

Adaptive Significance of Communal Oviposition in Wood Frogs (*Rana sylvatica*)

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Summary. 1. Wood frogs (*Rana sylvatica*) are one of the earliest anurans to breed in spring. Their breeding behavior is 'explosive', with most oviposition occurring within 2 to 6 days. Early breeding may reduce predation and ensure adequate developmental time for larvae, but it is accompanied by the risk of substantial egg mortality due to cold temperature.

2. Males amplex females throughout breeding ponds, and pairs move toward a communal oviposition site. Females usually deposit eggs on submerged twigs or vegetation directly contiguous to other egg masses. Late breeders oviposit at the edge of the growing clump, thus surrounding the egg masses of earlier breeders.

3. Egg masses in the center of a clump are insulated from thermal extremes in the surrounding water. Within a clump, central egg masses were warmer than peripheral egg masses, but egg masses at the edge of a clump were warmer than single egg masses deposited outside the clump.

4. Central egg masses had significantly greater hatching success than peripheral egg masses. Central egg masses also had significantly more eggs than peripheral egg masses, suggesting that larger females obtained central sites.

5. Because central egg masses have the greatest survivorship to hatching, wood frogs should be selected to breed early to obtain optimal oviposition sites. Breeding synchrony may result from this selection for early oviposition, with the ultimate limiting factors being how quickly frogs can emerge in the spring and when ice on ponds melts.

synchronously within a period of a few days. Although the dynamics of mating systems are strongly influenced by the length of the breeding period (Emlen and Oring 1977), ultimate factors determining timing have not been generally studied. In colonial birds, synchronized breeding has been attributed to biological advantages, e.g., predator deterrence (Kruuk 1964; Hoogland and Sherman 1976) or the facilitation of social foraging (Horn 1968; Ward and Zahavi 1973; Emlen and Demong 1975). Similarly, colonial nesting in some fishes may have evolved as a mechanism to reduce predation on fry (Dominey 1981; Gross and MacMillan 1981).

Temperate zone anuran amphibians demonstrate a variety of breeding systems (reviewed in Wells 1977), from highly synchronous choruses in which mate acquisition is largely the result of scramble competition for females to more prolonged aggregations where males vie for females by establishing territories that favor egg and larval survival (e.g., Howard 1978). Those species that breed earliest in the spring are usually synchronous breeders, and many deposit their egg masses in communal clumps.

Early breeding may be advantageous for anurans, especially those that deposit eggs in vernal ponds: (1) by completing oviposition early, frogs maximize the probability that tadpoles will metamorphose before the pond dries; and (2) because many potential predators are not active in early spring, larvae of early breeders may grow large enough to attain a size refuge from predation (e.g., Calef 1973; Heyer et al. 1975). Yet early breeding is a risky strategy, as eggs and larvae may be adversely affected by harsh environmental conditions. Spring weather can be unpredictable; temperatures frequently drop after mating is complete, and eggs sometimes become ensheathed in ice (Wright 1914; Wright and Wright 1949; Licht 1971; this study).

The deposition of globular egg masses in communal clumps may represent an adaptation to these con-

Introduction

Breeding behavior in many animal species is carried on over seasons of weeks or months, but in others breeding activity is 'explosive', i.e., all mating occurs

ditions. Because of the compounded insulation effects afforded by clumping, egg masses in communal aggregates are often warmer than the surrounding water and single unclumped egg masses (Savage 1950; Herreid and Kinney 1967; Merrell 1970; Licht 1971; Hassinger 1972; Howard 1980; Waldman and Ryan, in press; Seale, in press). I report here evidence that in one anuran amphibian, the wood frog (*Rana sylvatica*), these thermal advantages may have important effects on larval survivorship, and suggest that selection on frogs to obtain favorable egg deposition sites may influence the timing of breeding activities.

Materials and Methods

Wood frogs were observed in five ponds in Tompkins County, New York during March and April 1978 through 1981. Four ponds (denoted YB1, YB2, YB3, and YB4) are located in Yellow Barn State Forest near Dryden, New York; one pond (denoted SW) is located in the Sapsucker Woods Preserve near Ithaca, New York. All four ponds in the Yellow Barn forest are permanent woodland ponds, ranging in altitude from 575 to 610 m. YB1 (15 × 12 m) and YB4 (50 × 30 m) had clear water and were generally free of submerged vegetation; YB2 (11 × 4 m) and YB3 (18 × 12 m) had considerable algae and submerged vegetation. All had little emergent vegetation, and maximum water depth ranged from 0.5 to 0.8 m. Pond SW (altitude 325 m) had clear water, little submerged but considerable emergent vegetation, and generally dried completely by midsummer. Maximum depth was 0.5 m.

Wood frogs were sexed, measured, and marked as they entered pond YB4 during 1978. Body lengths were measured from the tip of the snout to the distal end of the ischium, and individuals were marked by sewing unique combinations of colored plastic beads through the skin beneath each tympanum. Because arrival of frogs to the pond was highly synchronous, only the first 140 individuals entering the pond were marked. Individual marking of the entire population would have necessitated delaying and consequently disrupting the onset of breeding activity, and thus was ruled out. Moreover, observers' activity appeared to interfere with the frogs' normal mating behavior. For these reasons, subsequent observations were made on unmarked individuals.

Breeding behavior was observed during one or two 60 min periods each night between 19.00 and 05.00 h. I observed frogs with a head lamp, standing at a constant location at the edge of a pond during each observation period. Wood frogs usually stopped calling and many submerged immediately after I moved, but breeding activity resumed after 10–20 min. Although males called both during daylight and evening hours, most mating activity occurred between 22.00 and 03.00 h.

To establish spatial oviposition patterns with time, I recorded the locations of all egg masses present in pond SW on mornings following each night of breeding activity during 1980 and 1981. I placed marked stakes in the ground near each set of egg masses so that relative positions of new egg masses on consecutive days could be accurately mapped.

After breeding was complete, temperatures were measured in the centers of egg masses located at various positions within clumps and in isolated single egg masses. These data were compared with water temperatures 10 cm outside the egg masses (5 cm below the water surface). Temperatures were taken with a Schultheis quick-reading thermometer in the center of representative egg masses. In addition, the proportion of each egg mass's surface area exposed to surrounding water was estimated. For this study, that portion

of an egg mass that was directly exposed to solar radiation (near the water surface) was not considered; the remaining surface area not in direct contact with surrounding egg masses was considered 'exposed'. Repeated estimates on egg masses agreed within ten percent.

To test whether larval survival differed by egg mass location within clumps, I compared the hatching success of central and peripheral egg masses in four clumps, each in a different pond (YB1, YB2, YB3, SW), during 1980. Development was monitored from oviposition until 2–3 days before hatching at which time I removed five random egg masses from the center (0–25% surface area exposure) and five random egg masses from the periphery (40–90% exposure) of each clump. Each egg mass was placed in an individual container, and most larvae hatched within a few hours at room temperature. The number of larvae that had hatched, or for which hatching appeared imminent (developmental stage 19 or greater [Gosner 1960]), and the number of dead embryos and larvae in each egg mass were then recorded. Some egg masses could not be immediately counted; these were preserved in 10% formalin, and when later counted, differentiation between those larvae that had hatched, or were about to hatch, and unsuccessful embryos and larvae was clear. Two central egg masses from the clump sampled in pond SW decayed extensively before preservation, and were not counted.

Results

Description of Breeding Behavior

Wood frogs overwinter in logs, stumps, and under leaf litter in woodlands (Wright 1914; Wright and Wright 1949), and near Ithaca, they usually migrate to breeding ponds within days after surface ice has melted, often while snow remains on the ground. In this study, breeding dates ranged from 24 March to 21 April. However, in any given pond, most breeding activity was completed within two to six days after males began calling. Wood frogs first arriving at a pond moved very sluggishly and were easily captured, suggesting that they had recently emerged from hibernation.

Breeding was synchronous. At pond YB4 in 1978, 24 males and one female arrived at the water on the first night of breeding activity (18 April), but over 500 frogs arrived within 90 min the following night. Most females deposited eggs the same night they arrived, and three large clumps consisting of between 50 and 370 egg masses were formed in two nights of breeding. Although males subsequently called for several days from locations near the clumps, few new egg masses were deposited and these were either added onto clumps or deposited singly away from the clumps. This was a typical pattern for all ponds, but there usually was only one communal oviposition site per pond. For example, in the same pond in 1980, all 686 egg masses were deposited in a single clump. In pond YB4, and often in other ponds, clumps were deposited at different locations within the pond each year, but they were always deposited in shallow water (<0.4 m depth).

Mating behaviors were generally similar to those described by Banta (1914), Howard (1980), and Berven (1981). Males called, and amplexed females, throughout ponds early during the breeding period, but were most concentrated near oviposition sites after pairs began to spawn. Once amplexed, the female (clashed by her mate) usually began swimming toward an oviposition site. Unpaired males actively disrupted spawning pairs near egg mass clumps, attempting to dislodge amplexed males. Pairs responded by kicking attackers away with their hind legs, or alternatively by submerging and reapproaching the clump after several minutes.

At the oviposition site, females grasped submerged twigs, stems or vines with their forelegs, and quickly oviposited around this vegetation (typically within 6 to 20 min). This posture enabled pairs to spawn despite interference from unpaired males, and ensured that egg masses were affixed to submerged vegetation. Because egg masses were usually deposited directly abutting one another (or up to 1 cm apart), twigs in the center of a clump quickly became covered, and later breeding females consequently tended to move to the edge of a clump to obtain appropriate oviposition sites.

Most central egg masses were thus deposited by early breeding females, as illustrated by data collected in 1981 at pond SW. On 29 March, wood frogs arrived at the pond during the late afternoon and early evening. Males promptly started calling, and between 22.00 and 23.30 h that night, 13 egg masses were deposited together in a single clump. By 05.00 h the next morning, the size of the clump had grown to 32 egg masses, and by 01.00 h 31 March, 129 egg masses had been deposited in the clump. All matings occurred within 48 h of the first males' arrival at the pond; no new egg masses were subsequently deposited, despite several additional days of intermittent calling by males. Except for three egg masses found near the center of the clump, all egg masses deposited on the second night were outside those deposited the first night (see Fig. 1).

Temperature Elevation Within Egg Clumps

Egg masses within clumps were warmer than water outside the clumps. Data collected on a typical clump consisting of 113 egg masses (and on single egg masses deposited outside the clump) are shown in Fig. 2. Temperature elevation was inversely correlated with the percentage of egg mass surface area exposed to surrounding water ($r = -0.85$, $n = 35$, $P < 0.0001$). Isolated egg masses were 0.6–2.2 °C warmer than water 10 cm outside the egg mass, egg masses at the edge of the clump were 1.0–5.0 °C warmer, and those in

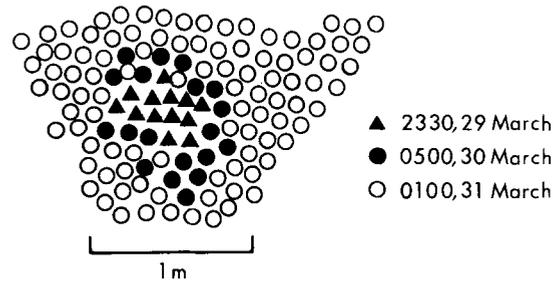


Fig. 1. Locations of egg masses within a communal clump in pond SW in 1981. Egg masses deposited on 29 March, the first night of breeding, were subsequently surrounded by egg masses of later breeding pairs

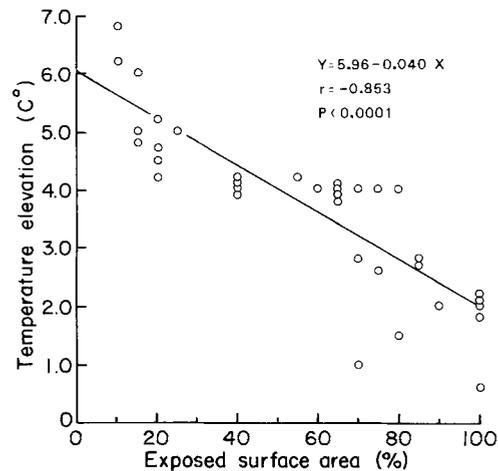


Fig. 2. Temperature elevation of egg masses above ambient water (24.0 °C) as a function of percent surface area of the egg mass exposed to water in a typical clump. See text for procedure used in estimating surface area. Temperature elevation is inversely correlated with percent exposure

the center, maximally insulated from surrounding water, were 4.2–6.8 °C warmer. Overall, central egg masses were significantly warmer than peripheral masses within the clump ($P < 0.0001$, Mann-Whitney *U*-test), and peripheral egg masses in the clump were significantly warmer than isolated egg masses outside the clump ($P < 0.0001$, Mann-Whitney *U*-test). In this clump, as in many others, egg masses were arranged in an essentially two-dimensional layer with all egg masses within 5 cm of the water surface. Some clumps were three-dimensional, however, with egg masses deposited on top of one another. In this case, temperatures in submerged egg masses were generally lower than those at the surface (see Hassinger 1972). Moreover, these data were collected on a sunny afternoon between 14.00 and 16.00 h. Temperature elevation was generally less on cloudy days and at night (Waldman and Ryan, in press; Seale, in press). Howard (1980) suggests that clumped egg masses are warmer than surrounding water only in those situations in which water circulation around the clump is limited,

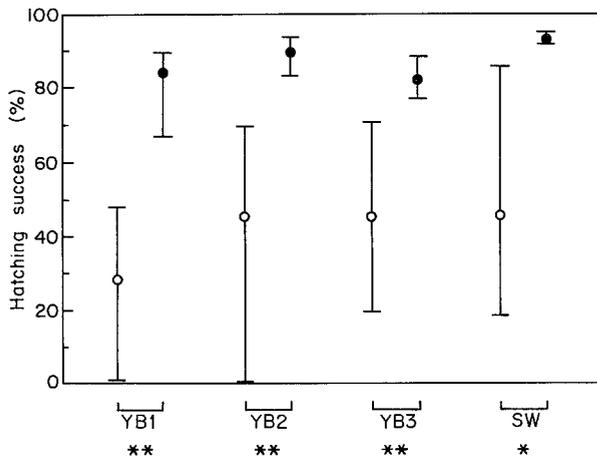


Fig. 3. Percent hatching success for representative peripheral (○) and central (●) egg masses in four clumps, each in a different pond. Means and ranges (bars) are shown. In each clump, hatching success is significantly greater in central egg masses than in peripheral egg masses (Mann-Whitney *U*-test: * $P < 0.02$; ** $P < 0.01$)

or in areas with low water levels and abundant vegetation. Although the magnitude of the temperature elevation may have been affected by these factors, egg mass clumps in all ponds sampled in this study during daylight and evening hours were warmer than the surrounding water.

Differential Hatching Success Within Clumps

In each of the four clumps sampled, hatching success in central egg masses ($\bar{x} = 86.3\%$, $SD = 6.8$) was significantly greater than that in peripheral egg masses ($\bar{x} = 41.6\%$, $SD = 23.2$) (Fig. 3; in each pond $P < 0.02$; overall $P < 0.0001$, Mann-Whitney *U*-test, one-tailed). Variation in hatching success was greater among peripheral egg masses than among central egg masses, perhaps because of greater variability in exposure. This effect appeared not to be dependent on the number of egg masses in the clump, although all clumps were relatively large (YB1: 95 egg masses; YB2: 86 egg masses; YB3: 71 egg masses; SW: 113 egg masses). Most eggs were successfully fertilized (98.9% of 727 sampled in three peripheral egg masses) and mortality generally occurred in early embryonic stages, when larvae are most susceptible to temperature fluctuation (Herreid and Kinney 1967; Zweifel 1977). I saw little evidence of egg predation, although on two occasions over four years newts (*Notophthalmus viridescens*) were observed apparently biting jelly remnants after eggs had hatched. In some locations leeches may attack eggs and early embryos (Cory and Manion 1953), but I saw no leech infestation during this study.

Besides having higher proportions of successfully

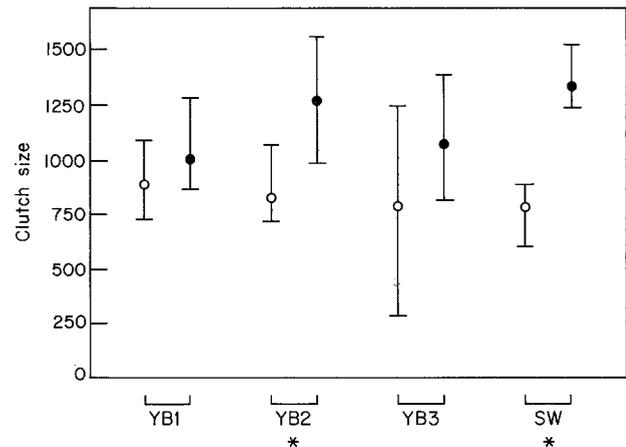


Fig. 4. Total number of eggs (live and dead) contained in representative peripheral (○) and central (●) egg masses. Means and ranges (bars) are shown. Data are presented for the same egg masses shown in Fig. 3. Central egg masses have significantly larger clutch sizes than peripheral egg masses in ponds YB2 and SW (Mann-Whitney *U*-test: * $P < 0.02$)

hatching eggs, central egg masses had more eggs than peripheral egg masses (Fig. 4; central: $\bar{x} = 1153$, $SD = 230$; peripheral: $\bar{x} = 823$, $SD = 206$). This difference was significant in two of the four clumps sampled ($P < 0.02$, Mann-Whitney *U*-test, one-tailed), but was highly significant overall ($P < 0.0001$, Mann-Whitney *U*-test). Thus, greater hatching success in central egg masses was confounded by larger clutch sizes. However, differential hatching success between central and peripheral egg masses is not attributable to this clutch size difference alone. Considering just central egg masses to control for temperature differences, hatching success and clutch size were not correlated ($r = 0.056$, $n = 18$, $P = 0.32$). Notably, the largest mean clutch size for central egg masses was found in the clump consisting of the largest number of egg masses (pond SW), but this mean is based on three samples only.

Discussion

Given the harsh environmental conditions to which wood frog eggs are exposed, deposition of egg masses in communal aggregates may be critical to embryonic survival. As suggested in previous studies (Herreid and Kinney 1967; Hassinger 1972; Howard 1980; Seale, in press), clumped egg masses are warmer than surrounding water. The darkly colored eggs may act as 'black bodies', warming more quickly than surrounding water in sunlight (Savage 1950, 1961; Hassinger 1970) and retaining this heat when the water cools because of the insulation provided by their jelly envelopes (Beattie 1980). The globular shape of the egg mass increases the effectiveness of this insulation

(Moore 1940), and clumping further restricts water flow around eggs (Licht 1971). Greater hatching success in central than in peripheral egg masses may be attributable to the more favorable temperature regime thus conferred. Although wood frog embryos are physiologically adapted to tolerate cold (Moore 1939, 1940), warmer temperatures in central egg masses apparently enable greater proportions of larvae to develop normally, and may enable them to develop more rapidly.

Generally, early breeders appear to obtain central egg deposition sites within clumps, and their eggs are surrounded by those of later breeding pairs. Indeed, early clutches may act as social releasers for the deposition of other egg masses around them. Howard (1980) experimentally introduced four egg masses into a pond prior to the onset of breeding activity, and found that all pairs breeding in the pond thereafter deposited their eggs at the site of the introduced clump. Although physical features of a pond may also be important in determining where frogs deposit their egg masses (Seale, in press), deposition of egg masses around those previously deposited can be thermally advantageous. Because egg masses deposited at the edge of a clump are warmer than those deposited outside a clump, this strategy would be adaptive for late breeding pairs even if their egg masses are not subsequently surrounded by others. By increasing the size of the clump, late breeders also increase the temperature elevation in central egg masses (Waldman and Ryan, in press; Seale, in press).

Selection on wood frogs to obtain optimal egg deposition sites might explain why these frogs breed synchronously (Waldman and Ryan, in press). By breeding early, wood frogs can increase the likelihood that their egg masses will be surrounded by those of later breeding pairs. The ultimate factors limiting how early frogs can deposit their eggs may be how quickly they can emerge from hibernation in the spring and when ice on ponds melts.

Large females may have some advantage over smaller females in obtaining central oviposition sites. Egg masses in central positions within clumps tended to be larger than those at the edge, and as clutch size in several amphibian species, including wood frogs, is positively correlated with body mass (Salthe and Duellman 1973; Collins 1975), those central egg masses may have been deposited by larger females. How larger females might obtain central oviposition sites is unclear. Possibly they emerge and migrate to ponds earlier than small females, thus allowing them to deposit eggs first. Although I did not collect sufficient data to test this hypothesis for females, males arriving at pond YB4 on the first night of breeding activity in 1978 were significantly larger than

those arriving the second night (mean snout-vent lengths [mm]: 18 April, 52.4 [SD=2.7, $n=24$]; 19 April, 50.6 [SD=3.8, $n=32$]; $P=0.044$, t -test, two-tailed). As a consequence of their inability to obtain central sites, small females might suffer high egg mortality. Delayed sexual maturation of female wood frogs (Bellis 1961; Collins 1975) might be selected as a result of the inability of small females to obtain favorable oviposition sites, coupled with an increased risk of mortality associated with breeding (Banta 1914; Huheey and Stupka 1967; Howard 1980; Seale, in press; personal observation).

Synchronization of breeding with good weather conditions may also be important. Because young embryos are more vulnerable to injury by cold than those more advanced in development (Herreid and Kinney 1967), egg masses deposited by late breeding pairs might still be at a vulnerable stage if weather turned abruptly colder soon after peak breeding. Hatching success data presented in this study were obtained in a mild spring in which breeding activity was not soon followed by cold weather. Presumably, differential survival between central and peripheral egg masses would be even greater during springs such as 1978 and 1979 when ponds froze over a few days after breeding. However, under some environmental conditions (e.g., when temperatures are unseasonably warm), communal oviposition might actually reduce survivorship in central egg masses because of heat stress (see Zweifel 1977), oxygen depletion (but see Savage 1950), or increased rate of fungal infestation.

I have demonstrated an advantage of clumping of egg masses in space, and have suggested that those frogs that breed the earliest are likely to benefit most from this grouping, leading to selection for clumping of breeding activities in time as well. Other selection pressures may also favor synchronous breeding in frogs. For example, larvae of *Rana temporaria* prey upon conspecific (as well as heterospecific) eggs; because eggs deposited before the first larvae in a pond begin feeding are not predated, selection for early oviposition should be strong (Heusser 1970). Moreover, in species for which synchronous breeding is adaptive, hormonal mechanisms may interact with environmental conditions to precisely determine when mating occurs (e.g., see Obert 1975). Further work is needed to clarify the physiological and evolutionary factors that influence the timing of breeding activities.

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