



Influence of Temperature and Water Potential on Survival of Hatched, Terrestrial Larvae of the Frog *Pseudophryne bibronii*

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HERPETOLOGICAL NOTES

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INFLUENCE OF TEMPERATURE AND WATER POTENTIAL ON SURVIVAL OF HATCHED, TERRESTRIAL LARVAE OF THE FROG *PSEUDOPHRYNE BIBRONII*.—In autumn, *Pseudophryne bibronii* lays eggs on land in moist areas beneath stones, thick vegetation, or other surface objects that are flooded later in winter. The embryos develop inside the jelly capsules to Gosner (1960) stage 26–28 when they are capable of hatching if the nest is flooded (Woodruff, 1976; Bradford and Seymour, 1985). Development of the larvae continues after hatching, and successful metamorphosis depends on the availability of standing water. However, we have occasionally observed hatched larvae in the field where standing water had disappeared. These larvae rested on moist soil under stones where they were closely clustered together. Because survival of these larvae clearly depended on future rainfall, we became interested in how long they could survive on land. Our experiments controlled two factors, temperature and water potential of the substrate, which we felt were of critical importance to survival.

Material and methods.—We collected 10 clutches of eggs at different developmental stages from sites in the Mount Lofty Ranges, near Adelaide, South Australia, in May 1987. We cleaned the eggs and incubated them at 12 C on Whatman No. 1 filter paper saturated with distilled water (Bradford and Seymour, 1985). When the embryos reached Gosner stage 28, in July 1987, we initiated hatching by submerging the eggs in distilled water overnight. We randomly divided the hatchlings into eight groups of 20 individuals each and distributed the groups in an array of two water potentials (0 and –25 kilopascals (kPa)) at each of four temperatures (7, 12, 17, 22 C). These conditions bracket the environments of natural clutches (Bradford and Seymour, 1985; Seymour and Bradford, 1987). Temperatures under a stone at the field site ranged between 8 and 23.5 C at the time of the study.

Larvae were placed on stacks of 20 Whatman No. 1 filter papers that were either resting in a pool of free water (0 kPa) or wetted to a specific

water content that was known to produce a water potential of –25 kPa. The relationship between water content and water potential of the filter paper had been previously determined with a pressure plate apparatus (Seymour and Piiper, 1988). To keep the humidity around the embryos practically saturated, filters were placed in closed plastic containers with a few minute holes in the cover. We weighed the containers and replaced any evaporative water loss when it appeared. The number of living larvae was determined periodically by touching them with a plastic spoon. If no movement was elicited, we confirmed death by submerging them in water and checking for any signs of life.

Results.—Both water potential and temperature affected survival times (Fig. 1). At a water potential of –25 kPa, the larvae survived for less than 5 d at all temperatures. Survival at 0 kPa was significantly longer than at –25 kPa and some individuals survived up to 21 d at 12 C, close to the normal incubation temperature.

Survival of the 0 kPa group was directly influenced by temperature. Probit analysis for this group showed LD₅₀ values of 6.9, 7.6, 14.6, and 53.8 d at 7, 12, 17, and 22 C, respectively, all significantly different ($P < 0.05$). Data at –25 kPa were insufficient for Probit analysis, but there was a similar temperature effect.

The larvae at 0 kPa appeared similar to larvae from the natural environment. They glistened and were well formed. On the other hand, larvae at –25 kPa were duller and appeared somewhat dehydrated.

Discussion.—The terrestrial eggs of *P. bibronii* are well adapted to survive long periods of dry weather. After reaching the hatching stage, the eggs can remain alive for over 100 d at 12 C while they wait for sufficient rain (Bradford and Seymour, 1985). Hatching occurs only after flooding of the eggs for several hours which tends to ensure that larvae emerge into sufficient standing water to complete metamorphosis (Bradford and Seymour, 1988b). Our study demonstrates that if larvae hatch, but are unable to remain in standing water, they are still able to survive for extended periods if the soil water potential remains high. This ability has obvious selective value because the pattern of rainfall in southern Australia is inconsistent

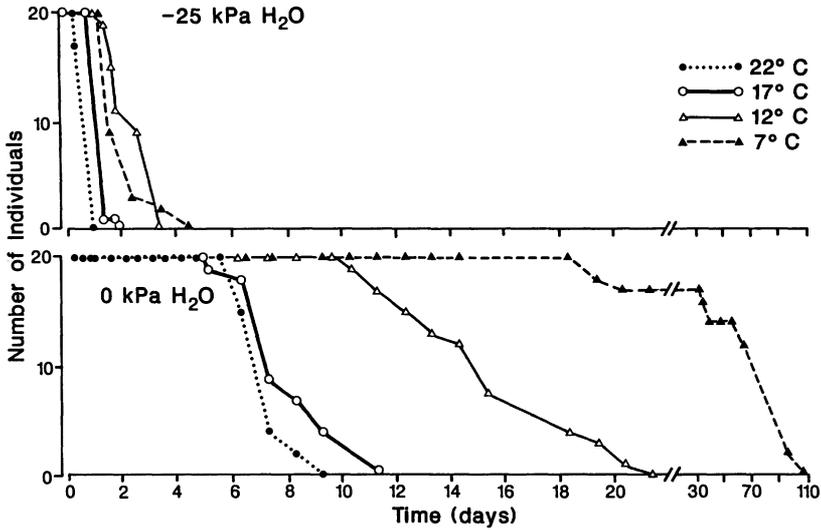


Fig. 1. Number of living terrestrial larvae of *Pseudophryne bibronii* kept on filter paper at 0 and -25 kPa water potential and selected temperatures.

during the larval stages of development (Climate of Australia, 1983).

The cause of death of terrestrial larvae is not known. Starvation is ruled out because aquatic larvae can live for about 100 d without food at 12 C (Bradford and Seymour, 1985), but the terrestrial larvae died within 21 d at the same temperature (Fig. 1). Moreover, aquatic larvae are markedly more active and would have higher rates of energy consumption. Osmotic and ionic regulation probably are not important factors because, at 0 kPa water potential, the availability of water to terrestrial larvae is theoretically similar to that available to totally aquatic larvae. Considerable water must have been absorbed osmotically through the skin and eliminated via the kidneys. The apparent dehydration on substrates of -25 kPa water potential obviously affected survival (Fig. 1), but this is not the entire answer because unhatched eggs are known to survive extended periods at water potentials of -50 kPa (Bradford and Seymour, 1988a). Nitrogen balance may be an additional factor leading to death if the larvae were poisoned by urea accumulating in the water held in the filter paper. Impaired respiration may have also occurred. In contrast to aquatic larvae that use gills for gas exchange, terrestrial larvae have only the skin. In aquatic larvae, rate of oxygen consumption doubles after hatching (Bradford and Seymour, 1985). If terrestrial larvae also demand this high rate of oxygen

consumption, but cutaneous exchange becomes limiting, development may become retarded, leading ultimately to death. Problems of nitrogen balance or gas exchange would lead to earlier deaths at higher temperature, in agreement with the data.

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TEMPORAL VARIATION IN THE DISPERSION OF A TROPICAL ANURAN.—Long-term observations of a riverine population of harlequin frogs, *Atelopus varius* (Bufonidae), in Costa Rica suggest that the frogs aggregate along the river during the dry season, but distribute themselves more uniformly during the wet season (Crump and Pounds, pers. obs.). Frogs in aggregations during the dry season had a higher (per frog) probability of attack by a sarcophagid fly, *Notochaeta bufonivora* (Pounds and Crump, 1987). Female flies larviposit onto the frogs; the fly larvae feed internally, and cause death within a few days (Crump and Pounds, 1985). Because these frogs are aposematically colored and contain a potent nerve poison (tetrodotoxin) in their integument (Kim et al., 1975) they probably have few predators other than these flies. Thus predation by *Notochaeta* may be an important source of mortality at our study site. Earlier, we hypothesized that frogs aggregated within the habitat, despite the increased risk of attack, because of variation in patch quality (Pounds and Crump, 1987). We presented evidence that frog density was higher in wetter patches, specifically in waterfall spray zones. In the present paper, we evaluate this hypothesis by examining variation in patterns of dispersion along a temporal gradient of habitat patchiness (number of weeks elapsed since the beginning of the dry season). If clumping results from habitat selection in a

patchy environment, then the degree of clumping should vary with the degree of patchiness. As the dry season progresses and the habitat becomes increasingly patchy, frogs should exhibit a more clumped distribution pattern. Because frog density and territoriality (males were territorial during the first quarter of the dry season) also may affect dispersion (Fretwell and Lucas, 1970), we also examine their effects in our analysis.

Study system and methods.—We conducted this study near Santa Elena, Puntarenas Province, Costa Rica, along the headwaters of the Rio Lagarto, a Pacific slope stream in the Cordillera de Tilaran mountains. At our study site (1140 m elev), the stream averaged about 3 m in width, contained frequent waterfalls, and was flanked by riparian forest. Because of a rain-shadow effect, the study site experienced a marked dry season from mid-Nov. to late May. A gradual decline in stream volume and a gradual contraction of waterfall spray zones during the dry season were accompanied by progressive drying of adjacent habitat and accentuation of differences between wet and dry areas. Consequently, patchiness of the hydric environment varied along a temporal gradient, ranging from a uniformly wet habitat (at the end of the wet season) to a mosaic of extremely dry patches interspersed with wetter areas (at the end of the dry season) (Crump and Pounds, pers. obs.). For a more detailed description of the study site, see Crump and Pounds (1985).

Harlequin frogs were abundant, averaging as many as 1/1.8 m of stream. Diurnally active, they typically sat fully exposed on boulders and rock faces within 3 m of the stream margin, yet they were essentially terrestrial, rarely entering water voluntarily. During the course of our study, breeding behavior of harlequin frogs was entrained on seasonal weather patterns (Crump, 1988). Male harlequin frogs defended territories against other males during the 6 mo wet season, which encompassed pre-breeding and breeding periods, and the early dry season (through Dec.). In contrast, during the remainder of the dry season, males did not display intrasexual aggression (Crump, 1988).

From Aug. 1982-June 1983, we performed weekly censuses (45 in all) along both sides of a 200 m length of the Rio Lagarto. Each side of the stream was subdivided into 40 adjacent quadrats, each 5 × 5 m. During these censuses, we marked (toe-clipped) 751 adult and subadult