Warmouth Sunfish, *Lepomis gulosus*, Banded Sunfish, *Enneacanthus obesus*, and Eastern Mosquitofish, *Gambusia holbrooki*. We also conducted a choice experiment to examine the survival rate of the two species of tadpoles when a predator is given a choice of both species simultaneously. *Lepomis gulosus* consumed the most tadpoles and ate significantly more tadpoles of *R. capito* than *R. sphenocephala*. *Gambusia holbrooki* injured the most tadpoles, especially *R. capito*. *Enneacanthus obesus* did not have an effect on behavior or survival of either anuran species. Tadpoles of both anurans increased hiding when in the presence of *L. gulosus* and *G. holbrooki*, but a greater proportion of *R. capito* hid than did *R. sphenocephala*. Our results suggest that *R. capito* are more vulnerable to predation by fish than are *R. sphenocephala*. The introduction of fish may play a role in population declines of certain anurans breeding in normally fish-free wetlands, and even small fish, such as mosquitofish, may have significant negative effects on the tadpoles of *R. capito*.

Communities of larval amphibians are structured in large part by changes in predation pressure along a gradient from temporary to permanent freshwater wetlands. (Wellborn et al., 1996). Anuran tadpoles possess a number of antipredator mechanisms, including species-specific unpalatability (Voris and Bacon, 1966; Grubb, 1972; Formanowicz and Brodie, 1982; Blouin, 1990), chemically mediated predator avoidance (Kats et al., 1988; Lefcort, 1996), and reduced activity (Woodward, 1983; Skelly, 1994; Anholt et al., 2000). However, the degree to which a tadpole possesses any of these defenses is related to habitat-induced requirements as opposed to a specific predatory threat (Relyea, 2001). In general, tadpoles from temporary wetlands tend to be relatively active, forage constantly, grow rapidly, and reach metamorphosis before the water disappears (Woodward, 1983; Wellborn et al., 1996). In wetlands with long hydroperiods, anuran tadpoles have slower growth rates and tend to be less active than those in temporary wetlands, and some are highly unpalatable to sympatric fish predators (Gunzburger and Travis, 2005). Thus, traits that may be favorable in one community type may be unfavorable in another (Wellborn et al.,

1996). Prey that do not normally coexist with a predator often do not have effective antipredator responses to that predator (Relyea, 2001). Lack of defensive adaptations is an important reason why temporary pond amphibian species cannot coexist with predatory fish in permanent water habitats (Woodward, 1983; Kats et al., 1988).

Comparisons of closely related species pairs that segregate along this hydroperiod gradient demonstrate that there are multiple mechanisms by which prey species may partition habitat (Werner, 1991, 1994). One example of this was illustrated by Werner (1994) using American Bullfrogs, *Rana catesbeiana*, and Green Frogs, *Rana clamitans*. *Rana catesbeiana* are commonly found in permanent wetlands with fish, whereas *R. clamitans* can coexist with fish but are more abundant in fishless habitats. These species differ in their vulnerability to fish and invertebrate predators; tadpoles of *R. clamitans* are more palatable to fish than tadpoles of *R. catesbeiana*. Tadpoles of *R. catesbeiana* are more active than *R. clamitans* and, therefore, are more vulnerable to predation from top predators in fishless ponds (for example, dragonfly larvae and ambystomid salamanders). Fish are beneficial to *R. catesbeiana* because they selectively consume the more efficient predators of the tadpoles (Werner, 1994). Thus, the behavioral and palatability differences between *R. catesbeiana* and *R. clamitans* account for their differential success between the two wetland types.

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Southern Leopard Frogs *Rana sphenoccephala* and Gopher Frogs *Rana capito* often are sympatric in the southeastern United States and are so alike in size and appearance as tadpoles that it is often difficult to distinguish between the two (Conant and Collins, 1998; Altig et al., 1998). However, these species differ greatly in their life history requirements. *Rana sphenoccephala* are habitat generalists occurring in virtually all freshwater habitats within their geographic range where they spend a large portion of their lives in aquatic habitats (Butterfield et al., 2005). In contrast, *R. capito* are rare and require specific habitats for both the aquatic and terrestrial life stages. As adults, *R. capito* spend the vast majority of their life in terrestrial habitats and reside underground in the burrows of Gopher Tortoises *Gopherus polyphemus* and rodents, *Podomys floridanus* and *Peromyscus polionotus* (Gentry and Smith, 1968; Franz, 1984; Lips, 1991), in fire-maintained longleaf pine/turkey oak forests (Jensen and Richter, 2005). Within this environment, the availability of temporary isolated wetlands is essential for *R. capito*, which will breed only in semipermanent naturally fishless ponds (Moler and Franz, 1987; LaClaire and Franz, 1990; Eason and Fauth, 2001). The introduction of predatory fish into historically fishless breeding sites has been suggested as a cause of population declines in this species (Jensen, 1995).

The relative importance of fish predation to the distribution of these species has not been evaluated experimentally. If predation by fish during the larval stage contributes to habitat segregation in these species, then the tadpoles of *R. sphenoccephala* should have higher survival rates and more effective antipredator responses than tadpoles of *R. capito* when exposed to fish predators. We evaluated the effect of fish predation on the survival and behavior of tadpoles of *R. sphenoccephala* and *R. capito*. The three species of fish used in our experiments represent a range of predatory capabilities, including two species of centrarchids, the large-gaped Warmouth Sunfish, *Lepomis gulosus*, and relatively much smaller gaped Banded Sunfish, *Enneacanthus obesus*, and the Eastern Mosquitofish *Gambusia holbrooki*, a much smaller Poeciliid fish (Boschung and Mayden, 2004). These fish species are commonly found in sites where *R. sphenoccephala* breed.

MATERIALS AND METHODS

Tadpoles.—Tadpoles were raised from three *R. sphenoccephala* and two *R. capito* egg masses. Eggs were collected from 9–14 February 2006 from Blue Pond, a semipermanent fishless pond on the Ordway-Swisher Biological Station located

in western Putnam County, Florida. We placed each egg mass in a shallow plastic wading pool (1.10 m diameter \times 20 cm deep) outside at the USGS Florida Integrated Science Center in Gainesville, Florida. The pools were filled to 15 cm deep with well water and covered with a mesh screen to keep out predators. After the tadpoles hatched, they were fed daily a mixture of ground rabbit pellets and TetraMin[®] fish flakes. A subset of tadpoles from each egg clutch was raised through metamorphosis in large outdoor mesocosms (cattle tanks, 1.24 m diameter \times 0.69 m deep) to confirm species identification.

Predatory Fish.—We collected the fish using dipnets, aquatic funnel traps, and seining from Anderson Que Lake and Lake Suggs on the Ordway-Swisher Biological Station prior to the start of the experiments. The fish were separated by species and kept in holding tanks (30 cm diameter \times 76 cm deep) equipped with a flow-through well water system; they were fed frozen bloodworms daily. Approximately one hour before each trial, the fish were given enough food to reach satiation to ensure that all the predators started each experiment at the same hunger level. The total length of each fish was measured at the completion of each trial. Fish were not reused for any experiment.

Experiment 1: Comparison of Fish Predators.—The first experiment examined the survival and behavior of *R. capito* and *R. sphenoccephala* tadpoles in response to three species of fish predators. We conducted a randomized factorial experiment using all possible combinations of the two species of tadpoles (either *R. capito* or *R. sphenoccephala*) and four predator treatments (*L. gulosus*, *E. obesus*, *G. holbrooki*, and Control, no predator). This experiment was conducted from 27 February through 1 March 2006. Each treatment was blocked by clutch and each block was replicated twice. Forty 10-gallon aquaria (50 \times 25 \times 30 cm) were filled to 24 cm deep with well water and aerated with an air stone. Two refuges were added to each aquarium by constructing a 15 \times 45 cm strip of 1 \times 2 mm mesh screening tied in a knot to mimic aquatic vegetation. Water was not added or removed from the aquaria during the experiment, allowing any chemical cues emitted from the tadpole or fish that might influence behavior to remain in the water.

For each aquarium, we haphazardly selected 30 tadpoles of either *R. capito* or *R. sphenoccephala* (not a combination of the two species) from the wading pools and added them to the aquaria, according to the prescribed treatment. A random sample of five tadpoles from each clutch was photographed along with a ruler in a shallow container and the total length of each

was later measured using Image J image processing and analysis software (mean total length 13.92 ± 1.73 SD mm for *R. sphenoccephala* and 15.25 ± 1.98 SD mm for *R. capito*). Tadpoles were fed a pinch of food (3 : 1 mixture of ground rabbit pellets and TetraMin® fish flakes) and allowed to acclimate to their new environment for 48 h prior to the addition of fish. For each species of fish, individuals of similar size within each species were selected among those collected. The total length ($\bar{x} \pm$ SD) of the predators was 40.87 ± 3.5 mm for *L. gulosus*, 44.85 ± 6.4 mm for *E. obesus*, and 29.75 ± 2.0 mm for *G. holbrooki*. One predator was added to each aquarium, excluding controls.

The experiment was stopped after 46 h, before mortality in any treatment reached 100%. The number of tadpoles visible outside refuges was recorded; predators were removed from the tanks; and surviving tadpoles were removed, placed into shallow containers, counted, and examined for injuries, such as pieces of the tail missing. To confirm identification, all surviving tadpoles were transferred to cattle tanks and raised to metamorphosis.

The response variables analyzed were number of tadpoles surviving, proportion of tadpoles hiding, and number of tadpoles injured. The proportion of tadpoles hiding was calculated by subtracting the number of tadpoles visible outside of refuges from the total number of surviving tadpoles and dividing this value by the total number of surviving tadpoles. We evaluated survival, frequency of injury, and proportion hiding using two-way analysis of variance (ANOVA) with species of tadpole and predator treatment as factors. The data were transformed to better fit the assumptions of normality. Survival and injury data were subjected to the natural logarithm transformation, and proportion tadpole hiding data were subjected to the arcsine-square-root transformation. Bonferroni post hoc tests were conducted to evaluate differences between pair wise means for all significant effects in each ANOVA.

Experiment 2: Choice Experiment.—The second experiment examined survival of the two anuran species when a fish predator (*L. gulosus* and *G. holbrooki*) was given a choice of both simultaneously. *Enneacanthus obesus* did not consume or injure a significant number of tadpoles in Experiment 1; hence, they were not used in Experiment 2. This experiment was conducted in two intervals: from 8–10 March 2006 using *L. gulosus*; and from 5–7 April 2006 using *G. holbrooki*. The choice experiment consisted of two treatments (predator or control) blocked by egg clutch; each block was replicated twice. This experiment was performed after Experiment 1; thus, the tadpoles were larger

than in Experiment 1. There were insufficient numbers of tadpoles remaining in one of the three clutches of *R. sphenoccephala*; hence, tadpoles from two clutches each of *R. sphenoccephala* and *R. capito* were used. The tadpoles were different sizes in the two intervals; thus, the results from using these two predators were analyzed separately. Aquaria were arranged as in the first experiment, except we added two additional mesh refuges to each tank to provide more cover for tadpoles. We haphazardly selected 15 tadpoles of each species from the wading pools and added them to each aquarium. Tadpoles were allowed to acclimate for 24 h before the addition of predators. Mean total length ($\bar{x} \pm$ SD) of tadpoles in the *L. gulosus* trial was 22.24 ± 2.88 mm for *R. sphenoccephala* and 20.01 ± 2.59 mm for *R. capito*. In the *G. holbrooki* trial, the mean was 23.98 ± 1.84 mm for *R. sphenoccephala* and 25.52 ± 2.73 mm for *R. capito*. The mean total length ($\bar{x} \pm$ SD) of predators was 57.38 ± 1.1 mm for *L. gulosus* and 31.90 ± 4.0 mm for *G. holbrooki*.

Tadpole behavior was not quantified in this experiment because of the difficulty of distinguishing between the two species of tadpoles in the aquaria during the experiment. *Lepomis gulosus* and *G. holbrooki* choice experiments were stopped after 30 and 28.5 h, respectively, before 100% mortality was reached in any of the treatments. Tadpoles were then removed, counted, and inspected for injuries. Survivors from these experiments were also transferred to cattle tanks and raised to metamorphosis to confirm species identification. Survival of tadpoles was almost 100% with *G. holbrooki*, and there were no injured tadpoles surviving with *L. gulosus*. Thus, we did not analyze these response variables. We performed paired *t*-tests to compare the survival of the two tadpole species with *L. gulosus* and to compare the number of tadpoles injured by *G. holbrooki*.

RESULTS

Experiment 1: Evaluation of Fish Predators.—None of the tadpoles were missing or injured in the control treatments at the end of the experiments. Therefore, the absence of tadpoles in treatments with fish predators was attributed to predation. Survival of tadpoles for each species was not affected by clutch (*R. sphenoccephala* ANOVA, $F_{1,8} = 0.46$, $P = 0.52$; *R. capito* ANOVA, $F_{1,8} = 3.8$, $P = 0.09$). Tadpole survival was significantly affected by predator treatment ($F_{3,24} = 16.07$, $P < 0.01$). Bonferroni comparisons indicated that tadpole survival was lowest with *L. gulosus*, but there was no difference in survival between tadpole species. The number of tadpoles consumed by *E. obesus* and *G.*

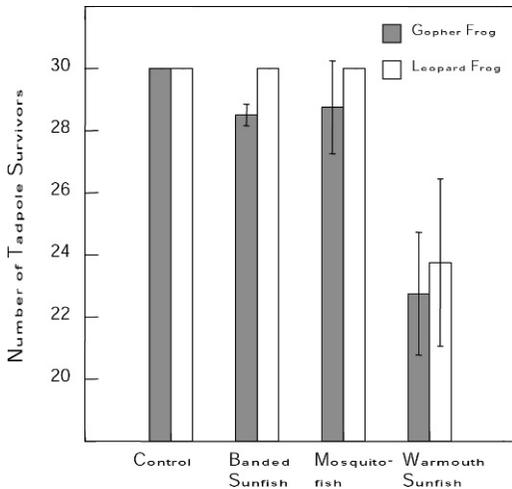


FIG. 1. The number of Gopher Frog, *Rana capito* and Southern Leopard Frog, *Rana sphenoccephala* tadpoles not consumed in each predator treatment of Experiment 1.

holbrooki was almost negligible and was not different from controls (Fig. 1).

Tadpole injuries were significantly affected by predator treatment ($F_{3,24} = 7.87$, $P = 0.01$), and there was a significant interaction of predator treatment and tadpole species ($F_{3,24} = 4.0$, $P = 0.02$). The occurrence of injury in *R. capito* tadpoles with *G. holbrooki* was significantly higher than all other treatments (Fig. 2).

In all predator treatments, tadpoles of *R. capito* hid more often than did those of *R. sphenoccephala* ($F_{3,24} = 20.31$, $P < 0.01$). Predator treatment played a significant role in tadpole hiding behavior ($F_{3,24} = 3.0$, $P = 0.05$). The proportion of tadpoles hiding was significantly higher with *L. gulosus* than for any of the other predator treatments or the control treatment (Fig. 3).

Experiment 2: Choice Experiment.—*Lepomis gulosus* consumed significantly more *R. capito* than *R. sphenoccephala* (paired *t*-test, $t_7 = -3.05$, $P = 0.02$). A mean of 11.0 ± 3.01 SD tadpoles of *R. sphenoccephala* survived in each replicate, compared with 7.75 ± 2.62 SD tadpoles of *R. capito*. The frequency of injuries by *G. holbrooki* did not differ significantly between *R. sphenoccephala* and *R. capito* (paired *t*-test $t_7 = -0.41$, $P = 0.70$).

DISCUSSION

Our results suggest that the presence of fish predators had a greater effect on survival and behavior of the tadpoles of *R. capito* than the tadpoles of *R. sphenoccephala*. However, as in previous studies, there was significant variation in the effectiveness of different fish species as predators (Hecnar and M'Closkey, 1997; Gunz-

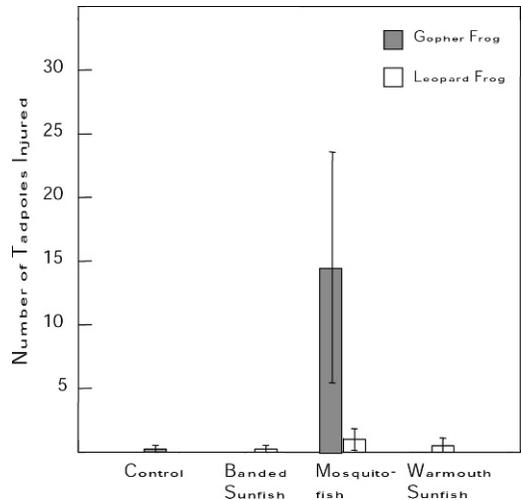


FIG. 2. The number of Gopher Frog, *Rana capito* and Southern Leopard Frog *Rana sphenoccephala* tadpoles injured for each predator treatment of Experiment 1.

burger and Travis, 2004). The presence of *E. obesus* did not affect survival or behavior of either tadpole species. This result is contrary to studies in which *E. obesus* were found to cause a reduction in the biomass and number of newly hatched tadpoles (Chalcraft and Resetarits, 2003) or to have an effect on tadpole activity level (Lawler, 1989; Binckley and Resetarits, 2002). Of the three fish species we tested, *L. gulosus* were the most voracious predators, consuming more tadpoles than *G. holbrooki* and *E. obesus* combined. *Lepomis gulosus* had

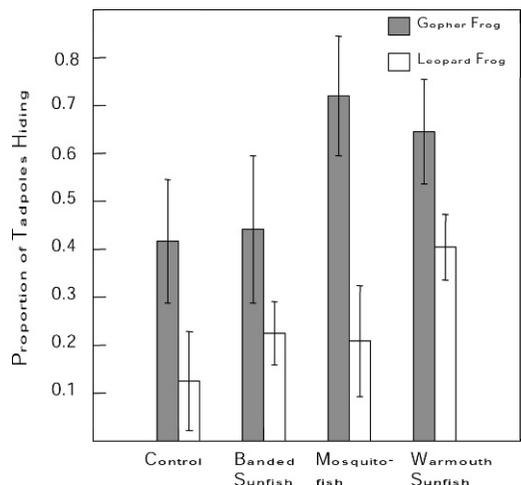


FIG. 3. The proportion of Gopher Frog, *Rana capito* and Southern Leopard Frog *Rana sphenoccephala* tadpoles hiding in each predator treatments of Experiment 1.

the largest gape size of the three fishes tested, and the tadpoles were small enough for them to consume whole. *Lepomis gulosus* consumed tadpoles until they reached satiation regardless of the species, although when fed a combination of both species, they consumed significantly more *R. capito* than *R. sphenoccephala*. It appears that in the absence of alternative prey, either species was sufficiently palatable to *L. gulosus*, but when both tadpole species were present, *R. capito* were more susceptible to predation.

In addition to direct predation, injuries to tadpoles, particularly on the tail region, have strong effects on swimming performance and ability to escape from future predator attacks (Huey, 1980; Semlitsch, 1989). Even though *G. holbrooki* did not consume many tadpoles, they inflicted the greatest amount of injury. In some cases, not a single tadpole in a trial was unharmed. This result is consistent with a small feeding trial by Braid et al. (1994). They observed that introduction of the mosquitofish *Gambusia affinis* with tadpoles of the Dusky Gopher Frog *Rana capito sevosa* resulted in significant injury and eventual mortality of all of the tadpoles in the trial. In Experiment 1 of our study, when *G. holbrooki* were fed each species individually, *R. capito* were more vulnerable to attacks. However, in Experiment 2 when both species were fed to the fish at the same time, both tadpole species were injured at nearly equal rates. It appears as though *R. sphenoccephala* were less palatable than *R. capito*, but when the two species were together, *G. holbrooki* were unable to distinguish clearly one species from the other.

Fish not only influence the survival of anuran tadpoles through direct predation but may also affect tadpole development by causing them to alter their behavior. The presence of predators may be sensed by tadpoles through direct chemical cues or cues from injured conspecifics, and most tadpoles, even those previously unaccustomed to the presence of predators, reduce their activity in response (Richardson, 2001). Reduced activity means less time foraging, which leads to a reduction in growth (Lawler et al., 1999; Anholt et al., 2000) and delayed metamorphosis (Babbitt, 2001). Our behavioral observations revealed that, *R. capito* were more prone to hiding in the presence of predatory fish than were the tadpoles of *R. sphenoccephala*. Despite their increased hiding behavior, *R. capito* still suffered higher injury rates from *G. holbrooki* in Experiment 1 and higher predation with *L. gulosus* in Experiment 2. These results present the opposite pattern typically observed for larval anurans of temporary ponds, which is higher activity levels than of the permanent pond breeding species. Unlike other temporary pond species, *R. capito* has a relatively long

larval period ranging from 87–225 days (Semlitsch et al., 1995; Palis, 1998; Jensen and Richter, 2005). This is even longer than the larval period of approximately 50–75 days observed for *R. sphenoccephala* tadpoles (Butterfield et al., 2005). Several studies have shown that *R. capito* typically breed in fairly large temporary to semipermanent bodies of water (Semlitsch et al., 1995; Eason and Fauth, 2001). Their reduced level of activity may be attributed to the stability of these ponds. *Rana capito* tadpoles would not have to contend with the threat of desiccation; thus, rapid growth is not essential for survival. However, the prolonged development of *R. capito* results in longer exposure to aquatic predators than *R. sphenoccephala*. In fishless habitats, some of the top aquatic predators of tadpoles are invertebrates (Woodward, 1983; Formanowicz, 1989; Werner, 1991; Skelly, 1994). One way tadpoles are able to survive with these predators is by reaching a size refuge, becoming too large for the invertebrate to catch and manipulate. Predation on tadpoles decreases as tadpole size increases (Travis et al., 1985; Semlitsch, 1989; Richards and Bull, 1990). The situation is different with fish large enough to swallow a tadpole whole, such as *L. gulosus*, and those not restricted by tadpole size, such as *G. holbrooki*. The prolonged larval period of *R. capito* may not allow them to develop quickly enough to escape this predation and could factor into their lower survival with fish.

Many examples of the negative impacts of the introduction of fish into historically fishless habitats on native amphibian populations have been documented. In particular, the introduction of fish to areas outside their natural geographic range may be most detrimental. For example, the Mountain Yellow-Legged Frog, *Rana muscosa*, has declined severely as a result of the introduction of salmonid fishes into previously fish-free lakes (Bradford and Tabatabai, 1993; Knapp and Matthews, 2000). Stocking sport fish is not the only cause for concern, because even small fish can have a large impact. The Eastern Mosquitofish *G. holbrooki* is of particular concern. *Gambusia holbrooki* are native to the southeastern United States and were first transported outside the United States in 1905 as a means to control mosquito populations. They now occupy a worldwide distribution (Krumholz, 1948). Contrary to what their name suggests mosquito larvae are not the only component of the *G. holbrooki*'s diet. They also consume the eggs (Grubb, 1972) and tadpoles (Braid et al., 1994; Gamradt and Kats, 1996; Morgan and Buttemer, 1996; Goodsell and Kats, 1999; Pyke and White, 2000) of many species of amphibians. They will even prey on amphibian tadpoles when alternative prey, such as mosquito larvae, are available

(Goodsell and Kats, 1999; Lawler et al., 1999). *Gambusia holbrooki* are very efficient predators, can occur at densities as high as 0.55/m² (Baber et al., 2002), and are able to forage in vegetated habitats that would otherwise serve as refuge from larger predators (Baber and Babbitt, 2004). All sizes of tadpoles are at risk of predation. When a tadpole is too large to be consumed whole, they are then attacked in the tail and ventral region until they are immobilized and consumed (Pyke and White, 2000; Baber and Babbitt, 2004). *Gambusia holbrooki* have been shown to have detrimental effects on amphibian populations ranging from California to Australia (Gamradt and Kats, 1996; Morgan and Buttemer, 1996; Pyke and White, 2000; Hamer et al., 2002). The results of our study indicate that both large predatory centrarchid fish and smaller fish such as *G. holbrooki* can significantly alter the behavior and survival of anuran tadpoles unaccustomed to their presence. Preventing the introduction of fish into fishless habitats could be critical for the protection of particularly vulnerable species such as *R. capito*.

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