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Thermal Advantages of Communal Egg Mass Deposition in Wood Frogs (*Rana sylvatica*)

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Embryos of most anurans develop within a special microhabitat consisting of the jelly secreted around the eggs by the female parent. The jelly envelope covering each embryo effectively provides a buffer between it and the surrounding water; moreover, the three-dimensional structure of the gelatinous egg mass is thought to represent an adaptation to thermal stresses and gas exchange requirements likely to be encountered by the developing embryos. Jelly masses of North American ranid frogs can be categorized into two species-specific types related to these environmental factors: globular-shaped and surface film forms (Moore, 1940). Frogs that breed early in the spring deposit their eggs in globular masses, which may facilitate the concentration and retention of heat (obtained from solar radiation) within the egg masses. Such traits may be particularly adaptive in the cold water characteristic of ponds in early spring. In contrast, frogs breeding in late spring and summer generally deposit their eggs in monolayer surface film masses. Because embryos of these species develop in much warmer conditions, their metabolic rates are higher than those of early-breeding species and the oxygen tension in the water is lower; thus this egg mass form may represent an adaptation to maximize surface area for gas exchange (reviewed in Salthe and Mecham, 1974). In some instances, this surface film structure may also functionally cool the eggs (Ryan, 1978).

Wood frogs (*Rana sylvatica*) are the most northerly distributed ectothermic tetrapod in North America, with a range extending from north of the Arctic Circle to Georgia. In temperate regions, wood frogs breed in early spring, frequently before ice has completely melted from breeding ponds. Wood frogs deposit their egg masses in communal clumps within limited areas, thereby compounding insulation effects provided by their individual egg masses. Although several investigators have suggested that clumping of egg masses warms embryos (*R. sylvatica*: Herreid and Kinney, 1967; Hassinger, 1970; Howard, 1980; Seale, 1982; *R. temporaria*: Savage, 1950, 1961; Guyétant, 1966; Beattie, 1980; *R. pipiens*: Zweifel, 1968; Hassinger, 1970; Merrell, 1977; *R. aurora, R. pretiosa*: Licht, 1971), differences in temperatures of egg masses at various positions within clumps have not been investigated.

We studied egg masses in two woodland ponds near Ithaca, New York during April 1978 and 1980. The ponds are shallow (less than 0.8 m depth) permanent pools, with little submerged or emergent vegetation. Most egg masses were deposited in clumps in the shallowest water (less than 0.25 m depth), attached to submerged vines, reeds, and twigs. Generally, all egg masses in a pond were deposited at one site, leading to the formation of one clump per pond. However, in 1978 at one pond, six clumps consisting of variable numbers of egg masses were formed, allowing us to compare characteristics of egg masses based upon clump size within the same pond. Clumps consisted of between 3 and 150 egg masses.

To investigate the temperature of egg masses in relation to their positions within a clump, we measured temperatures of some egg masses (approx. 3 cm within each egg mass) both at the center and at the periphery of clumps, as well as those of single egg masses deposited outside clumps. We then compared these temperatures with that of the surrounding water, 10 cm outside the clump (5 cm below the water surface). All temperature data were obtained with a Schultheis quick-reading thermometer. To quantify the "exposure" of each egg mass to the surrounding water, we visually estimated the percentage surface area of each egg mass not in direct contact with surrounding egg masses (on its lateral and ventral surfaces). Observations were made on clumps consisting of various numbers of egg masses, and in clumps on both sunny and overcast days.

Although most egg masses within clumps were warmer than the surrounding water, egg masses in central locations within a clump were warmer than those at the edge of that clump. Temperature elevation of egg masses was inversely correlated with their exposed surface area. Moreover, egg mass temperatures increased (in all clump positions) as the size of the clump increased (Fig. 1). This finding suggests that the presence of additional egg masses in a clump provides added insulation, improving the heat retention capacity of the clumped egg masses.

The correlation of temperature elevation of an egg mass with its surface area exposure was apparent both on sunny and on cloudy days. Figure 2 shows temperature elevation of egg masses as a function of their position within a clump of 36 egg masses on two successive afternoons. The first day was sunny and central egg masses were 3.0-3.2°C above ambient. Weather conditions the following afternoon were overcast, with intermittent rain and drizzle throughout the day. Clumped egg masses were still warmer than the surrounding water, but the magnitude of the tem-

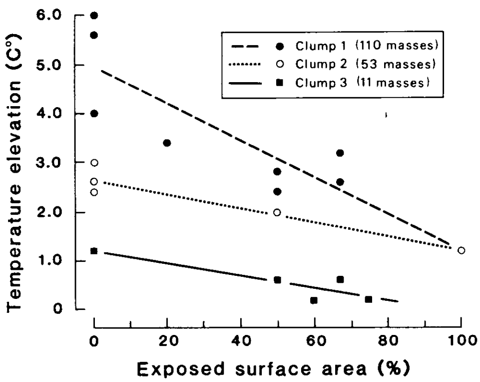

FIG. 1. Temperature elevation of egg masses above the surrounding water (16.8–17.0°C) as a function of their estimated exposure to outside water. Data and least square regression lines are shown for egg masses contained within three different clumps in the same pond. For each clump, temperature elevation was inversely correlated with egg mass surface area exposure (Clump 1 [110 egg masses]: $r = -0.82$, $N = 8$, $P < 0.02$; Clump 2 [53 egg masses]: $r = -0.93$, $N = 5$, $P < 0.05$; Clump 3 [11 egg masses]: $r = -0.90$, $N = 5$, $P < 0.05$). Data were collected on 23 April 1978 between 1400 and 1600 h in clumps all located in one pond. Sky conditions were sunny (12.5°C air temperature).

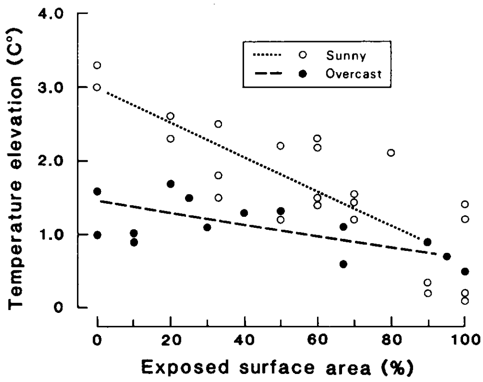

FIG. 2. Temperature elevation of egg masses above the surrounding water in a single clump of 36 egg masses on two consecutive days. 19 April 1980 was sunny and the water temperature was 23.8°C; 20 April was cloudy with intermittent rain and the water temperature was 17.5°C. On both days, temperature elevation was inversely correlated with egg mass surface area exposure (19 April: $r = -0.82$, $N = 23$, $P < 0.01$; 20 April: $r = -0.72$, $N = 14$, $P < 0.01$), but the maximum temperature elevation was about twice as high on the sunny as on the cloudy day. On both days, data were collected between 1400 and 1600 h.

perature elevation was reduced to about half that of the previous sunny afternoon.

Because egg masses are clumped in space, embryos gain a temperature advantage that may be important in ensuring larval survival under cold spring conditions (Waldman, 1982). All breeding pairs benefit by depositing their clutches at a single site in a pond, because temperature elevation of egg masses within a clump is proportional to the number of egg masses in it. The propensity of wood frogs to oviposit at a communal site may thus derive from this clump-size advantage. However, egg masses in the center of a clump presumably benefit more than those at the edge because central egg masses are warmer. Besides providing protection from cold, warmer temperatures might enable individuals in central egg masses to grow more quickly than those in peripheral egg masses. As a result, important selective advantages in competitive ability (possibly continuing after metamorphosis) would accrue to larvae from central egg masses. In addition, accelerated growth rates may enable these larvae to rapidly attain a size refuge from predation, and presumably maximize the likelihood that they will metamorphose in ephemeral habitats (see review in Wilbur, 1980).

Wood frogs tend to deposit their egg masses around those previously deposited in a pond (Howard, 1980); hence selection to obtain central oviposition sites may explain in part why the breeding activity of wood frogs is clumped in time, as well as in space. Characteristically, wood frog breeding aggregations are short in duration, with all oviposition occurring within 2–10 days (Banta, 1914; Howard, 1980; Berven, 1981; Waldman, 1982). Indeed, breeding appears to occur at the earliest possible time; wood frogs migrate to breeding ponds just a few days after spring emergence, and may breed within a few hours after their arrival (Wright, 1914; pers. obs.).

Our results further suggest that the temperature of clumped egg masses may be above that of surrounding water under a wider range of environmental conditions than previously reported. Howard (1980) suggests that clumped egg masses are warmer than the surrounding water only when water circulation is limited and abundant emergent vegetation exists in a pond. Our study ponds were characterized by little emergent vegetation or other obstructions to water flow. Yet we recorded substantial temperature elevation in both central and peripheral egg masses. Ambient wind conditions might account for differences between Howard's results and our own; Howard (pers. comm.) collected his temperature data on rather windy days, whereas our data were collected on calm and moderately windy days. If wind conditions do affect the magnitude of temperature elevation experienced by egg masses, wood frogs might be selected to choose oviposition sites in those areas of a pond least exposed to wind (see discussion in Guyétant, 1976). We believe that the clumping of egg masses may provide a favorable microenvironment for wood frog embryos and larvae in many breeding habitats.

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