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EFFECTS OF SUBMERGENCE ON EMBRYONIC SURVIVAL AND DEVELOPMENTAL RATE OF THE FLORIDA APPLESNAIL, *POMACEA PALUDOSA*: IMPLICATIONS FOR EGG PREDATION AND MARSH MANAGEMENT

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**ABSTRACT:** *Aerial deposition of egg clutches by the aquatic Florida applesnail is believed to have evolved in response to aquatic egg predators. Adaptation to aerial conditions might, however, have rendered embryos intolerant of submergence, a potential occurrence in natural and managed marshes, rivers, and lakes. In this study, eggs were submerged in water for various durations in the laboratory to assess their ability to survive flooding; and clutches of known ages were submerged for several days in the field to determine if aquatic predators might decrease survival below levels expected to occur due to flooding alone. Submergence of clutches slowed embryonic development and increased mortality. Embryos that were within a few days of hatching at the time of submergence were not strongly affected. When younger embryos were submerged, none hatched; and most died in early stages of growth. Submergence of clutches in the field increased mortality above that in laboratory submergence, but factors other than predation, such as loss of adhesion and entanglement with floating debris, accounted for the losses. There was no evidence that aquatic predators were a significant factor in embryonic mortality. In managed wetlands that hold populations of *Pomacea paludosa*, flooding should occur slowly during the reproductive season (March through October), particularly in the first few months when clutch production is high, to avoid loss of as much as 2 wk of clutch production.*

AMPULLARIID SNAILS (applesnails) of the genera *Pomacea* Perry and *Pila* Roeding deposit clutches of large eggs with calcareous shells on emergent vegetation of freshwater habitats (Perera and Walls, 1996). The two genera have long fossil histories, and there are numerous reports of the Florida applesnail, *Pomacea paludosa* (Say), in fossil strata since the late Pliocene (2 mya) (Dall, 1892; Tucker and Wilson, 1932; Henderson, 1935; Smith, 1937; Taylor, 1966; Hoerle, 1970; McGinty, 1970; Thompson, 1984; Petuch, 1992; Perera and Walls, 1996). It is generally believed that the New World genus *Pomacea* evolved the habit of aerial deposition of clutches in response to loss to aquatic predators such as its sympatric confamilial *Marisa* Gray (Robins, 1971; Paulinyi and Paulini, 1972), which deposits submerged gelatinous clutches (Perera and Walls, 1996). Because mean elevation of clutches above the surface of the water is only 150–200 mm (Hanning, 1979; Turner, 1996), a moderate rise in water level of 11–14 mm/d would sub-

merge many clutches during the 2-wk period of development, potentially subjecting embryos to physiological stress and aquatic predators. The purpose of this study was to measure the physiological tolerance of embryos to submergence and to evaluate the potential of aquatic predation to reduce further the survival of embryos.

**METHODS**—Clutches were collected from emergent stems (primarily common cattail, *Typha latifolia* L.) at a water-filled borrow pit (28° 7' 24" N, 80° 42' 28" W) northwest of the intersection of U.S. Interstate Highway 95 and Florida State Road 518, west of Melbourne, Florida. The lake, known locally but unofficially as Clear Lake, is steep sided and was formed by the excavation of carbonate rock to build the roadbed for the interstate highway. In addition to a dense, stable population of applesnails, Clear Lake contains *Lepomis microlophus* (Gunther) (redear sunfish) and *Trionyx ferox* (Schneider) (Florida soft-shelled turtle), known predators of adult applesnails (Chable, 1947; Wilbur, 1969; Dineen, 1974; Dalrymple, 1977), and several other species of *Lepomis* Rafinesque that possibly eat hatchling applesnails (Snyder and Snyder, 1971; Jaynes, 1993). Blue Cypress Water Management Area (BCWMA) East (described in Turner, 1996) contains the same predators (Snyder, 1997). Both Clear Lake and BCWMA East sites were used to study predation.

Clutches are laid at night within an adhesive mass of extracapsular mucus (jelly) that dries within a few hours after sunrise. Clutches that are found to be invested with jelly are, therefore, within several hours of oviposition. Jellied clutches were collected at Clear Lake in August and September 1993, transferred to standard (25 mm by 76 mm), glass, microscope slides, and allowed to dry in an inclined position under full-spectrum fluorescent lighting (Daylight, General Electric Co.) at 27–32°C and 59–82% relative humidity. The upright orientation of the clutch on the original plant stem was maintained during this study; i.e., care was taken not to invert the stem and clutch. When the clutches were dry, each was placed at a slight incline in a beaker and allowed to incubate under a photoperiod of 12 h of light and 12 h of darkness for 14 or 21 d. Each beaker was provided with at least a few millimeters of water into which hatchling snails could fall. During incubation, filtered lake water was added to the beakers to submerge selected clutches at ages of 1, 4, 8, and 12 d; the ratio of water volume to clutch volume was approximately 150:1. Control clutches were not submerged. Lake water was coarsely filtered (Whatman no. 1) to remove larger microorganisms.

After 14 or 21 d of incubation, clutches were removed for dissection to determine the stages and viability of embryos. Stages of development included hatchlings, shelled embryos, and unshelled embryos. To stage shelled embryos further, each embryo was placed over graph paper with 1-mm spacing, and the size of the body shell was estimated as the number of grid-squares covered. The following criteria, from most to least reliable, were used to recognize a live embryo: heartbeat; withdrawal of the body into the shell; active epidermal ciliation; foot expanded and appressed to an intracapsular gas bubble.

Low production of clutches at Clear Lake during the summer drought of 1993 precluded optimal experimental design: replication was low ( $r = 2$  or  $3$ ), and the clutches had to be incubated in three trials. Each trial included two control clutches, but not all possible combinations of treatments (four ages at submersion and two days of sacrifice) were included in each trial. Additional jellied clutches were harvested at Clear Lake during April–May 1994 and allowed to develop in the laboratory at similar temperature, humidity, and lighting as in 1993. Clutches were dissected at regular intervals and evaluated for stage of development to produce a representative series of embryogenesis under aerial conditions.

The field phase of studies on submersion attempted to assess the potential of predation to inflict mortality before death that would be expected to have occurred by submergence alone (i.e., in the absence of predators) based on results of the laboratory phase. Jellied clutches were collected from emergent stems in Clear Lake in 1993 at regular intervals and held in the laboratory for later use. At the start of each of two trials, therefore, clutches of several ages

were available for submergence. In addition, enough jellied clutches were found in Clear Lake at the start of the Clear Lake trial to include 0-d-old (jellied) clutches. The two trials were conducted at Clear Lake and BCWMA East. Ages for the Clear Lake trial were 0, 1, 4, 7, and 11 d; those for the BCWMA East trial 2, 6, 9, and 13 d.

Poles made from half-inch (21-mm outside diameter) polyvinylchloride (PVC) plumbing pipe were cut to 1.5-m lengths and driven vertically into the substratum. Clutches were attached by their plant stems to the PVC poles with plastic cable-ties, free ends of which were cut to reduce the chance of fouling by windblown or waterborne debris. Each pole held a pair of clutches of the same age, one clutch (aerial clutch) about 300 mm above the water level and one (submerged clutch) about 50 mm below the water level. At Clear Lake, 10 poles were set along the northern shore at water depths of 510–810 mm and secured to *Typha latifolia* with cable-ties. Pairs of clutches were assigned to the poles haphazardly, and they were oriented toward open water. At BCWMA East (27° 40' 21.2" N, 80° 38' 19.2" W), 15 poles were set in two ranks, one along the sawgrass (*Cladium jamaicense* Crantz) edge and the other within the nearby mixed shallow marsh and about 5.1 m from the sawgrass edge; depths were 280–440 mm. Assignment of clutches to poles was haphazard, and those on poles along the sawgrass edge faced open water.

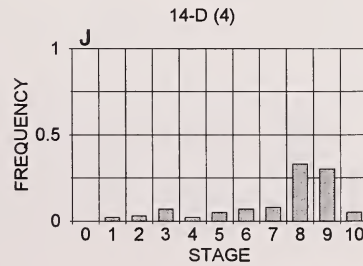
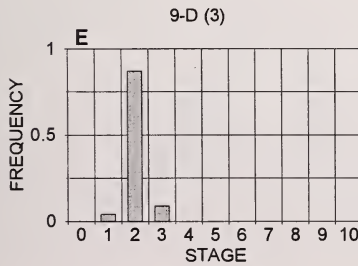
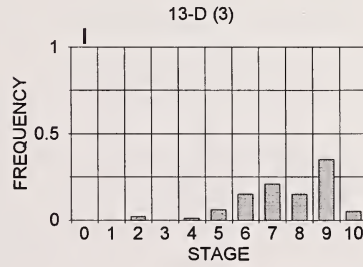
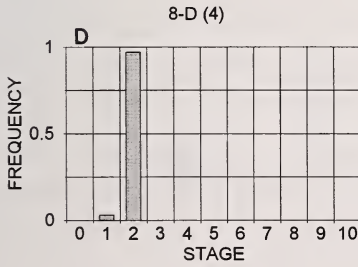
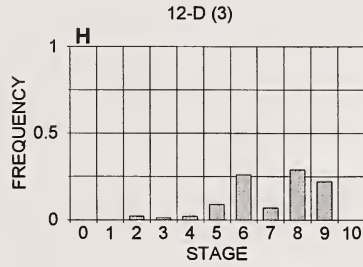
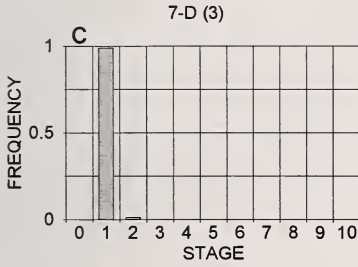
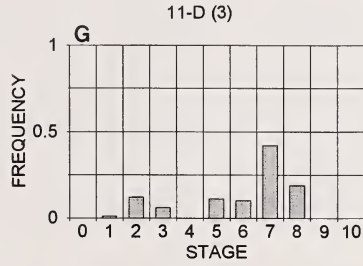
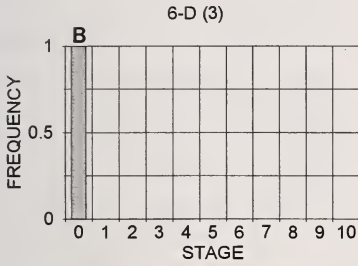
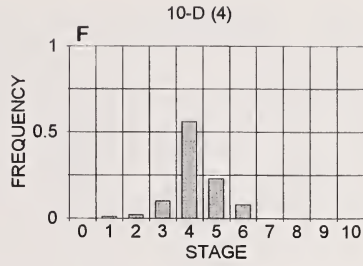
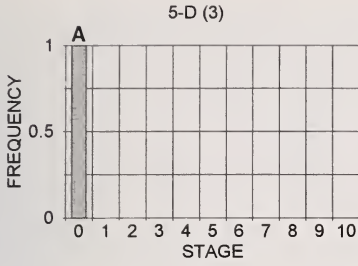
Visibility in the water column at Clear Lake was excellent: The bottom of the lake at the base of the PVC poles could be seen from the surface, and there was no macroscopic debris floating or suspended in the water. Visibility at BCWMA East was poor: *Utricularia vulgaris* L. (common bladderwort) and plant debris filled nearly the entire water column along the sawgrass edge and in the mixed shallow marsh; only a few centimeters of free water remained at the surface. During these trials, water level dropped about 30 mm at Clear Lake and about 20 mm at BCWMA East, leaving none of the submerged clutches exposed. Clutches were harvested after 3 d in June 1993 in the Clear Lake trial and after 7 d in July 1993 in the BCWMA East trial. Notes on gross condition of clutches and eggs were made in the field and laboratory, and eggs from the BCWMA East trial were individually dissected.

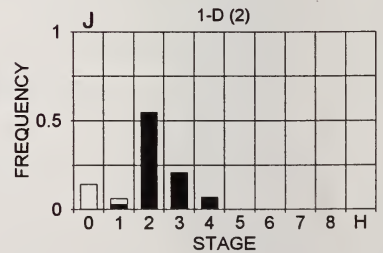
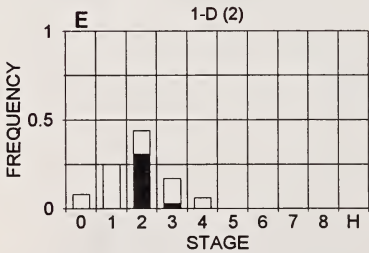
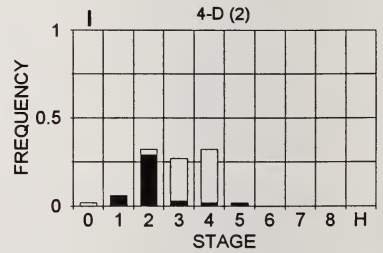
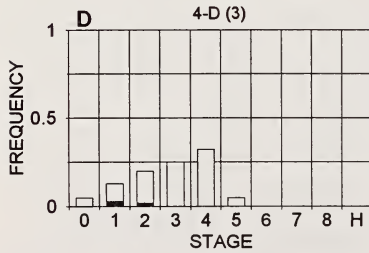
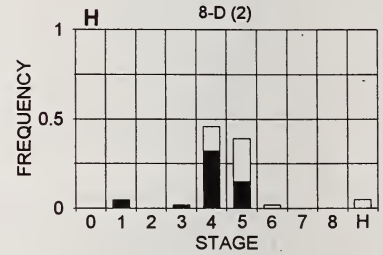
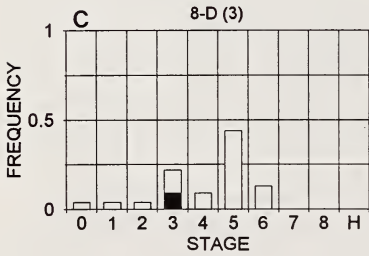
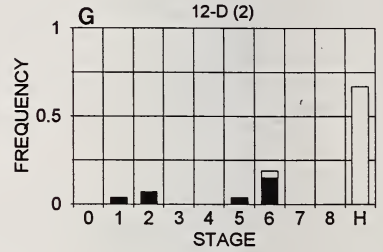
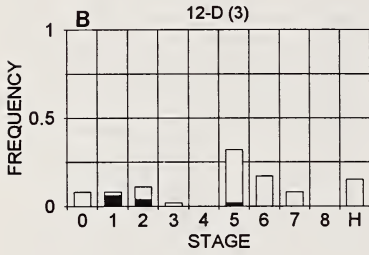
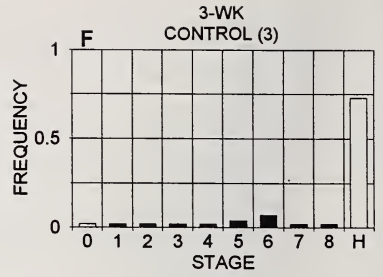
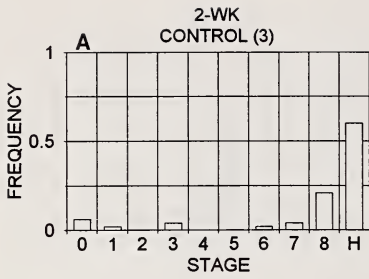
**RESULTS**—Under aerial conditions in the laboratory, embryos of *Pomacea paludosa* remained small (< 1 mm square) and lacked a body shell for the first 4 d of development. Shelled embryos reached Size-class 1 (1 mm square) by Day 7 and grew slowly to Size-class 4 at 10 d, by which time the size distribution spread over six classes (Fig. 1F). As embryogenesis progressed, the modal size class decreased in frequency (Fig. 1F–H), and the distribution became increasingly skewed toward the smaller size classes. By Day 14, 68% of the embryos had attained size-classes 8–10 (Fig. 1J). Clutches at 14 d were sacrificed before hatching occurred.

Submergence in all treatments slowed the rate of embryonic development and increased mortality in the laboratory (Fig. 2). The severity of effects was directly proportional to the duration of submergence and inversely proportional to age at submergence. Nevertheless, submerged embryos in all treatments continued to grow beyond their predicted size at time of submergence (cf. Fig. 1 and Fig. 2). For example, embryos submerged

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FIG. 1. Relative size-frequencies of shelled embryos of *Pomacea paludosa* under aerial conditions in the laboratory. No embryo of clutches sacrificed before 5 d of incubation bore a body shell. Values in parentheses are the numbers of clutches used.





at 8 d at a predicted Size-class 2 (Fig. 1D) attained size-classes 3–6 during the subsequent 6 d of submergence (Fig. 2C).

Success of hatching after 14 d was highest in the control (aerial) group, and the modal size of unhatched embryos in the controls was the largest of all groups (Fig. 2A). Moderate hatching occurred in clutches submerged at 12 d of age (Fig. 2B), but hatching did not occur in any clutches submerged at younger ages (Fig. 2C–E). Growth was retarded in all submerged clutches compared to the control (Kolmogorov-Smirnov test for goodness of fit to an extrinsic hypothesis,  $P < 0.05$  for each of four comparisons,  $n = 23$ –60). Although modal size declined in clutches submerged at younger ages, submergence did not arrest growth. For example, after 14 d of embryogenesis, clutches submerged at ages of 4 d and 1 d (Fig. 2D, E) grew body shells of sizes equivalent to those of 8–10-d embryos incubated under aerial conditions (Fig. 1D–F). Mortality occurred only in submerged clutches; total embryonic mortality during the first 14 d of incubation was 12% of unhatched shelled embryos, and 97% of all deaths occurred among the smallest embryos (size-classes 0–3).

Extension of incubation time to 21 d (Fig. 2F–J) did not allow embryogenesis to progress except in control clutches and in clutches submerged at 12 d of age, as shown in the increased proportion of hatchlings. The two juveniles that hatched in the 8-d group (Fig. 2H) fell from the uppermost eggs of one clutch that had become partly exposed due to excessive evaporation in the beaker. Mortality was 67% among unhatched shelled embryos of clutches incubated for 21 d.

Submergence of clutches in the field gave little evidence for loss to aquatic predators. Only 5 of the 309 eggs in 10 aerial clutches were damaged during the 3-d trial at Clear Lake (93–100% survival; Table 1). There was no evidence of hatching in aerial clutches or of damage due to recreational use of jet-propelled watercraft. Two additional eggs from one aerial clutch were lost entirely from their attachment to the plant stem; the same clutch included two broken eggs. Survival of eggs in submerged clutches at Clear Lake was much lower and more variable (44–99%; Table 1). Of 362 eggs in 10 submerged clutches, 19 were broken; but 12 were empty of contents (no residual yolk or albumen) and belonged to clutches for which control clutches in the laboratory began hatching on the date that this trial was concluded; the other seven were on PVC poles that sustained loss or damage

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FIG. 2. Effects of laboratory submergence on relative size-frequencies of embryos. Clutches were submerged at ages 12, 8, 4, or 1 d and remained submerged until the day of sacrifice. Controls were not submerged. A–E, clutches sacrificed after 2 wk of incubation. F–J, clutches sacrificed after 3 wk of incubation. Stage 0 included only embryos that lacked a body shell. Hatchlings (H) were not sized. Shelled embryos were scored as live (white parts of histogram bars) or dead (black), but unshelled embryos could not be scored. Values in parentheses are the numbers of clutches used.

TABLE 1. Condition of paired aerial and submerged clutches in the field. Two pairs of clutches were used for each age at Clear Lake and four pairs (three for 6-d-old clutches) at BCWMA East. Data do not include eggs that were damaged in handling at the start of the trial.

Age at start (d)	Percentage of eggs after 3 or 7 d in:							
	Aerial clutches				Submerged clutches			
	Whole	Lost	Broken	Hatched	Whole	Lost	Broken	Hatched
Clear Lake, 3 d								
0	100	0	0	0	44.4	55.6	0	0
1	98.2	0	1.8	0	98.6	0	1.4	0
4	93.4	3.3	3.3	0	83.0	11.0	6.0	0
7	98.8	0	1.2	0	83.9	16.1	0	0
11	100	0	0	0*	70.5	9.8	19.7	0*
BCWMA East, 7 d								
2	96.9	3.1	0	0	90.6	6.3	3.1	0
6	86.7	0	1.3	12.0	100	0	0	0
9	54.1	1.3	0	44.6	82.3	12.9	3.2	1.6
13	32.1	25.9	0	42.0	9.9	16.8	22.8	50.5

\* Control clutches in laboratory began to hatch on last day of trial.

to their aerial clutches. Another 66 eggs were lost from submerged clutches: 40 from jellied, 0-d-old clutches, which presumably lost adhesion; 11 eggs from the PVC pole holding the aerial clutch that had 2 lost and 2 broken eggs; 6 from a submerged clutch that presumably had begun to hatch, based on hatching of control clutches in the laboratory; and 9 from a PVC pole with an aerial clutch in which 2 eggs were broken.

Dissection of eggs retrieved from the trial at BCWMA East after 7 d improved the ability to discriminate between hatching and other conditions of eggs. Survival of eggs was higher and less variable in aerial (74–99% whole and hatched eggs; Table 1) than in submerged clutches (60–100%). All but one egg were lost or crushed in a pair (i.e., aerial and submerged) of clutches on one PVC pole, indicating the occurrence of an unknown event. Except for this pair of clutches, 8 eggs were lost and 1 broken out of 333 eggs of 14 aerial clutches; and 31 eggs were lost and 11 broken out of 303 eggs of 14 submerged clutches. More than half of the eggs lost from submerged clutches represented an entire clutch on a pole that had become surrounded by floating debris; and 7 of the 11 broken eggs of submerged clutches were empty (no residual yolk or albumen) and belonged to clutches that had begun to hatch. Hatching rates of 13-d-old eggs were high and similar in submerged (50.5%) and in aerial (42.0%) clutches; and the rate for 9-d-old eggs was far poorer in submerged (1.6%) than in aerial (44.6%) clutches (Table 1).

DISCUSSION—The large gelatinous eggs of *Marisa cornuarietis*, in the same family as the Florida applesnail, are laid underwater (Perera and Walls, 1996). They swell from 3 mm diameter at oviposition to 5 mm as water is



imbibed soon afterward (Michelson, 1955). It is not, therefore, valid to assume that the large eggs of *Pomacea paludosa*, with diameters of 4–6 mm (Ryder, 1889; Wallace et al., 1956; Hepler, 1974; Hanning, 1979), would die from submergence due to physiological stress. But the Florida applesnail has probably evolved a physiological dependence on aerial incubation. More than 100 yr ago, Ryder (1889) warned that submergence kills the embryos. Other authors since have parroted his warning, and only Hurdle (1973) has offered new data. Hurdle (1973) found submergence to delay hatching but not to prevent it. Submergence loosened the extracapsular adhesive mucus after 1 wk, and 45% of clutches lost eggs by detachment within 2 wk. Unfortunately, Hurdle's (1973) clutches were of unknown ages at the start of submergence, and he gave no data on mortality within clutches. A subsequent experiment (Hurdle, 1974) gave similar results, with submergence for 1 wk followed by a post-submergence period of continued embryogenesis; but no information was given on age of clutches or on mortality within clutches. In the present study, also, embryogenesis was delayed by submergence in the laboratory. After 3 wk, however, embryogenesis had not progressed beyond stages at 2 wk in clutches that were submerged at ages of 1, 4, and 8 d; and mortality at 21 d of incubation was high. Clutches that were submerged at 12 d of age had already achieved a moderate size of shelled embryo; some hatched within another 2 d and many by the end of the experiment at 21 d.

Many smaller embryos are capable of crawling when freed from their eggshells (Turner, unpublished observations), but only embryos with body shells similar in diameter to their eggshells will hatch. The mechanism of hatching is unknown in *P. paludosa*. Hatching does not seem to be aided by weakening of the eggshell by chemical dissolution or radular scraping, for inspection by scanning electron microscopy gives no evidence for either mechanism (Turner and McCabe, 1990). If hatching is size dependent, it might be accomplished by outward pressure from extension of the foot. Based on this hypothesis, submerged eggs would hatch only if they contained late-stage embryos that could achieve hatching size before death from physiological stress; and smaller embryos, competent to live if freed, would remain unhatched, lacking both the aid from implosion by water pressure on a weakened eggshell and the ability to extend the foot across the diameter of the egg.

Aposematism—the linkage of a conspicuous warning (such as coloration) with a penalty (such as unpalatability) against predation—must be an effective mechanism for protecting the large yolky eggs of the Florida applesnail from terrestrial predators (Snyder and Snyder, 1971; Romer, 1972; Orians and Janzen, 1974), for most claims of predation on its eggs are poorly documented (Bailey, 1925; Blatchley, 1932; Ligas in Snyder and Snyder, 1971; Abreu, 1976; Kushlan, 1978). There seems to be general agreement in the literature on applesnails that the major selective pressure for aerial deposition of clutches was the presence of aquatic predators. It seems un-

likely, however, that aposematism would have evolved prior to or parallel with aerial oviposition, for aposematism might have been equally as effective against aquatic vertebrates in the past as it appears to be against terrestrial predators today. Indeed, some potential aquatic predators reject eggs offered to them (Snyder and Snyder, 1971).

Other advantages to depositing aerial clutches might be the more favorable incubation temperature and oxygen concentration for embryogenesis; the production of larger hatchlings from larger eggs that could survive only in a well-oxygenated environment; avoidance of mechanical damage from drift material in a high-density medium and from clumsy adults climbing stems to breathe at the surface; avoidance of clutch cannibalism; reduction of microbial growth by exposure of the eggshell to ultraviolet light. None of these possibilities has been studied, although mechanical damage from drift material is implicated in some results from fieldwork of the present study. Oxygen concentration might be a critical factor, for diurnal and seasonal maxima and minima of dissolved oxygen (DO) can differ up to 5–80-fold in marshes and sloughs that hold populations of the Florida applesnail (Belanger et al., 1985; Platko, 1986; Browder et al., 1994). In the present study, DO was not monitored during submergence in the laboratory, but the ratio of water volume to clutch volume was kept high (150:1). Diurnal DO curves are not available for BCWMA East (Snyder, 1997) and Clear Lake.

Whatever the selective pressures might have been for evolution of aerial deposition of clutches, the eggs of the Florida applesnail are now intolerant of submergence, perhaps because of reduced permeability of a calcareous eggshell. Embryos apparently die from physiological stress or other factors before they are eaten by predators. Damage incurred by experimentally submerged clutches in Clear Lake and BCWMA East marsh was low and could not be specifically attributed to predation; other factors easily accounted for shell breakage and loss: hatching, weakened adhesion to stems, impact of or snagging by waterborne debris, impact from adjacent moving stems, and unknown factors that also caused damage to companion aerial clutches.

The potential for submergence by rising waters and for loss of eggs and embryos to predation or other factors probably varies widely according to age of the clutch. Jellied clutches are easily dislodged from their attachment to stems upon submergence. Jellied clutches are, however, the least likely stage in a stand of clutches to be submerged because of the height to which water level must rise in the several hours between oviposition and the desiccation of extracapsular mucus. Early stages in embryogenesis of the Florida applesnail also are the most unpalatable (Snyder and Snyder, 1971; Romer, 1972) but have the least physiological tolerance to submergence. Late-stage embryos, on the other hand, are most prone to submergence by flooding unless they are attached to a vigorously growing plant stem: Water level could rise above clutch height during the 2-wk incubation period. Moreover, unpalatability diminishes as embryogenesis proceeds (Romer, 1972), and

late-stage embryos are the most likely to survive submergence physiologically and to hatch under water. Submergence of clutches with late-stage embryos might increase hatchling mortality due to predation. Snyder and Snyder (1971) speculated that bluegill sunfish eat juvenile applesnails in the field as the fish did in laboratory studies. Jaynes (1993) has repeatedly observed sunfish lying in wait beneath clutch-bearing stems in Hunter's Lake, Hernando County, Florida, and consuming hatchling snails as they fall through the water column. Hatching might be the only stage at which submerged clutches experience substantial predation. Predation on hatchlings, whether from submerged or aerial clutches, warrants further study.

The warning of Ryder (1889) must be heeded: submergence of applesnail clutches kills them. Hanning's (1979) determination of the reproductive season from March through October in Lake Okeechobee also seems to hold for BCWMA East and Clear Lake. The potential impact of increases in water level during this season depends upon the distribution of clutch elevations. The distribution that exists at any time reflects recent hydrologic history: If water level is declining, younger, physiologically more sensitive clutches would occupy a lower broad zone on stems, and a greater proportion of them than older clutches would be submerged by subsequently rising waters; if water level is steadily rising, cohorts of older, less sensitive clutches would be submerged in succession. Only clutches nearest to hatching would provide some hatchlings during a period of rapidly rising water. If water level were to increase too rapidly, as much as 2 wk of clutch production in the area would be lost. Production during the first few months of oviposition is probably most critical, for there is evidence that snails hatching early in the year provide the spawning population for the autumn and following spring (Martin, 1973; Hurdle, 1974; Hanning, 1979). In general, however, the biological significance of lost clutches is unknown, for the population dynamics of the Florida applesnail have been little studied.

The distribution of clutch cohorts should be monitored and applied to a dynamic model that could be developed to predict mortality at known or desired rates of flooding. The challenge to effective management is the decision on what level of mortality to accept, considering other priorities in wetlands management. Monitoring water levels will be critical for long-term maintenance of snail populations as a food supply for the snail kite and other predators. Predation on submerged clutches, at least, need not be a consideration.

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