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NOTE

FACTORS AFFECTING HATCHING SUCCESS OF GOLDEN APPLE SNAIL EGGS: EFFECTS OF WATER IMMERSION AND CANNIBALISM

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Abstract: The golden apple snail (*Pomacea maculata* Perry) is an invasive species that lays its eggs out of water but is otherwise aquatic. To investigate this behavior and potential management techniques, we conducted experiments to examine the physical effects of immersion and underwater egg predation on hatching success. Predation on submerged eggs by *P. maculata* adults reduced hatching success by ~99%. In predator-free conditions, hatching success was reduced 75% by immersion in water and was negatively correlated with time submerged. Our results suggest that both underwater egg predation and low immersion tolerance may be exploited to limit the spread of *P. maculata*.

Key Words: biological control, invasive management, invasive species, *Pomacea*

INTRODUCTION

Invasive species are present in many ecosystems throughout the world and are a major threat to global biodiversity (Bruton 1995, Courchamp et al. 2003, Henderson et al. 2006). Invasive species impact community composition and habitat structure in both terrestrial and aquatic ecosystems (McChesney and Tershy 1998, Canonico et al. 2005, Levin et al. 2006, McCabe et al. 2006). Whether through direct interactions with agriculture or indirect effects via reductions in biodiversity or ecosystem function, the economic impacts of invasive species can be remarkably high, in excess of $314 billion each year for six large nations (Pimentel et al. 2001). Because patterns of invasions by exotic species can be hard to predict (Buchan and Padilla 1999), a thorough understanding of the demography of exotic species is often essential in designing effective methods of control. Here we focus on the egg laying behavior and hatching success of *Pomacea maculata* Perry (Ampullariidae, synonyms: *P. gigas* Spix, *P. insularum* D'Orbigny; Cowie and Thiengo 2003), an invasive member of the golden apple snail complex.

Golden apple snails, including *P. maculata*, *P. canaliculata* Lamarck, and *P. bridgesii* Reeve, are indigenous to South America (one species, *P. paludosa* Say, is native to peninsular Florida). *Pomacea canaliculata* was first introduced to Taiwan in 1980 for aquaculture (Naylor 1996), but it was a commercial failure in Asian markets (Halwart 1994) and export to Europe was terminated due to health regulations (Naylor 1996). After the snails lost commercial value, they were discarded into waterways and canals, and dispersed into ponds and rice paddies where they quickly established large populations (Ito 2002). In cooler and more seasonable climates, such as their native South American habitat, golden apple snails usually reproduce only once in summer or autumn; however, the year-round warmth of southeast Asia allows *P. canaliculata* to reproduce three to four times per year (Carlsson and Lacoursière 2005) and facilitates increased growth rates, substantially shortening the time until a female's first oviposition (Estebenet and Martín 2002). *Pomacea canaliculata* has become a serious pest throughout southeast Asia (including Japan and the Philippines) and in Hawaii due to its feeding on lotus, taro, and young rice seedlings (Yusa et al. 2006), and it is considered to be a potential invader of Australia (Baker 1998). Additionally, *P. canaliculata* has been found to alter ecosystem functioning in Asian wetlands by reducing the presence of aquatic plants, thereby prompting planktonic algae to become dominant and water to become turbid (Carlsson et al. 2004a). Recently *P. maculata*, a close relative of *P. canaliculata* with highly similar life history characteristics, has been found in Texas bayous (Howells 2005, pers. observation E. Siemann and C. Gabler). Because the climate of coastal Texas (similar to that of southeast Asia) allows the snails to reproduce earlier and more frequently during their lifetimes, these species of apple snails may achieve similar population growth and establish themselves as invasive species.

Efforts to control apple snails in Asia have included draining rice paddies for a period after planting, using pesticides, and employing biological control agents (Yusa and Wada 1999). Past studies have examined a variety of animals as possible biocontrol agents, including ducks (Teo 2001), fish (Ichinose and Tochihara 2003, Yusa et al. 2006, Carlsson et al. 2004b), leeches (Aditya and Raut 2005), fire ants (Stevens et al. 1999), crabs (Carlsson et al. 2004b, Yusa et al. 2006), turtles (Yusa et al. 2006), and the Norway rat (Yusa et al. 2006). In some cases, these predators have proven effective in reducing snail survival, but problems remain. Some predators consume apple snails in laboratory conditions but do not consume them in the field (Yusa et al. 2000). Further, non-native control agents have the potential to become invasive species themselves (Lever 2001). A greater understanding of the egg laying behavior and hatching success of apple snails (particularly *P. maculata*) would augment our understanding of the establishment and spread of golden apple snails and may lead to more efficient management and control of this invader.

Past studies have primarily emphasized predation on juvenile and adult *P. paludosa*, *P. canaliculata*, and *P. bridgesii* (Stevens et al. 1999, Teo 2001, Carlsson et al. 2004b, Aditya and Raut 2005, Yusa et al. 2006). Some studies have examined factors influencing the hatching rates of these species' eggs such as inbreeding (Fujio et al. 1997) and water submersion (Turner 1998, Pizani et al. 2005), but none have specifically investigated *P. maculata*. Water submersion is of particular importance because apple snails lay egg masses on trunks or stems of plants or on walls above the water. This is done at night, possibly to avoid desiccation or predation (Albrecht et al. 1996). Laying eggs out of the water creates an additional cost to females (Estebenet and Martín 2002), but this behavior may be explained by the fact that apple snail eggs face different and perhaps reduced risks, especially in terms of predation, than do juveniles and adults. The eggs are conspicuously bright pink, but very few animals eat them, likely because they are unpalatable (Snyder and Snyder 1971). However, fire ants (*Solenopsis geminata* Fabricius and *S. invicta* Buren), invasive species in the apple snail's introduced range, attack both adult *P. paludosa* (Stevens et al. 1999) and *P. canaliculata* eggs (Yusa 2001).

Female apple snails may lay their eggs out of the water not only to avoid aquatic predators, but also to avoid negative effects of the water itself on hatching success of their eggs. These effects may include altering the permeability of the egg capsule (Pizani et al. 2005), reducing oxygen availability due to low levels of dissolved oxygen (Turner 1998), or lower incubation temperatures in water as compared to air temperatures (Turner 1998). In fact, eggs of the Florida apple snail, *P. paludosa*, showed reduced embryonic development and hatching success when submerged in water (Turner 1998). However, Turner (1998) found no evidence of predation on submerged eggs of this native apple snail.

Due to the differences in egg morphology between *P. maculata* and *P. paludosa*, the eggs of *P. maculata* may respond differently to water submersion and predation than those of *P. paludosa*. The eggs of the non-native apple snail *P. maculata* are smaller (approximately 1–2 mm in diameter) and are laid in larger numbers in each clutch than eggs of *P. paludosa* (approximately 3–6 mm in diameter). Thus, *P. maculata* clutches may contain many more interior eggs that have no contact with the surrounding medium. Therefore, we examined the water tolerance of *P. maculata* eggs. Additionally, adult *P. maculata* consume juveniles in captivity (pers. observation E. Siemann and C. Gabler), so we also quantified the effects of predation (i.e., cannibalism) on submerged eggs. In the first experiment, we compared hatching rates of eggs kept above water to those of submerged eggs without a predator and those of submerged eggs with a predator (adult *P. maculata*). We performed a second experiment focused only on submersion, which more closely mimicked natural submergence conditions. In coastal Texas bayous, heavy rains or tidal flows may cause water levels to rise quickly and remain elevated for hours to days. Therefore, eggs laid above the water level on a stationary object such as a retaining wall or tree trunk may become submerged temporarily rather than continuously. In the second experiment, we examined hatching success of eggs submerged intermittently for different periods of time.

METHODS

Both experiments were conducted in a greenhouse at Rice University in Houston, Texas, USA from October through November 2007. Adult *P. maculata* individuals were gathered from Horsepen Bayou in Pasadena, Texas. These adults then laid eggs in captivity, and once the eggs clutches had dried, the eggs were collected for use in the two experiments.

Predator Exposure Experiment

In this split-plot experiment with six replicates, we compared the hatching success of eggs kept above water, eggs kept below water, and eggs kept below

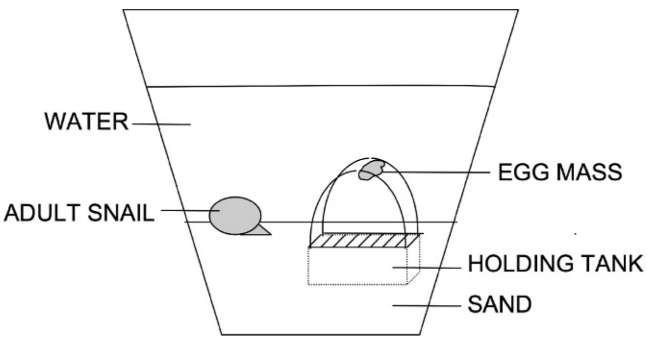

Figure 1. Predator treatment tank diagram. An egg mass, kept from floating to the surface by an arch made of window screen and vinyl-coated hardware cloth, was placed in each 12-L tank with one adult apple snail. When eggs hatched, juveniles fell into the holding tank, where they were inaccessible to the adult apple snail.

water and exposed to a predator. Each of six egg clutches was cut into three pieces, roughly equal in size. Each piece from an individual egg clutch was then randomly assigned to one of three treatments: 1) a predator-free treatment in which eggs were submerged in water for the duration of the experiment, 2) a predator treatment in which eggs were submerged in water with a single adult *P. maculata* present for the duration of the experiment, or 3) an above water control where the section of egg clutch remained dry throughout the experiment. The ages of the six clutches varied due to a limited number of egg clutches, but because one piece of each clutch was assigned to each treatment any age effects were standardized among the three treatments.

For the six above-water controls, eggs were placed on top of a plastic mesh bench liner covering a 250-mL plastic cup filled with approximately 175 mL of water (municipal tap water, aged 24 hours). As juveniles emerged, they fell into the water and could be counted. For the predator-free water immersion treatment, eggs were placed in a plastic cup filled with water under fiberglass window screen to keep eggs from floating to the surface. These cups were then submerged in 4-liter containers of water (three cups in each container) to minimize water temperature fluctuations. For the predator treatment (Figure 1), eggs were placed in 12-liter tanks with a single *P. maculata* adult. The adult snails weighed approximately 95–115 g each. Because *P. maculata* adults eat juveniles in captivity, eggs were placed above a container covered with vinyl-coated hardware cloth that allowed newly emerged juvenile snails to drop into the container and be inaccessible to the adult snail. Eggs were kept from floating to the surface of the water by attaching an arch made of window screen and vinyl-coated hardware cloth to the top of the juvenile-holding container. This arch had openings at both ends large enough for an adult snail to fit through and sides sturdy enough for the adult snail to climb up to reach the eggs. Adult snails were given Romaine lettuce as an alternative food source, so that predation on snail eggs could not be attributed to lack of food.

For the first week of the experiment, water temperatures were allowed to fluctuate between night and day, but after one week, heaters were used at night to maintain a constant temperature of 28°C in the greenhouse. Water was cleaned daily by removing any floating particles (such as wilted lettuce in the predator enclosures) and replacing some of the tank water with clean, aged tap water. Additionally, water was aerated each day.

In the underwater predator treatment, juveniles were removed and counted daily in order to minimize predation on juveniles. Hatching was assumed to be complete when there were less than 15 eggs remaining (control clutch pieces averaged 185 juveniles) and those eggs were no longer pink or floating. In the other two treatments, all juveniles were counted at least once a week. Hatching was complete after four weeks. One clutch did not produce any juveniles and was excluded from the analysis.

The number of hatched snails per clutch had a right-skewed distribution so data were square root transformed to fit a normal distribution. Analysis of variance was used to test whether hatching success depended on clutch or treatment. A partial difference test on means, adjusted for the effect of clutch, was used to examine differences in hatching success among the three treatment levels. SAS was used for all analyses (SAS Institute, Inc. 2004. v. 9.1. Cary, North Carolina, USA).

Length of Immersion Experiment

This split-plot experiment with six replicates examined the hatching success of eggs that were immersed in water for different amounts of time. Each of six egg clutches was cut into three pieces, roughly equal in size. Each piece from an egg clutch was then randomly assigned to one of three treatments: 1) submergence for one day followed by dry conditions, 2) submergence for three days followed by dry conditions or 3) an alternating two-day submergence and two-day dry treatment (2 cycles over 8 days) followed by dry conditions. As in the predator exposure experiment, clutch age varied due to a limited supply of egg clutches, but equal distribution of clutch pieces among treatments standardized any age effects.

Each clutch piece was placed into a separate PVC tube with fiberglass window screen secured to the ends by duct tape at one end and a rubber band at the other. Tubes were placed in either dry plastic cups or plastic cups filled with aged, municipal tap water to impose dry versus wet conditions. Tubes were checked daily on days 2 through 15 and any hatched snails were counted and discarded by temporarily removing the rubber banded screen.

The number of hatched snails per clutch had a pronounced right-skewed distribution so data were *ln*[number hatched +1] transformed to fit a normal distribution. Analysis of variance was used to test whether hatching success depended on clutch or treatment. Partial difference, adjusted means contrast tests were used to examine differences in hatching success among the three treatment levels.

RESULTS

Predator Exposure

Hatching success varied significantly by treatment ($F_{2,8}$ = 6.2, p = 0.02) but did not vary among clutches ($F_{4,8}$ = 2.4, p = 0.14). In adjusted means contrast tests, hatching success within clutches was significantly greater for eggs that remained above water compared to those left underwater either with or without exposure to a predator (Figure 2A). Hatching success on average was lower with predator exposure as compared to underwater predator-free conditions. Of successfully hatched eggs that were incubated above water, only 28% on average would have hatched when incubated underwater, and only 1% would have hatched when incubated underwater and exposed to a predator. Adult snails consumed 99% of the submersed eggs, although we do not know what percent of these were viable.

Length of Immersion

Hatching success varied with both clutch origin ($F_{5,10}$ = 6.5, p = 0.006) and treatment ($F_{2,10}$ = 4.5, p = 0.04). Hatching success was greater for the one-day immersion treatment than the alternating treatment in adjusted means contrast tests (Figure 2B).

DISCUSSION

Both experiments showed that immersion in water reduced hatching success of *P. maculata* eggs. Eggs

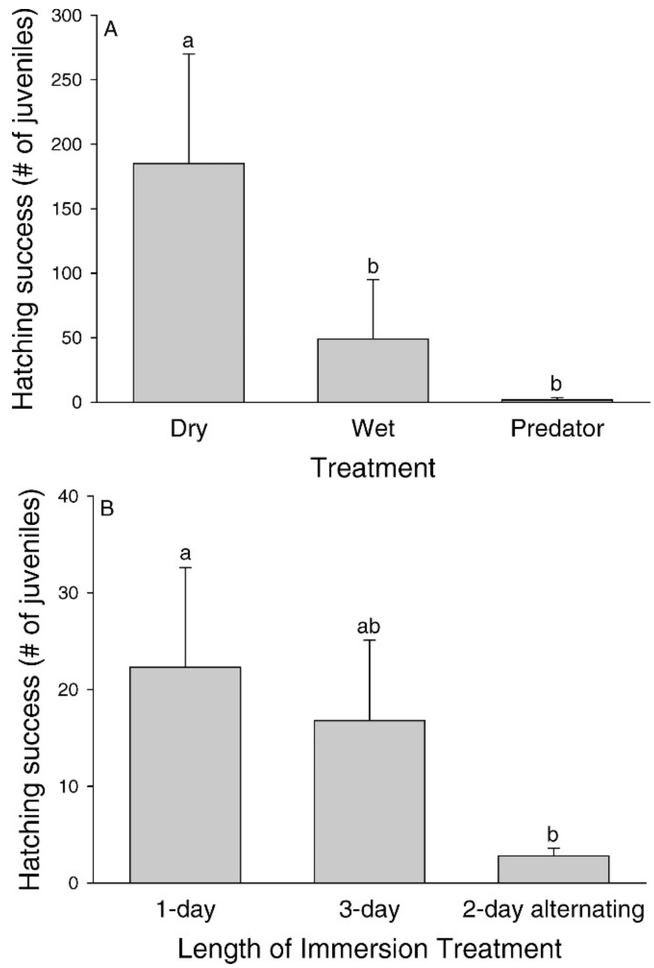

Figure 2. Mean hatching success of *P. maculata* eggs in A) the predator exposure experiment and B) the length of immersion experiment. For each experiment, values with the same letter indicates treatments that were not significantly different (adjusted means contrast tests). Error bars represent 1 S.E.

were able to withstand short-term exposure to water, but had a lower tolerance to longer and repeated submersion. It seemed that egg clutches could not withstand exposure to water because the majority of the clutches that were submerged broke apart into individual eggs. This apparent inability of the clutch to maintain its structural integrity in water may have contributed to the reduced hatching rate in water compared to dry conditions, as interior eggs that may otherwise have been buffered by exterior eggs were exposed to water. Water immersion may contribute to hatching failure by reducing oxygen availability to developing embryos, thereby preventing proper embryonic development, or by causing premature hatching (Turner 1998, Pizani et al. 2005). When immersed egg clutches break apart into small pieces, it is possible that individual eggs experience lower predation, perhaps by presenting a less conspicuous target, but eggs could experience higher predation by becoming accessible to small predators. Avoidance of aquatic egg predators, including cannibalistic adult snails, may have selected for the laying of eggs out of water, and the physiological adaptations of eggs necessary for surviving in a dry environment may have resulted in the inability to remain viable when immersed in water (Turner 1998). In this scenario, predator avoidance is the ultimate cause for laying eggs out of the water and the narrow environmental tolerances are a consequence, although the design of this experiment did not specifically test this hypothesis.

We note that the use of different-sized containers for the predator-free and predator-exposure treatments could have had some effect on egg hatching. In both treatments, however, eggs were surrounded with at least a few liters of water to buffer any temperate changes, and the water was cleaned and aerated daily in both treatments. Additionally, the adult apple snails consumed nearly all (~99%) of the eggs, leaving very few with which to see the effect of water immersion itself in the predator-exposure experiment. Most importantly, eggs in the dry and wet treatments were in the cups of the same size, which allowed us to make comparisons between hatching success in dry and immersed conditions.

P. maculata eggs were readily consumed by adult snails. Cannibalism in apple snails is not limited to adults consuming eggs because we have observed adults consuming juveniles as well, although it was prevented in our study because juveniles were protected from the adult snail. This suggests that the rates of cannibalism in our study may be low compared to that which would be observed with consumption of both eggs and juvenile snails. Of course, overall rates of cannibalism could be higher or lower in artificial settings compared to rates in field settings. Our predator snails were kept in small tanks, and may have exhibited elevated rates of cannibalism because of the easy access to the eggs. Nevertheless, the finding of significant cannibalism suggests that although *P. paludosa* eggs are considered to be unpalatable and are rejected by some aquatic predators (Snyder and Snyder 1971), *P. maculata* eggs are vulnerable to predation by adult apple snails.

Cannibalism can fulfill nutritional deficiencies (Simpson et al 2006), and in the case of egg cannibalism by adult snails, it may be related to protein or calcium deficiency. A congener, *P. bridgesii*, has been found to prefer animal food to plant food (Aditya and Raut 2001). Because diet quality can have strong effects on survival, growth, and fecundity, it is possible that cannibalism plays an important role in population dynamics and invasions of the golden apple snail complex. Cannibalism can also have important effects on population dynamics because of feedbacks between adult density and juvenile survival (Claessen et al 2004). Field studies that determine the relationships among cannibalism and population growth in *P. maculata* would be useful.

Although it is energetically more costly for a female snail to lay eggs above water (Estebenet and Martín 2002) because she may be exposed to predation by terrestrial and aerial animals, heavy predation pressure on eggs in the water may be favoring this behavior. Previous study of *P. paludosa* by Turner (1998) found little evidence of predation on eggs in the field. However, given the significant differences in the egg morphology and the differences in native ranges between *P. paludosa* and *P. maculata*, predation cannot be ruled out as a selection pressure for laying eggs above water. In fact, Turner (1998) states that there is general agreement in apple snail literature that the major selective force for laying eggs above water was the presence of aquatic predators. It is possible that factors other than predation, such as increased oxygen availability for developing embryos or preventing silt build up on eggs, may have contributed to laying eggs above water. Although we know little about *P. maculata* egg predation in the field, predation may help keep the species in check in its native range and may serve to help control its population growth in its introduced range.

Our results suggest that periodic flooding of fields and streams may help control apple snail populations by limiting hatching rates and exposing eggs to aquatic predators, including adult apple snails. Flooding could be an attractive control method because it eliminates the need for chemical controls. However, it may need to be done multiple times during the growing season due to the ability of the apple snails to produce multiple clutches per season in their non-native ranges. A cycle of alternating flooding and normal conditions may be especially efficient, as this would reduce hatching success because eggs laid above the water during normal conditions would be submerged later, reducing the need to continually raise water levels as new eggs are laid. Cannibalism or predation by other snails may also help keep populations in check, although more work is needed to evaluate the impacts of predation on population dynamics. By increasing our knowledge of apple snail life history, we will be better able to predict snail impacts and devise methods of controlling emerging pest populations.

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