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In order to attain maximum reproductive fitness, temperate zone anurans are inextricably dependent upon the successful completion of a suite of seasonal reproductive events. In anurans, the annual sequence includes the propagation of gametes, the location of a mate, the selection of a breeding site, the fertilization of the eggs, and the development of the eggs and young (Duellman and Trueb, 1986). To facilitate the production of offspring, one form of sexual selection, male-male competition, has evolved. This behavioral pattern has been revealed in the mating behavior of certain frog species, such as wood frogs (*Rana sylvatica*), which have relatively short, but intense breeding seasons (Berven, 1981). When male-male competition is in effect, large dominant males aggressively force smaller, less dominant males into areas where those males are less likely to find a female. In more drastic encounters, several aggressive males may clasp onto a single female forming a "mating ball" (Phillips and Wade, 1990). Apparently, these mating balls can result in the death of female wood frogs, as was observed in populations from Indiana (Phillips and Wade, 1990) and Michigan (Howard, 1980). At the Indiana breeding site, only two females were found dead, and only three females died at the Michigan site. In the following, we report on high breeding mortality in a wood frog population from northcentral Arkansas and suggest possible causes of the mortality.

Throughout its range, the wood frog, the most boreal of all the North American ranid frogs, is well known for its brief, explosive breeding activity which typically occurs in late winter or early spring (Martof, 1970). In northern Arkansas, breeding characteristically follows heavy, late winter (primarily February), rainfall (Trauth et al., 1989, 1995; Cartwright et al., 1998); wood frogs migrate to temporary or permanent pools of water (e.g., woodland ponds and man-made wildlife ponds) where oviposition of eggs occurs. At several ponds, relatively, large communal adult aggregations have been observed.

Monitoring selected wood frog breeding populations in the Sylamore Ranger District (SRD) of the Ozark National Forest of northcentral Arkansas began in 1987. Over a span of 14 years, the timing and duration of the breeding season has varied only slightly over the years (Cartwright et al., 1998). On occasion, we have observed the carcasses of a few dead wood frogs within these ponds; however, in those instances, no collection of dead frogs occurred.

On the night of 26 February 2000 a survey of a large woodland pond (commonly called Stout Pond) was conducted between 1800 and 2030 h, and a total of 140 dead adult *R. sylvatica* was found. The pond lies within a large depression in an oak-hickory forest in Stone County (T16N, R12W, S30) just south of St. Hwy 14 and ca. 1.12 km east of the Baxter-Stone county line. The pond was partially filled with water (maximum depth 40 cm) following rains on the 25th and 26th with rainfall totals of 2.44 and 3.20 cm, respectively, as recorded at Mountain View. The pond was searched repeatedly by criss-crossing and walking the perimeter during the deafening calls of approximately 850 male wood frogs. Ecological associates included spring peepers (*Pseudacris crucifer*), ringed salamanders (*Ambystoma annulatum*), spotted salamanders (*A. maculatum*), and central newts (*Notophthalmus viridescens louisianensis*). Because very few non-amplectant females were observed and because 100s of wood frog egg masses had already been laid in all areas of the pond, we assumed that most of the breeding activity had occurred on the night of the 25th. This presumption is bolstered by the condition of the dead frogs; i.e., many showed more advanced signs of morbidity than others, although some had obviously died very recently prior to collection.

The dead frogs were transported to the herpetology laboratory at Arkansas State University on the night of the 26th and were fixed in 10% formalin. Later, all specimens were transferred to 70% ethanol for permanent storage. The following body size data were gleaned from these specimens: average female snout-vent length (SVL) = 60.1 mm (range, 54.7 - 66.0 mm) in 58 of 65 individuals; average male SVL = 51.2 mm (range, 45.9 - 58.2 mm) in 67 of 75 individuals.

The condition of the specimens varied from little or no body damage to total dismemberment. Many frogs exhibited obvious signs of avian predation, and some had even been partially scavenged. The types of injuries sustained by both sexes were mostly puncture wounds which caused partial-to-complete abdominal wall rupturing in many specimens. In 40 females (61.5%), small tears or tri-cornered puncture wounds were evident in the skin just behind the

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head, on the back, and laterally along the external body wall. This was accompanied by, in many individuals, a protrusion of oviducts, eggs or both from the lateral wounds. Some females were missing one or the other hind leg. We found three peculiar instances of extra-coelomic displacement of ova occurring outside of the coelomic cavity. Ova were displaced into the subcutaneous spaces in the groin, lower back , thighs, and axillary region (Fig. 1). This observation is best explained as a result of a tearing or puncturing of the abdominal wall so as to allow ova previously ovulated to move freely or to be squeezed out of the coelom and into interstitial spaces. Forty-nine males (65.3%) had similar dorsal piercing, wounds near the head and some along the back. Because several feathers (unidentifiable to species) were found floating on the surface of the water, we, therefore, tentatively conclude that an avian predator (e.g., a wading bird, Order Ciconiformes) likely caused the majority of puncture wounds.

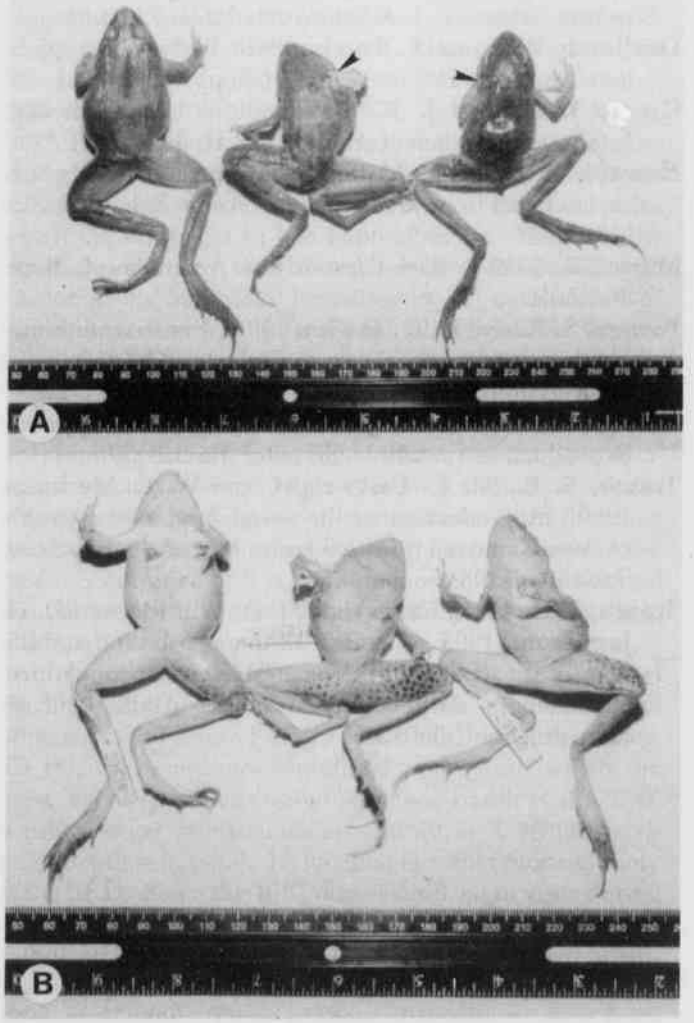

Fig. 1. Extra-coelomic eggs of *Rana sylvatica*. A. Dorsal view of specimens (left to right, ASUMZ 23638-40); arrows point to puncture wound areas. B. Ventral view of specimens in A reveals eggs lying subcutaneously in the thigh of ASUMZ 23638; in the right axillary region, groin, and thighs of ASUMZ 23639, and in the left thigh of ASUMZ 23640.

Although wood frog mortality could have resulted directly from the piercing wounds inflicted by a bird, the significance of death stemming from mating balls is the likely cause of death and cannot be over emphasized. Females that die in mating balls apparently do not reproduce, as was observed by Howard (1980) in a Michigan population (see below for comments on gravid specimens). Even though further collection data are warranted, it is probable that females weakened or dying in mating balls express lower vitality levels due possibly to agedness or pathogen/parasite exposure. This would make them highly susceptible to avian or other predators (e.g., raccoons, Trauth et al., 1995). Persistence of vitality late into life and resistence to pathogens and parasites are probably inherited traits (Greer and Baker, 1992). Weakened or diseased organisms are typically less active than healthier ones (Greer and Baker, 1992) and would be more likely to succumb to attacks by predators. Reduced activity levels can result in reduced muscle performance (Powers and Howley, 1990). Consequently, unhealthy females with reduced muscle tone would be less capable of resisting the grasp of a male or several males and, accordingly, would be less capable of avoiding predatory aquatic birds. Males who grasp weakened females "violently" during amplexus may reduce their own fitness as well if they remain amplexed with these females following the female's death.

Although it is unclear whether the male's strong grasp combined with a female's reduced strength could result in peritoneal ruptures leading to egg extrusions, 58 dead females (89.2%) were gravid (and, thus, were removed from the breeding population). In addition, four males were found amplexed to dead females. This should, coincidentally, reduce resource competition between adult frogs and between developing larvae during the ensuing summer. As stated previously, many of the observed dead females had skin ruptures in addition to extra-coelomic egg extrusions. Further data collection will be necessary in order to determine if these symptoms were initially the result from male grasping or secondarily by predators/scavengers foraging on dead or dying frogs. If egg extrusions are due to male grasping, female mortality via this mechanism may be even more prevalent than our data suggest.

Male grasping may be an effective mate health evaluative mechanism. If males are capable of recognizing female muscle tone, or female death, they could release the amplexed female (explaining the prevalence of dead

females without amplexed males) and select a new one, even if that means fighting off a currently amplectant male (explaining numerous observations in the past of multiple males amplexing single females in wood frog populations). The more capable a male is at utilizing this mechanism, the better he can avoid investing gamete currency in poor females during an explosive breeding chorus where females are plentiful and male-male competition is relatively low. Males incapable of recognizing the death of their amplectant female probably continue swimming around the pond grasping their dead mate (explaining observations of live males grasping dead females). The living male continues to grasp the female in anticipation of egg release until his energy stores are exhausted, at which time he may be pulled under the water by the dead female and drowned (explaining the observations of some dead pairs in amplexus). This scenario would be highly selective against male phenotypes incapable of recognizing the death of their amplexed mate.

The population characteristics of the wood frog chorus in our pond, though, was such that sex ratios at the onset of mating activity may have been close to 1:1 (based on the number of egg masses present). At first, this may greatly reduce male-male competition and provide the opportunity for males to evaluate females resulting in high ovipositional success. However, with the overwhelming preponderance of males (as witnessed during the second night of breeding), high male-male competition for late-breeding females likely culminated in the weakening/deaths of both sexes.

In conclusion, a total of 140 dead wood frogs (*Rana sylvatica*) was collected in a flooded, woodland depression/pond in the Ozark National Forest of northcentral Arkansas following two days (25-26 February 2000) of heavy rains and intensive breeding activity by this species. Among the dead females, 89.2% (58 of 65) were gravid individuals; four of these females were found in amplexus with live males, and three females exhibited extra-coelomic egg extrusion. Signs of avian predation were noted (61.5 and 65.3% in females and males, respectively) and could have caused the death of some individuals. Breeding mortality in wood frogs has been reported before in the literature (northern Indiana and central Michigan) and may help explain similar unpublished observations in a Virginia population (Keith Berven, pers. comm.). The suspected cause of death in females, as suggested by previous authors, could have resulted from abdominal crushing related to the intense "mating balls" formed by multiple-amplectant males on a single female. Likewise, this type of mating behavior could also cause reduced male vitality, thus explaining the observed dead males.

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