

Juvenile Frogs Compensate for Small Metamorph Size with Terrestrial Growth: Overcoming the Effects of Larval Density and Insecticide Exposure

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New Species of *Telmatobius* (Anura: Leptodactylidae) from Humid Paramo of Peru and Bolivia

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ABSTRACT.—A new species of *Telmatobius* is described from humid paramo of southeastern Peru and western Bolivia. Males of the new species differ from those of *Telmatobius sanborni*, the only other species of *Telmatobius* in the area, mainly by lacking hypertrophied forearms and having smaller nuptial spicules; in addition, color patterns are different. The apparent low diversity of forest *Telmatobius* in southern Peru may be an artifact of lack of research on this group of frogs in this region.

Considerable effort has been expended in recent years to understand the diversity, evolution, and conservation needs of frogs of the genus *Telmatobius* (Lavilla and De la Riva, 2005). Although the number of species of the genus has risen from 30 species known in the 1980s (Frost, 1985) to 55 species recognized currently (Lavilla, 2005), several threats are affecting these interesting frogs; hence, their diversity might be reduced in the near future. Particularly, chytridiomycosis may be responsible of local extinctions or declines in some species (Merino-Viteri et al., 2005; Seimon et al., 2005). Unfortunately, as is the case with other anurans, this phenomenon is taking place while we are still far from having a complete understanding of the species richness, distribution, biogeography, and phylogenetic relationships of members of the genus *Telmatobius*. Simultaneously with some initiatives trying to improve the knowledge on the conservation status of *Telmatobius* and the reasons for the decline or extinction of certain populations, taxonomic research continues to add species new to science.

Humid forests and paramos on the Andean slopes of Peru and Bolivia support a rich anuran fauna. In these communities, frogs of the genus *Telmatobius* are usually present, but their actual species diversity is still poorly known. Lehr (2005) recognized 22 species of *Telmatobius* in Peru; at least nine of them are forest dwellers (Wiens, 1993; Lehr, 2005). Most of these Peruvian forest species occur in the northern part of the country; two (*Telmatobius brevirostris*, *Telmatobius punctatus*) occur in central Peru (Departamento de Huánuco), and only one, *Telmatobius sanborni*,

has been reported from the humid Andean forests in southern Peru (Departamento de Puno; De la Riva, 2005; Lehr, 2005). In Bolivia, 14 species of *Telmatobius* occur; nine of them are forest or humid paramo inhabitants (De la Riva, 2005). Two of these nine species, *T. sanborni* and an undescribed species, were found close to the Peruvian border during herpetological surveys carried out in recent years in the Cordillera de Apolobamba. Further examination of unidentified *Telmatobius* in the collection of the University of Kansas obtained during the 1970s in southern Peru, revealed specimens similar to those of the unnamed species from Bolivia. The purpose of this paper is to contribute to the knowledge of the genus *Telmatobius* in Peru and Bolivia by describing this new species.

MATERIALS AND METHODS

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Drawings were made using a camera lucida. The order of characters in the diagnosis follows De la Riva (2005), and those of the description follow De la Riva and Harvey (2003). Comparisons between the new species and other Bolivian and Peruvian forms are based on the information provided by De la Riva (2005) and Lehr (2005). Webbing formulae are those of Savage and Heyer (1967) as modified by Myers and Duellman (1982). Specimens were measured with a digital caliper to the nearest 0.01 mm, but, following Hayek et al (2001), we rounded all measurements to one decimal point. Museum abbreviations are CBF, Colección Boliviana de Fauna, La Paz, Bolivia; KU, Natural History Museum, University of Kansas, Lawrence, Kansas, USA; and MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain.

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FIG. 1. Dorsal (above) and ventral (below) views of *Telmatobius timens* sp. nov. (left, CBF 5674, adult female, 61 mm in SVL; right, CBF 5679, holotype, adult male 53.6 mm in SVL).

SYSTEMATICS

Telmatobius timens sp. nov.

Figures 1–3

Holotype.—CBF 5679, an adult male, collected at Valle de Tojoloque, Provincia Franz Tamayo, Departamento de La Paz, Bolivia, 14°44'33.5"S, 69°01'10"W, 3750 m, collected on 19 October 1999 by James Aparicio.

Paratypes.—CBF 5677 and MNCN 42017, males; CBF 5672–74 and MNCN 42018, females; and CBF 5675 and CBF 5680, juveniles, all from the vicinity of the type locality, collected by J. Aparicio between 19 and 23 October 1999. KU 139040–41, immature and juvenile respectively, from north slope Abra Acanacú, 27 km north-northeast (by road) of Paucartambo, Departamento de Cusco, Peru, 3450 m, collected on 16



FIG. 2. *Telmatobius timens* sp. nov., adult male (KU 162958) from Abra Acanacú, (KU slide 5000; photo by W. E. Duellman).

January 1971 by W. E. Duellman and T. H. Fritts; KU162958-89, adult males from Abra Acanacú, 25 km north-northeast (by road) of Paucartambo, Departamento de Cusco, Peru, 13°12'S, 71°42'W, 3520 m, collected on 7 February 1975 by W. E. Duellman and L. Trueb.

Diagnosis.—*Telmatobius timens* can be distinguished readily from any other species of *Telmatobius* by the following combination of characters: (1) snout-vent length (SVL) of males to 61.0 mm, females to 58.3 mm; (2) head in lateral profile moderately high, with short, rounded snout; (3) snout rounded in dorsal view; (4) lips not flared; (5) postcommisural gland present; (6) tympanum absent; supratympanic fold short; (7) forelimb of males moderately robust, without humeral spine; (8) base of prepollex broadened posteriorly, bearing nuptial pad barely in contact with the inner palmar tubercle; nuptial spicules moderately large, not closely arranged; (9) toes from two-thirds to fully webbed; plantar surface smooth; (10) tarsal fold weak or absent; (11) dorsal skin with scattered flat pustules; (12) dorsum gray, with dark gray dots; (13) venter gray, ventral surfaces of limbs orange or yellow with brown blotches; and (14) iris brown.

Species of *Telmatobius* usually share a great number of characters and show considerable variation, but typically there are one or two characters that combined with others allow determination. In the following comparisons, only the most relevant characters are considered. Because species of *Telmatobius* are highly endemic and restricted to particular habitats, comparisons are not made with highland, puna species (except *T. jelskii* and *T. marmoratus*; see below), with non Peruvian-Bolivian species, or with forest and

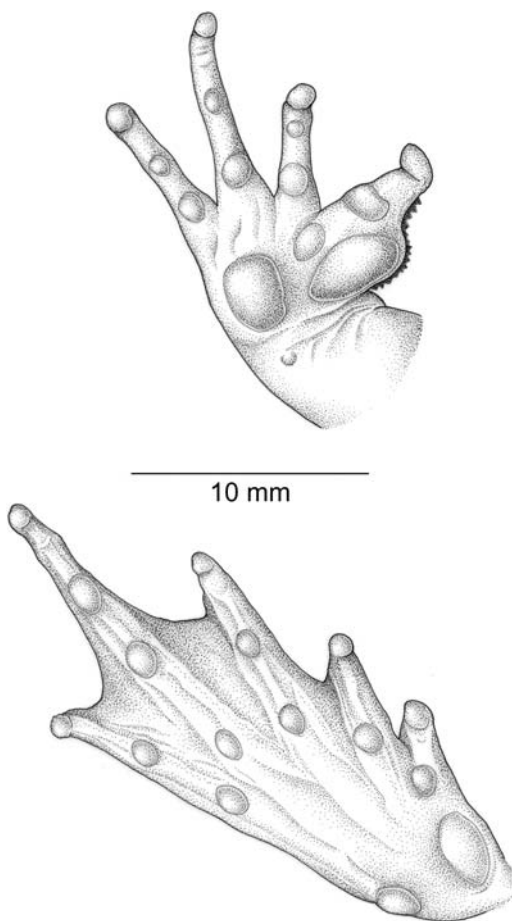


FIG. 3. Plantar and palmar surfaces of *Telmatobius timens* sp. nov. (holotype, CBF 5679).

paramo species from northern Peru, which occur a considerable distance from *T. timens*.

Telmatobius timens differs from *Telmatobius sanborni* in that males possess nonhypertrophied forelimbs (hypertrophied in *T. sanborni*), small nuptial spicules (large), gray dorsum with dark gray dots (green or grayish-green with or without black irregular blotches), and ventral surfaces of limbs with orange or yellow and brown blotches (yellow or orange color mostly absent); additionally, the toes of *T. timens* have far more webbing than those of *T. sanborni*. No other described species of *Telmatobius* are known from the forests and humid paramos of the Andean slopes of southeast Peru. *Telmatobius bolivianus* and *Telmatobius verrucosus* occur in northwest Bolivia (Departamento de La Paz), but these species have not been found in sympatry with *T. timens*. *Telmatobius timens* is distinguished from *T. bolivianus* in that male lack a protruding humeral spine (present in *T. bolivianus*) and the

nuptial pads are composed of moderately large and not closely arranged spicules (spicules minute and closely arranged). *Telmatobius timens* differs from *T. verrucosus* in possessing dorsal skin with scattered flat pustules (dorsal skin rugose or tuberculate in *T. verrucosus*) and moderately large nuptial spicules (large and long) and nonhypertrophied forelimbs in males (hypertrophied). Several forest *Telmatobius* exist in central Bolivia (Departamentos de Cochabamba and Santa Cruz), far from the range of *T. timens*, and all of them are easy to distinguish. *Telmatobius edaphonastes* is uniformly dark brown and has no more than vestigial webbing. *Telmatobius sibiricus* has a dorsal pattern consisting of large dark irregular blotches, barred upper lips, and nuptial excrescences made up of minute, closely arranged spicules. *Telmatobius simonsi* is similar to *T. sibiricus* and, additionally, differs from *T. timens* in possessing minute keratinized spicules on the soles of the feet. *Telmatobius yuracare* differs from *T. timens* in having a protruding humeral spine in males. *Telmatobius* sp. nov., from Cochabamba and the easternmost part of Departamento de La Paz, has nuptial pads composed of small spicules and a greenish-brown dorsum with small black and yellow flecks (De la Riva, 2005). In Peru, the two forest species that occur closest to *T. timens* (but still more than 600 km airline distance) are *Telmatobius brevirostris* and *Telmatobius punctatus*. *Telmatobius timens* can be distinguished from *T. brevirostris* mainly by having dorsal skin with scattered flat pustules (dorsal skin smooth in *T. brevirostris*) and nuptial pads bearing moderately large and not closely arranged spicules (spicules minute and closely arranged). *Telmatobius timens* differs from *T. punctatus* in possessing dark gray dots on a gray dorsum (dark brown to olive dorsum with yellow reticulations or small yellow blotches).

One highland species, *T. marmoratus*, lives in the same general area of *T. timens*, both in Peru and Bolivia, and the two species might be found in the same valleys; however, *T. marmoratus* always inhabits puna or dry subparamo between 3100 and 4500 m and never has been found in humid forested areas (De la Riva, 2005; Lehr, 2005). *Telmatobius timens* is readily distinguished from *T. marmoratus* by having nuptial pads bearing moderately large and not closely arranged spicules (small, closely arranged spicules in *T. marmoratus*), lips not flared (markedly flared), and ventral surfaces of limbs orange or yellow with brown blotches (yellow or orange coloration absent). Likewise, *T. jelskii* is another mostly highland species that extends into some valleys; the southernmost part of its range approaches that of *T. timens* (Lehr, 2005). *Telmatobius timens* is readily distinguishable from *T.*

jelskii by having lips not flared (flared in *T. jelskii*), nuptial pads bearing moderately large spicules (small) and head moderately high (flattened).

Description of the Holotype.—An adult male, medium-sized, robust, SVL 53.6 (Fig. 1). Head length (measured from rictus to tip of snout) 27.6% of SVL, wider than long; head width (measured at level of rictus) 33.9% of SVL; head length 81.2% of head width; head moderately high in lateral profile, subtriangular in dorsal view, with round, short snout; nostrils small, not protruding, oriented dorsolaterally, closer to tip of snout than to eye; internarial region convex; eye large, its length 35.2% of head length, oriented anterolaterally; canthus rostralis indistinct, loreal region slightly concave; lips not flared; maxilla and premaxillae with small pointed teeth, embedded in the labial mucosa; dentigerous processes of vomers straight, bearing small fanglike teeth, between small, oval choanae; tongue rounded, attached anteriorly to floor of mouth, free posteriorly for about one-third of its length; vocal slits absent; tympanum and tympanic annulus absent; supratympanic fold short, extending obliquely from behind eye to posterior margin of postcommisural gland.

Forelimbs moderately robust; relative length of fingers II < I < IV < III; webbing absent between fingers; tips of fingers swollen; fingers lacking lateral fringes; thenar tubercle large, elliptical, depressed; palmar tubercle oval, approximately the same size as thenar tubercle; one subarticular tubercle on the base of each finger and at penultimate phalangeal articulation on Fingers II and IV; one round supernumerary tubercle between thenar and palmar tubercles; palmar surface smooth, without keratinized spicules; base of prepollex broadened posteriorly, bearing nuptial excrescence composed of keratinized, black, small conical spicules loosely arranged, barely reaching posterior margin of thenar tubercle, extending dorsally from base of prepollex to base of distal phalange on Finger I (Fig. 3).

Hind limbs moderately robust; tibia length 51.5% of SVL; tibia length 93.9% of foot length (measured from proximal border of inner metatarsal tubercle to tip of fourth toe); relative length of toes I < II < III < V < IV; webbing formula $II^{1/2}-2III-2^{1/2}III1-3IV2-1V$; webbing extending as lateral fringes to tips of toes; tips of toes swollen, approximately same size as those of fingers; outer metatarsal tubercle oval, approximately one-fourth size of elliptical inner metatarsal tubercle; subarticular tubercles round to oval, well developed; supernumerary tubercles absent; plantar surface smooth, lacking keratinized spicules; tarsal fold absent (Fig. 3).

Skin of dorsum and dorsal surface of head moderately rugose, with low, flat, poorly marked pustules; some small tubercles on head; dorsal

TABLE 1. Measurements of adult *Telmatobius timens* sp. Nov. Abbreviations are HW, head width; HL, head length; ED, eye diameter; IND, Internarial distance; IOD, Interocular distance; END, eye-nostril distance; EW, eyelid width; TL, tibia length; FL, foot length; SVL, snout-vent length.

Number	Sex	HW	HL	ED	IND	IOD	END	EW	TL	FL	SVL
162958KU	M	19.2	16.4	6.1	4.1	4.0	3.1	4.9	25.3	29.8	58.3
162959KU	M	18.8	17.1	6.1	4.1	3.8	3.1	3.8	26.6	29.2	58.2
CBF 5679	M	18.2	14.8	5.2	3.9	4.0	3.3	3.7	27.6	29.4	53.6
MNCN 42017	M	15.0	12.7	4.7	3.2	3.7	2.7	3.2	20.9	22.4	42.2
CBF 5677	M	14.0	12.2	4.5	3.2	3.3	2.8	2.9	21.7	22.2	40.6
CBF 5674	F	18.8	15.4	5.8	4.5	3.9	3.2	4.1	29.6	32.6	61.0
MNCN 42018	F	14.8	12.5	4.6	3.8	3.8	2.5	3.6	21.0	22.5	43.1
CBF 5673	F	14.7	11.9	5.2	3.8	3.7	3.4	3.5	23.0	24.9	43.7
CBF 5672	F	13.2	11.6	4.5	3.6	3.7	2.8	3.2	17.9	19.0	39.1

surface of limbs mostly smooth; skin of venter and ventral surfaces of limbs smooth; keratinized spicules absent from any part of body other than nuptial excrescences; cloacal opening unornamented, located just below dorsal level of thighs.

Coloration of the Holotype.—In alcohol, the holotype is uniformly dark gray above; the venter and throat are pale gray; the ventral surfaces of limbs are dark gray with irregular cream blotches. The palmar and plantar surfaces are dark gray with the tubercles pale gray. In life, the general color pattern was similar, but the cream blotches on limbs were yellow.

Measurements of the Holotype.—Measurements in millimeters. SVL 53.6; head width 18.2; head length 14.8; eye diameter 5.2; internarial distance 3.9; interocular distance 4.0; eye-nostril distance 3.3; eyelid width 3.7; tibia length 27.6; foot length 29.4.

Variation.—Bolivian specimens are quite uniform in color pattern; the extension of the yellow-orange blotches of the ventral surfaces of limbs is variable, from almost no blotches to yellow coloration covering most of the lower surfaces of thighs. The dorsum often has a pattern consisting of dark gray rounded or irregular blotches; this pattern is more marked in the specimens from Peru (Fig. 2). The following color in life descriptions for Peruvian specimens are based on field notes by W. E. Duellman from 16 January 1971 and 7 February 1975, respectively: KU139040–41 exhibited “dorsum black with dull olive-green mottling or reticulations; venter dull gray with black spots and reticulations; dull yellow in axilla and on ventral surfaces of thighs; iris dull brown”; KU162958–59 exhibited “dorsum dull dark brown (with pale green flacks in smallest individual); throat, chest and ventral surfaces of limbs dull lavender; ventral surfaces of limbs spotted with pale orange in some individuals; belly bluish-gray; iris dull reddish-brown; eye-shine orange-red.”

In general, webbing is quite a variable character in *Telmatobius*, and Peruvian specimens of

T. timens have more extensive webbing and a more marked tarsal fold than Bolivian ones. Ranges of some morphometric ratios of nine adults of the type series are head length 80.9–90.7% of head width; head length 23.3–30.2% of SVL; eye-nostril distance 50.6–66.4% of eye length; tibia length 43.2–53.3% of SVL; tibia length 84.6–97.5% of foot length (see Table 1).

Ecology and Distribution.—This species is known only from the localities described for the holotype and paratypes in Bolivia and Peru (Fig. 4). These localities are above the upper limit of the cloud forest or elfin forest, on the Amazonian slopes of the Andes. The Bolivian locality, Valle de Tojoloque, is about four hours (by foot) from the small community of Quiara, and it lies in an area of humid paramo. The Tojoloque River is a tributary of the Pelechuco River, which belongs to the Beni basin and flows into the Amazonian lowlands. The valley is deep and humid, with an elevational range approximately between 3000 and 4200 m. The tree line is around 3500 m a.s.l. The type locality is in the Cordillera de Apolobamba, within the Area Natural de Manejo Integrado Apolobamba, a protected zone of 483,743 ha with an elevational range of 800–6200 m, and encompassing puna highlands to montane and lowland rain forest (SERNAP, 2000). The two Peruvian localities where *T. timens* has been found are close to each other at Abra Acanacú, a pass in the Cadena de Paucartambo, on the northwestern end of the Cordillera de Carabaya. Duellman (1978) described the locality and provided a detailed map of the area. The airline distance between Tojoloque (Bolivia) and Abra Acanacú (Peru) is approximately 300 km. The species presumably is present in the intervening area, mostly in the poorly surveyed Peruvian Departamento de Puno. Although *T. timens* has not been collected in cloud forest, this possibility should not be discarded, for species of *Telmatobius* that occur in humid paramos or the upper limit of the “ceja de monte” (e.g., *T. sanborni*)

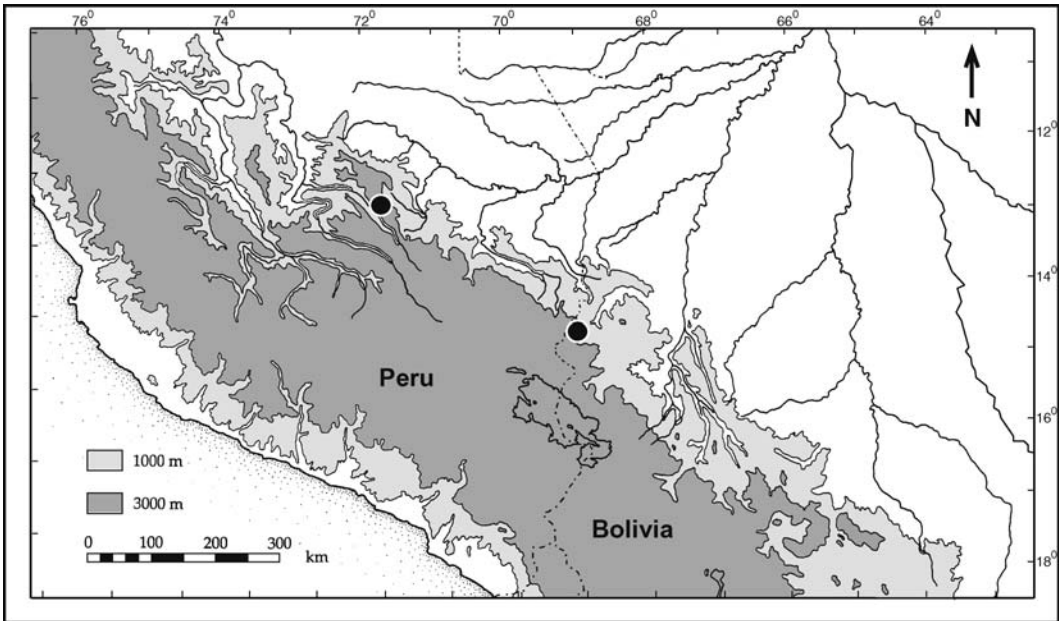


FIG. 4. Distribution of *Telmatobius timens* sp. nov. in Bolivia and Peru.

often inhabit both types of ecosystems (De la Riva, 2005).

The holotype was found at night in a small pool 50 cm in depth. The Bolivian paratypes were collected sitting on rocks in the Tojoloque River and at a small tributary, at elevations between 3550 and 3600 m. At Abra Acanacú, frogs were in paramo, sitting on rocks, ground, in crevices, and in moss adjacent to streams at night; at this locality, *T. timens* was found with *Gastrotheca excubitor*, *Gastrotheca marsupiata*, *Phrynopis peruvianus*, and *Phrynopis cophites* (W. E. Duellman, pers. comm.).

Etymology.—The specific name, the Latin word *timens* means frightened, scared, or alarmed. The name is used in references to the possible arrival of the fungal infectious disease to Bolivia. Chytridiomycosis has already affected other species of *Telmatobius* in Ecuador and Peru.

DISCUSSION

As stated above, the *Telmatobius* fauna of the humid Andean forests and humid paramos of southern Peru is poorly known. Only *T. sanborni* and *T. timens* have been reported from departments of Puno and Cusco, and they are the only two paramo-forest species reported from the huge region extending some 800 km (airline) from Huánuco to the Bolivian border. In contrast, nine paramo-forest species occur in northern and central Peru (Wiens, 1993; Lehr, 2005) and nine in Bolivia, where up to three species can be found at

a single locality (De la Riva, 2005). It might seem that the Amazonian Andean slopes of the Peruvian departments of Pasco, Junín, Ayacucho, Apurímac, Cusco, and Puno represent a gap in the distribution of *Telmatobius* forest-dwelling species, because no forest species have been reported in the first four departments. However, this apparent low diversity is an artifact, as suggested by specimens deposited in collections and unstudied for years. Indeed, a high diversity is expected because species of *Telmatobius* are highly endemic and species turnover takes place within a few tens or, at most, hundreds of kilometers (see Wiens, 1993; De la Riva, 2005; Lehr, 2005). Many specimens of *Telmatobius* in the collection at the University of Kansas Natural History Museum from many localities in southern Peru have not been assigned to any described species. This material presumably consists of several species whose study will require careful comparisons, revision of type specimens and nomenclature, the use of field data, and, in some cases, fresh additional material to delimit species and unravel the taxonomic complexity of the populations involved.

The southern limits of distribution of *T. jelskii* and *T. brevirostris*, two variable species formerly considered polytypic, are not well known (Sinsch et al., 1995); this fact has greatly contributed to the unclear taxonomic situation of the forest *Telmatobius* of southern Peru. *Telmatobius jelskii* is mostly a highland species that occurs in the departments of Ayacucho, Huancavelica and

Junín (Rodríguez et al., 1993). Ecologically it is like the parapatric *Telmatobius marmoratus*, which is found more to the south (Vellard, 1951, 1955). Vellard (1955) proposed four subspecies for *T. jelskii*, which were invalidated by Sinsch et al. (1995). Intraspecific variation in *T. jelskii*, coupled with the different altitudes and habitats where the species occurs, make it difficult to identify certain populations. Franco et al. (1999) tentatively identified as *T. jelskii* specimens of *Telmatobius* from Machu Picchu and some localities nearby in the Departamento de Cusco. The taxonomic status of these populations requires additional work, including more studies on variation, distribution, and the specific limits of *T. jelskii*. However, the northern distribution of *T. sanborni* is unknown; specimens identified as *T. sanborni* have been collected in the Departamento de Cusco as far north as Amparaes (13°10'S, 71°57'W; KU196616, 196626) and Abra Málaga (13°09'S, 72°20'W; KU173401–02).

Chytridiomycosis is an emerging infectious disease that is destroying amphibian species populations throughout the world (Stuart et al., 2004). In the Neotropics, it seems to be progressing from north to south (Young et al., 2001; Lips et al., 2004). Infections by chytrid fungus have probably driven to extinction the three Ecuadorian species of *Telmatobius* (Merino-Viteri et al., 2005). Little is known about the situation in northern and central Peru, but chytrids have already been detected in *T. marmoratus* in Cusco (Seimon et al., 2005). It remains to be seen whether the taxonomic diversity of *Telmatobius* in southern Peru can be ascertained before this new plague destroys these anurans.

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Juvenile Frogs Compensate for Small Metamorph Size with Terrestrial Growth: Overcoming the Effects of Larval Density and Insecticide Exposure

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ABSTRACT.—I reared four species of anurans (*Rana sphenoccephala* [Southern Leopard Frog], *Rana blairi* [Plains Leopard Frog], *Rana clamitans* [Green Frog], and *Bufo woodhousii* [Woodhouse's Toad]) for seven to 12 months in small, outdoor terrestrial enclosures (1 × 2 m) to examine the consequences of larval competition (via density) and contaminant exposure (via the insecticide carbaryl). I added six *Rana clamitans*, eight *Rana sphenoccephala*, eight *Rana blairi*, and 10 *Bufo woodhousii* to terrestrial enclosures shortly after metamorphosis and recaptured them during the following spring. All anurans from low-density ponds were significantly larger than those from high-density ponds, but these size differences did not significantly affect survival to or size at spring emergence. However, *R. sphenoccephala*, *R. blairi*, and *R. clamitans* that survived to spring had been larger at metamorphosis on average than those that did not survive; in contrast, *B. woodhousii* that survived the winter were smaller at metamorphosis on average than those that did not survive. Carbaryl exposure affected mass at metamorphosis of *R. clamitans* and *B. woodhousii* that were added to enclosures, but this difference disappeared or did not increase by spring emergence. Overall, exposure to carbaryl during the larval period did not have any apparent effects on survival or growth during the terrestrial phase. In my study, anurans were able to offset small size at metamorphosis with terrestrial growth, although there was a trend of reduced overwinter survival for rapid species that metamorphosed at a smaller size.

Competition (Scott, 1990), predation (Morin, 1983), and length of the pond hydroperiod

(Semlitsch et al., 1996) are known to regulate larval development of amphibians and to influence mass, time, and survival to metamorphosis (Wilbur, 1987, 1997). Studies suggest these natural factors can influence size at metamorphosis, with larger metamorph size having positive effects on future reproduction, growth,

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and overwinter survival (Semlitsch et al., 1988; Smith, 1987; Berven, 1990). Furthermore, factors such as chemical contaminants influence size at metamorphosis (Boone and Semlitsch, 2002; Boone and James, 2003) and, therefore, may affect terrestrial survival and growth.

Although experimental studies have been conducted in the terrestrial environment (Pechmann, 1995; Chazal and Niewiarowski, 1998; Altwegg, 2003), few studies have followed amphibians from hatching through subsequent development in the terrestrial environment (but see Goater, 1994; Pechmann, 1994; Beck and Congdon, 1999; Parris, 2001; Relyea and Hoverman, 2003). Goater (1994) explicitly tested the ramifications of size at metamorphosis on the terrestrial life stage by rearing *Bufo bufo* (European Toad) at two larval densities resulting in a 48.5% difference in mass at metamorphosis. Subsequent rearing in terrestrial aquaria reduced this mass difference to 15% before winter hibernation under some environmental conditions. Goater (1994) found that under favorable terrestrial conditions, small size at metamorphosis may be quickly overcome, and suggested that metamorph size is a weak predictor of fitness. Growth in the terrestrial environment following metamorphosis may ameliorate the consequences of small size at metamorphosis, and small individuals may quickly reach sizes equal to individuals that had metamorphosed at a large size. However, often studies have found that differences in mass at metamorphosis did not converge after rearing in the terrestrial environment (anurans: Pechmann, 1994; Morey and Reznick, 2001; Altwegg and Reyer, 2003; Relyea and Hoverman, 2003; salamanders: Scott, 1994; Pechmann, 1994, 1995).

The objectives of my study were to determine whether larval exposure to carbaryl (near expected postapplication levels) and larval density had consequences for anuran survival and growth in the terrestrial environment. After cattle tank mesocosm studies designed to test for the effects of natural stressors (including density, as well as predation and pond drying) and carbaryl (Boone and Semlitsch 2001, 2002), I reared anurans in terrestrial enclosures. However, terrestrial studies were not designed identically or with the objective of being a single study replicated over time. Nevertheless, because of the similarity in design and unified objectives of the two studies, they are presented together here. This research represents the first attempt to test how both density and insecticide exposure in the larval environment influence the critical period following metamorphosis in the terrestrial environment.

MATERIALS AND METHODS

My field enclosures were located in an open field near the edge of a mixed oak forest in

Columbia, Missouri (Boone County) at the University of Missouri-Columbia Research Park. Each enclosure measured 1×2 m with a height of 0.7 m. Enclosures were constructed of steel sheet metal (buried 0.7 m in the ground) and were arranged in groups of four in 12 spatial blocks with adjacent enclosures sharing a common wall. Vegetation within the enclosures was maintained at ≤ 30 cm. I dug a pit (45 cm deep, 45 cm diameter) in the center of each enclosure, which was filled with leaf litter to serve as a potential overwintering site and covered with a square plywood board (45×45 cm). Additionally, four burrows (at a 45° slope, and approximately 20 cm deep, 40 cm long, 3 cm diameter) were made in the corners of each enclosure by hammering a round wooden dowel into the ground before metamorphs were added. I used densities of 3–5 frogs/m² in this study based on a preliminary study in the enclosures with *R. sphenoccephala* and *R. blairi* that yielded high survival ($76 \pm 6\%$) with three frogs/m² (unpubl. data). No additional food sources were supplied to the anurans in the enclosures, because anurans had access to naturally occurring invertebrates (pers. obs.).

My study consisted of two separate and independent experiments. In each experiment, the objective was the same and the methods were similar but not identical. The objective in each study was to determine how larval environmental conditions influenced overwinter mass, growth rate, and survival in the terrestrial environment. In both studies, differences in size at metamorphosis resulted from density or chemical exposure in the larval environment. I then determined how larval density and exposure to the insecticide carbaryl during larval development affected overwinter survival and mass at spring emergence.

The insecticide carbaryl (the active ingredient in Sevin) is a well-studied acetylcholinesterase inhibitor that has been used in numerous aquatic studies with larval amphibians in the laboratory and field (reviewed in Boone and Bridges, 2003), making it ideal for examination of effects of larval exposure in the terrestrial environment. Carbaryl is relatively short lived in the aquatic environment (3–4 days in cattle tank pond experiments; Boone and Semlitsch, 2002) and does not bioaccumulate (Cox, 1993). Carbaryl affects endpoints at metamorphosis (e.g., size at metamorphosis; Boone and Semlitsch, 2002; Boone et al., 2004) at postapplication environmental levels (≤ 4.8 mg/liter; Peterson et al., 1994).

I raised anurans in cattle tank ponds from hatching through metamorphosis. Before placement in terrestrial enclosures, each metamorph was weighed and uniquely toe-clipped. All anurans reared in a certain larval environment

were raised in terrestrial enclosures with anurans of the same species from the same larval treatment (e.g., *B. woodhousii* raised in ponds under low-density conditions with no exposure to carbaryl were placed in a terrestrial enclosure with other *B. woodhousii* from this same treatment). Individuals were recaptured and removed from enclosures the following spring so that mass, growth rate (= change in mass/days spent in the enclosure), and enclosure survival could be determined; enclosures served as the experimental unit. Mass at metamorphosis, growth rate, and mass at spring emergence were log-transformed to normalize the data and homogenize variances. Overwinter survival was angularly transformed. Data were analyzed with analyses of variance (ANOVA) to test for treatment effects and their interaction. Preliminarily, I used a number of covariates (including overwinter survival, mass at metamorphosis, and total time spent in the enclosure) in analyses; however, because each covariate was either not significant or did not change the effect, all covariates were eliminated to conserve error degrees of freedom. In all analyses, results from mass at metamorphosis may differ from results previously reported in the larval studies (Boone and Semlitsch, 2001, 2002), because only a random subset of the metamorphs was used in the present study.

Study I (1997): Rana clamitans and Bufo woodhousii.—One clutch of *B. woodhousii* and three egg masses of *R. clamitans* were reared from hatching through metamorphosis in outdoor 1000-liter cattle tanks ponds at low or high density (1:3 ratio; 27 and 81 *B. woodhousii* tadpoles, 30 and 90 *R. clamitans* tadpoles) that were exposed to a postapplication level of carbaryl (0, 3.5, or 7 mg/liter carbaryl) early in larval development (predator presence was also manipulated; for details, see Boone and Semlitsch, 2001). *Rana clamitans* clutches were mixed before placing tadpoles in the ponds. Only one clutch of *B. woodhousii* was used because of low availability of that species at the time the study was initiated. Use of a single clutch increases the probability that the observed effects may be a result of unique genetic distinctiveness of that clutch. Metamorphs collected from the cattle tank study were held in the laboratory and fed fruit flies and crickets ad libitum for no longer than three weeks until enough metamorphs were available to be added to enclosures.

I added 10 metamorphs of *B. woodhousii* to each enclosure (five frogs/m²) on 29 July. Metamorphs of *B. woodhousii* were placed in terrestrial enclosures according to their larval carbaryl and density treatments. Because of variation in the number of *B. woodhousii* that reached metamorphosis, the number of replicates varied among treatments. For *B. woodhousii*,

carbaryl controls were replicated twice in low and high density, exposure to 3.5 mg/liter carbaryl in low- and high-density ponds were replicated three times, exposure to 7.0 mg/liter carbaryl in high-density ponds was replicated twice, and exposure to 7.0 mg/liter carbaryl in low-density ponds was not included in the design because too few metamorphs were collected from these ponds. *Bufo woodhousii* were overwintered in a total of 12 enclosures. Measures at 7.0 mg/liter were not included in the analyses, because the interaction of carbaryl and density could not be tested (because of missing cells).

I added six metamorphs of *R. clamitans* to each enclosure (three frogs/m²) on 16 September with *R. clamitans* from ponds exposed to 0, 3.5, or 7.0 mg/liter carbaryl reared in separate enclosures. *Rana clamitans* reached metamorphosis in low-density ponds only. The number of replicates was constrained by the number of *R. clamitans* that reached metamorphosis, resulting in one enclosure for a chemical control, four enclosures for 3.5 mg/liter carbaryl treatment, and three enclosures for 7.0 mg/liter carbaryl treatment. Although *R. clamitans* are believed to overwinter in wetlands, which may be the norm, they may also overwinter in terrestrial environments (Lamoureux and Madison, 1999; Birchfield, 2002).

I searched enclosures every three to four days in the spring beginning 27 March to 18 May 1998. Data for each species were analyzed with an ANOVA to determine effects of larval density (*B. woodhousii* only), carbaryl exposure in larval development, and their interaction (*B. woodhousii* only) on mass at metamorphosis, mass at spring emergence, growth rate, and overwinter survival. A logistic regression was used to examine the relationship between probability of surviving until the spring and mass at metamorphosis, density, and their interaction. The carbaryl treatment was excluded, because it never significantly influenced the model.

Study II (1998): Rana sphenoccephala and R. blairi.—Five clutches of both *R. sphenoccephala* and *R. blairi* were reared from hatching through metamorphosis in outdoor 1000-liter cattle tank ponds at low or high density (1:3 ratio; 23 and 69 tadpoles of *R. sphenoccephala*, 45 and 135 tadpoles of *R. blairi*) that were exposed to a postapplication level of carbaryl (0, 3.5, or 7 mg/liter carbaryl) early in larval development (pond drying was also manipulated; for details, see Boone and Semlitsch, 2002). Metamorphs were added to enclosures within three days of tail absorption to minimize handling effects on mass at metamorphosis. I added eight *R. sphenoccephala* or *R. blairi* to each enclosure (four frogs/m²) beginning on 12 June and continuing until 10 July. *Rana sphenoccephala* and *R. blairi* were added to enclous-

sures according to larval density (low or high) and carbaryl exposure (0, 3.5, 7.0 mg/liter) to test the effects of these treatments on overwintering survival and mass; each treatment was replicated three times for each species (for a total of 36 enclosures). Enclosures were searched every three to four days in the spring beginning 21 May to 14 June 1999. Data were analyzed with an ANOVA to determine the effects of larval density, carbaryl exposure in larval development, and their interaction on mass at metamorphosis, mass at spring emergence, growth rate, and overwinter survival; additionally, I analyzed for effects of treatments and their interaction on time that metamorphs were added to the enclosures (which is a reflection of time to metamorphosis). A logistic regression was used to examine the relationship between probability of surviving until the spring and mass at metamorphosis, density, and their interaction; carbaryl treatment was excluded, because it never significantly influenced the model.

RESULTS

Study I (1997): *Rana clamitans* and *Bufo woodhousii*.—For *B. woodhousii*, metamorphs from low-density ponds were 1.6 times larger than those from high-density ponds when added to enclosures ($F_{1,6} = 8.69$, $P < 0.001$; Fig. 1A). Metamorphs from carbaryl control ponds were 1.2 times larger at metamorphosis than those exposed to 3.5 mg/liter carbaryl ($F_{1,6} = 8.69$, $P = 0.026$; Fig. 2A). Differences in size at metamorphosis attributable to density or carbaryl exposure did not result in significant differences in mass at spring emergence, growth rate, or overwinter survival. On average (± 1 SE), $25 \pm 7\%$ of *B. woodhousii* survived to the spring. According to logistic regression, probability of surviving to the spring was moderately affected by mass at metamorphosis ($\chi^2 = 3.28$, $P = 0.070$), larval density ($\chi^2 = 3.44$, $P = 0.064$), and the interaction of mass at metamorphosis with density ($\chi^2 = 3.36$, $P = 0.067$); the model had 73.1% concordance in predicting the data (AIC = 30.9). Generally, metamorphs that survived the winter were slightly smaller at metamorphosis (0.183 ± 0.013 g [low density], 0.144 ± 0.012 g [high density]) than those that did not survive the winter (0.229 ± 0.012 g [low density], 0.132 ± 0.010 g [high density]), but these differences were not significant.

Mass of *Rana clamitans* at metamorphosis was significantly and positively affected by carbaryl exposure in the aquatic environment ($F_{2,8} = 7.02$, $P = 0.017$; Fig. 2B). Carbaryl exposure moderately influenced mass of *R. clamitans* at spring emergence with exposure to 3.5 mg/liter ($F_{2,8} = 4.34$, $P = 0.053$) but did not influence growth rate or overwinter survival. *Rana clamitans*

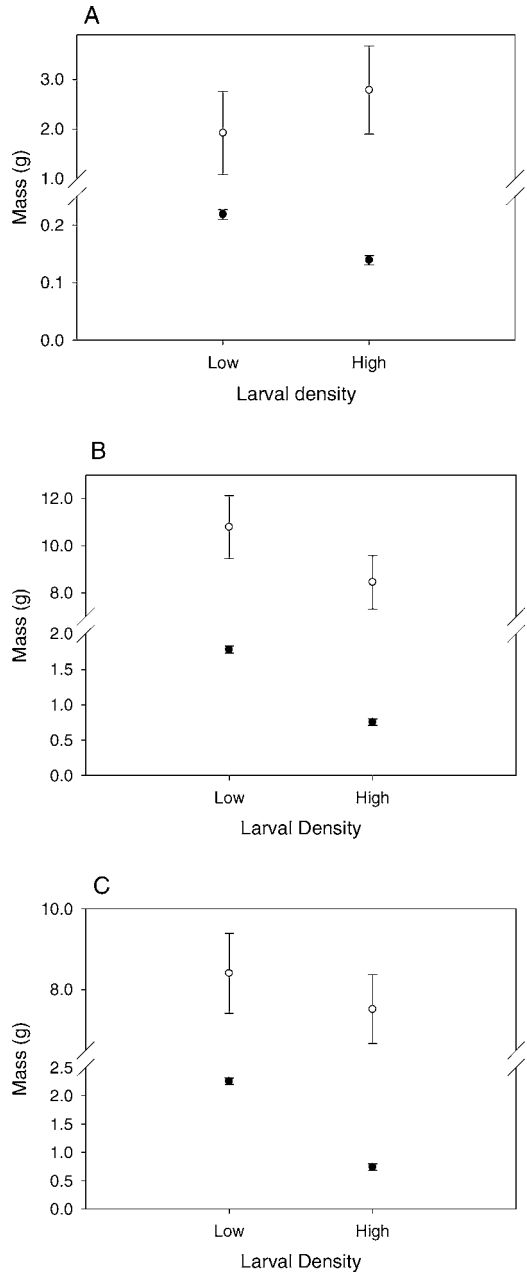


FIG. 1. Mass at metamorphosis (closed circles) and mass at spring emergence (open circles) in terrestrial enclosures for (A) *Bufo woodhousii*, (B) *Rana sphenocphala*, and (C) *Rana blairi* that were reared in low- and high-density aquatic environments. Significant differences between density treatments occur at metamorphosis for all species but not after collection in the spring. Error bars represent ± 1 SE.

reached metamorphosis almost exclusively in low-density ponds (results reported in Boone and Semlitsch, 2002); thus, effects of larval

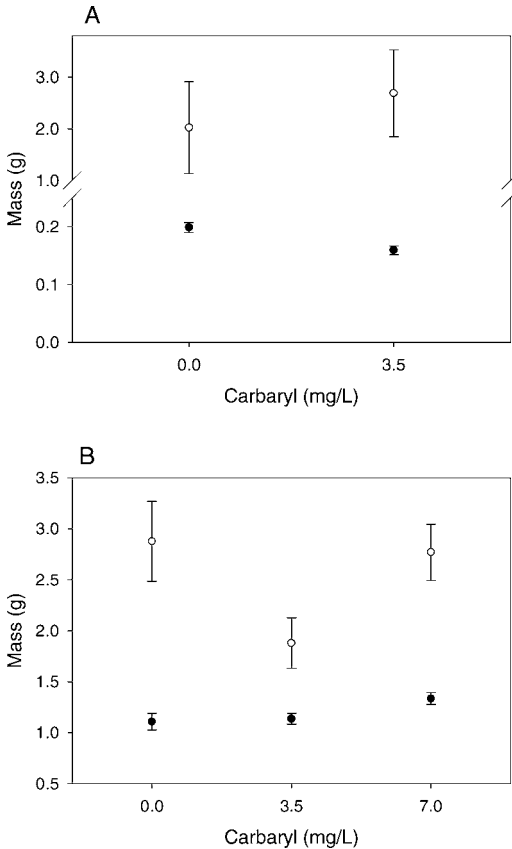


FIG. 2. Mass at metamorphosis (closed circles) and mass at spring emergence (open circles) in terrestrial enclosures for (A) *Bufo woodhousii* and (B) *Rana clamitans* that were exposed to carbaryl during larval development. Significant differences occur among carbaryl treatments for mass at metamorphosis for all species, and at spring emergence for *R. clamitans*. Error bars represent ± 1 SE.

density could not be determined in the terrestrial environment. On average (± 1 SE), $48 \pm 5\%$ of *R. clamitans* survived the winter. According to logistic regression, probability of survival to metamorphosis was moderately affected by mass at metamorphosis ($\chi^2 = 2.94$, $P = 0.087$); the model had 69.4% concordance in predicting the data (AIC = 30.9). Generally, metamorphs of *R. clamitans* that survived the winter were larger at metamorphosis (1.274 ± 0.053 g) than those that did not (1.131 ± 0.053 g), but differences were not significant.

Study II (1998): *Rana sphenocéphala* and *Rana blairi*.—For *R. sphenocéphala*, mass at metamorphosis was significantly greater in low-density ponds ($F_{1,7} = 180.63$, $P < 0.001$; Fig. 1B) but was not affected by carbaryl exposure or the interaction of density and carbaryl. *Rana sphenocéphala* from high-density ponds were added to

enclosures significantly later than those from low-density ponds ($F_{1,12} = 71.42$, $P < 0.001$); however, average date of addition differed only by 4.1 ± 0.34 days. Further, time to addition was influenced by an interaction of density and carbaryl ($F_{2,12} = 10.25$, $P = 0.003$), but again differences among treatments were small (Julian date for low-density ponds across carbaryl treatments: 307.7 ± 0.6 [0 mg/liter], 305.6 ± 0.6 [3.5 mg/liter], 304.4 ± 0.6 [7.0 mg/liter]; for high-density ponds: 309.1 ± 0.6 [0 mg/liter], 309.6 ± 0.6 [3.5 mg/liter], 311.3 ± 0.6 [7.0 mg/liter]). Carbaryl exposure did not influence the time metamorphs were initially introduced to the enclosures. Overwinter survival and growth rate were not significantly affected by treatments or their interactions. On average (± 1 SE), $23 \pm 5\%$ of *R. sphenocéphala* survived the winter. According to logistic regression, probability of surviving the terrestrial environment was significantly predicted by mass at metamorphosis ($\chi^2 = 3.91$, $P = 0.048$) and larval density ($\chi^2 = 4.47$, $P = 0.035$) but not the interaction of larval density and mass at metamorphosis; the model had 82.1% concordance in predicting the data (AIC = 39.7). Generally, metamorphs of *R. sphenocéphala* that survived the winter (1.562 ± 0.090 g) were larger than those that did not (1.213 ± 0.076 g).

For *R. blairi*, mass at metamorphosis was significantly reduced with increased larval density ($F_{1,10} = 626.52$, $P < 0.001$; Fig. 1C), and was positively affected by low carbaryl exposure ($F_{2,10} = 5.88$, $P = 0.021$) but not by treatment interactions. There were significant differences in date that metamorphs were added to enclosures attributable to density ($F_{1,12} = 25.0$, $P < 0.001$), carbaryl ($F_{2,12} = 169.3$, $P < 0.001$), and their interaction ($F_{2,12} = 26.15$, $P < 0.001$), but treatments additions differed by less than 10 days on average (Julian date for low-density ponds across carbaryl treatments: 306.7 ± 0.5 [0 mg/liter], 312.6 ± 0.5 [3.5 mg/liter], 310.4 ± 0.5 [7.0 mg/liter]; for high-density ponds: 300.4 ± 0.5 [0 mg/liter], 313.2 ± 0.5 [3.5 mg/liter], 309.8 ± 0.5 [7.0 mg/liter]). Overwinter survival, growth rate, and mass at spring emergence were not significantly affected by treatments or their interactions. On average (± 1 SE), $35 \pm 6\%$ of *R. blairi* survived the winter. According to logistic regression, probability of surviving the terrestrial environment was not significantly affected by mass at metamorphosis, larval density, or the interaction of larval density and mass at metamorphosis; the best fit model included only the intercept and had 28.1% concordance in predicting the data (AIC = 49.0). On average, metamorphs of *R. blairi* that survived the winter (1.588 ± 0.066 g) were slightly larger at metamorphosis than those that did not (1.465 ± 0.062 g), but differences were not significant.

DISCUSSION

Mark-recapture studies on the Wood Frog (*Rana sylvatica*), Mole Salamander (*Ambystoma talpoideum*), and Western Chorus Frog (*Pseudacris triseriata*) have indicated that differences in amphibian size and time to metamorphosis can influence individuals throughout their lifetimes by affecting terrestrial survival, lifetime size, and reproductive success (Smith, 1987; Semlitsch et al., 1988; Berven, 1990; Scott, 1994). My study, however, suggested that differences in size at metamorphosis can be overcome in less than one year from metamorphosis. My study includes a range of variation that was much smaller than the cohort-based studies previously mentioned, which could make detecting the consequences of metamorph size more likely, although my sample size was much smaller overall. I did not find a strong relationship between size at metamorphosis and probability of surviving the winter, although there was a trend of larger ranids having a greater probability of surviving the winter. Werner (1986) found positive correlations between size at metamorphosis and adult body size for North American ranids and hylids, but not for bufonids, suggesting that growth in the terrestrial phase may not be correlated with metamorphosis for all species and that species may use the aquatic and terrestrial habitats differently. For this reason, we may anticipate that not all species will demonstrate the relationships between metamorphic size and terrestrial survival and adult size. Species such as ambystomatid salamanders that reach a large proportion of their final adult size during the larval period (Semlitsch et al., 1988) may show the expected relationship between size at metamorphosis, and terrestrial growth and survival more strongly than species that complete most of their growth in the terrestrial environment. Additionally, relationships between aquatic and terrestrial growth and survival may vary temporally with size and time at metamorphosis, having lasting effects in some years but not in others.

In my study, mass at metamorphosis was significantly different between larval density treatments for *R. sphenoccephala*, *R. blairi*, and *B. woodhousii* and among carbaryl treatments for *B. woodhousii*, *R. clamitans*, and *R. blairi*. These results set the stage for differential survival and mass after overwintering, if size at metamorphosis greatly influenced these responses; however, these differences were not realized, and most frogs made up for small size at metamorphosis with terrestrial growth by the time they were captured in the spring. For instance, at metamorphosis *R. blairi* reared in low-density environments were three times larger than those reared in high-density environments. At spring

collection, juveniles from low-density ponds were still larger, but those from high-density ponds were only 10% smaller. This apparent compensation in size between smaller and larger metamorphs may have been in part a result of smaller metamorphs having a lower probability of surviving the winter, leaving only the larger individuals and resulting in an apparent "catch-up" effect. In general, however, ranids that metamorphosed at a small size remained smaller than individuals that metamorphosed at a larger size by the following spring, as we would anticipate from earlier work (Werner, 1986; Smith, 1987; Berven, 1990). Differences in size-classes may remain throughout the lifetime in ranids, or ranids may gradually overcome initial differences in size, as my data suggest.

Bufo woodhousii were able to compensate for small size at metamorphosis in my study and were not more susceptible to winter mortality than larger metamorphs. *Bufo woodhousii* from low-density larval environments were 1.6 times larger at metamorphosis than those from high-density ponds but were 1.4 times smaller than those from high-density ponds after overwintering. It is unlikely that differential survival in size classes would account for these differences because large animals were less likely to survive until spring, on average. It is surprising that smaller animals had greater survival, but this may have been a consequence of more effective use of hibernacula or that smaller individuals were no longer "smaller" by the time overwintering ensued. Overall, *B. woodhousii* were able to compensate for small size at metamorphosis in the terrestrial environment whether differences at metamorphosis were caused by density or chemical treatments. Goater's (1994) study in terrestrial aquaria with *B. bufo* (European Toad) and Beck and Congdon's (1999) study in terrestrial enclosures with *Bufo terrestris* (Southern Toads) also showed that, although size at metamorphosis may be significantly different, the disparities can be reduced over time. Size at metamorphosis for a species with a relatively short larval period may be less constraining than for species with long larval periods (Werner, 1986).

For all species that began with initial differences between treatment groups (whether caused by larval density or carbaryl exposure), it is surprising that their growth rates were not also significantly different. If animals from small size classes indeed gained more mass compared to animals that were originally larger, then we would expect significant different growth rates. However, even though initial differences in mass were significant, they were also small. For instance, with *B. woodhousii*, the average difference in mass at metamorphosis between animals from low- and high-density ponds was 0.082 g,

with little variation associated with mean mass (± 0.005); after overwintering, the difference between animals reared in low- and high-density ponds was on average 0.864 g, with larger variation within low- and high-density groups (approximately ± 0.864). The variation at the final size was much greater than initial size differences (or variation), and would make it difficult to distinguish differences in growth rates when only initial and final sizes were measured, as were in my study. Despite differences in growth rates not being significant, the differences in mass (as a percentage) between density groups became smaller over time, suggesting that smaller animals were, in fact, growing at greater rates.

Further, differences in size at metamorphosis associated with density or chemical exposure did not significantly influence the probability of overwinter survival in the terrestrial enclosures. The trend for ranids, however, was that metamorphs surviving until the spring were larger on average than those that did not survive until spring, whereas smaller *B. woodhousii* metamorphs appeared more likely to survive the winter. Overall, my study indicated that small size at metamorphosis does not strongly decrease the probability of surviving the winter. Although the enclosures may exclude important terrestrial predators and reduce the mortality that one may find in more natural studies (e.g., Smith, 1987; Semlitsch et al., 1988), my study suggests that small size at metamorphosis alone may not be disadvantageous for some species in some years. Generally, survival in these enclosures was moderate (23–48%), similar to the survival rates of ranids in Parris (2001) and of ambystomatid salamanders in Pechmann (1995), suggesting that small outdoor enclosures may be ideal for experimental manipulations of juvenile anurans in the terrestrial environment.

My main impetus with these studies was to determine whether effects of carbaryl exposure during the larval period extended beyond metamorphosis or if carbaryl's effect manifested itself differently than those caused by the natural stress of larval density. These data suggest that there were no latent effects from carbaryl exposure to larval amphibians for the responses measured. Even when there were differences at metamorphosis from carbaryl exposure, these effects either disappeared (i.e., *B. woodhousii*) or remained the same (i.e., *R. clamitans*). Because most of the effects of carbaryl found in the larval environment have been attributed to indirect effects from changes in the food web (Boone and Semlitsch, 2001, 2002; Mills and Semlitsch, 2004), it is not surprising that strong postexposure effects from carbaryl exposure were not apparent later in the terrestrial development.

This study proffers insight into anuran growth and survival in the terrestrial environment. My data, collected from a number of species, suggest that size at metamorphosis does not strongly or significantly influence growth and survival of these species in terrestrial enclosures in less than one year. My data also suggest that differences in life-history strategies of species, particularly in length of the larval period, may be important considerations when making general statements regarding the importance of measures at metamorphosis.

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