

## A New Species of *Eleutherodactylus* (Anura, Leptodactylidae) from the Massif de la Hotte, Haiti

S. BLAIR HEDGES, RICHARD THOMAS AND RICHARD FRANZ

*Eleutherodactylus amadeus* is described from the upper elevations of the Massif de la Hotte, Haiti. It is a small, polymorphic species with a repetitious, four-note call. It most closely resembles *E. heminota* (*auriculatus* group) but has glangular areas and smaller digital pads.

THE island of Hispaniola comprises two paleoislands presently separated by an arid corridor, the Valle de Neiba (Dominican Republic) and the Cul de Sac (Haiti). The distributions of the diverse Hispaniolan herpetofauna (>200 sp.) have long suggested that these two areas were isolated at some time in the past (Williams, 1961; Schwartz, 1980), presumably due to sea level changes. Recent geological studies, however, indicate that the North and South Islands may have been independent tectonic blocks that have only recently collided (Pindell and Dewey, 1982; Mann and Burke, 1984; Buskirk, 1985), implying a more ancient separation of the herpetofaunas.

Most of the South Island is composed of the narrow and mountainous Haitian Tiburon peninsula. The Massif de la Hotte lies near the end of this peninsula and rises to 2340 m (Pic Macaya). As in most of Haiti, the land in this region is devoid of its original vegetation, except for some high, inaccessible areas. A national park (Parc National Macaya) was created to protect some of those remaining stands of natural forest and associated animals in the Massif de la Hotte, and encompasses Morne Macaya and Morne Formon (above 1600 m).

For several months in 1984, a general biotic survey was conducted in Parc National Macaya by a team of biologists from the Florida State Museum under the direction of Charles A. Woods. During the course of field work, a small, undescribed species of *Eleutherodactylus* was frequently encountered and specimens were collected by RF and others. In July 1985, SBH and RT visited the region for several days and also collected specimens.

In the account below, the following abbreviations are used: E-N (distance between nostril and eye), EYE (horizontal diameter of eye), HW (greatest width of head), IOD (interorbital distance), SHL (shank length), SVL (snout-vent

length), THL (thigh length), TYM (horizontal diameter of tympanum), UF/FSM (University of Florida herpetology collections, Florida State Museum), and USNM (National Museum of Natural History, Smithsonian Institution).

*Eleutherodactylus amadeus* n. sp.

Fig. 1

*Holotype*.—USNM 258676, an adult male from Formon Ridge Camp, on the south slope of Morne Formon (Formon Ridge), 3.0 km N Base Camp (2.6 km N, 15.1 km W Camp Perrin, airline distance), Dept. du Sud, Haiti (18°20' 59"N, 74°00'38"W, 1650 m), one of a series collected by S. Blair Hedges and Richard Thomas on 13-15 July 1985.

*Paratypes*.—USNM 258677-690, UF/FSM 61185-226, 61228-234, 61238-245, 61247, paratopotypes; UF/FSM 61329, Plaines Formon, near village of Formon, on Ravine Formon, vicinity of Base Camp (0.0 km N, 15.2 km W Camp Perrin, airline distance), 1000 m; UF/FSM 61324-327, Plaines Formon, Trouing Siccol area, 2.5 km northwest Base Camp, 1240-1260 m; UF/FSM 61270-272, Plaines Formon, Trouing Jeremie area, Trouing Jeremie No. 5, ca 2 km northwest Base Camp; UF/FSM 61264-269, 61273-275, 61323, Morne Cavalier, 3.1 km northwest Base Camp, 1550 m; UF/FSM 61394-409, 61411-427, Morne Cavalier, spring on east slope, 0.5 km E Pic 1570, 2.8 km northwest Base Camp, 1530 m; UF/FSM 61261, 61331, Morne Formon, south slope, trail between Base Camp and Formon Ridge Camp, 1400 m; UF/FSM 61235-236, 61253-260, 61332-347, Morne Formon, south slope, basin southeast of Formon Ridge Camp, 2.8 km N Base Camp, 1500 m; UF/FSM 61178-184, 61348-352, 61354-382, Morne Formon, crest, trail between Formon Ridge Camp and Grande



Fig. 1. *Eleutherodactylus amadeus* (USNM 258691), paratype.

Ravine Camp, 3.6 km N Base Camp, 1800–1900 m; UF/FSM 61262, Morne Formon, crest, Brent's Crest Trail, between East and West trails, 3.8 km north-northwest Base Camp, 2040 m; UF/FSM 61171–176, Morne Formon, north slope, trail between Formon Ridge Camp and Grande Ravine Camp, 3.9 km north-northwest Base Camp, 1900 m; USNM 258691–721, UF/FSM 61165–170, 61177, 61383–88, Morne Formon, north slope, trail between Formon Ridge Camp and Ravine Camp, 4.1 km north-northwest Base Camp, 1700 m; UF/FSM 61237, 61389–391, Morne Formon, north slope, trail between Formon Ridge Camp and Grand Ravine Camp, 4.5 km north-northwest Base Camp, 1500–1530 m; UF/FSM 61263, Morne Formon, west slope, trail from Morne Cavalier to Pic Formon, 3.8 km northwest Base Camp, 1850 m, UF/FSM 61312–61318, Saddle between Morne Formon and Morne Macaya, 5.8 km northwest Base Camp, 1860–1900 m; UF/FSM 61319–322, Crest and Peak of Morne Macaya, 6.5 km north-northwest Base Camp, 2200–2340 m.

**Diagnosis.**—A small species of *Eleutherodactylus* ( $\bar{x}$  adult SVL = 18.7 mm [males], N = 15; 23.4 mm [females], N = 15) with smooth dorsum and relatively smooth venter (fine corrugations or indentations under magnification; usually not granular or areolate), moderately enlarged digital tips, and a variable dorsal pattern. It most closely resembles *E. heminota*, from which it differs in having supraxillary, inguinal, and postfemoral glandular areas (in preservative), smaller digital tips, ventral spotting, and a four-note, rather than one-note, call.

**Description.**—Head as broad as body, longer than wide; snout subacuminate in dorsal view, rounded in profile, overhanging lower jaw; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis straight, rounded (in cross section), indistinct; loreal region flat; lips not flared; IOD greater than width of upper eyelid, space flat (no cranial crests); no supratympanic fold; tympanum superficial with non-tuberculate membrane; occasionally one or two small tubercles posterior to angle of jaw; choanae round, moderate in size, not concealed by palatal shelf of maxillary arch; vomerine odontophores prominent, in two linear or slightly arched rows perpendicular to axis of body; tongue large, ovoid, slightly notched behind (in some); posterior one-half not adherent to floor of mouth; internal paired subgular vocal sac (absent in some adult males).

Skin of dorsum smooth, that of venter relatively smooth but with fine corrugations or indentations, usually not tuberculate or areolate (specimens from the highest elevations in the Massif de la Hotte [ $>2000$  m] are generally more tuberculate both dorsally and ventrally); no dorsolateral or discoidal folds; skin below vent coarsely areolate; anal opening not extended in sheath; supraxillary, inguinal, and postfemoral glands present in males and most females (visible only on preserved specimens); no ulnar tubercles, palmar tubercle single or bifid, thenar tubercle round or oval, both low and indistinct; several flattened supernumerary palmar tubercles present; subarticular tubercle round, non-conical, and slightly elevated; all fingers expanded at tips, fingers III–IV more than fingers I–II; fingertips often pointed; semi-circular pad present on ventral surface of fingertip (“pad” is used here sensu Lynch and Myers, 1983); “U-shaped” circumferential groove bordering distal two-thirds of pad, interrupted at distal end (if fingertip pointed); width of largest pad (III) one-half to three-quarters TYM, smallest (I) one-third to one-half TYM; fingers with indistinct lateral ridges; first finger shorter than second when adpressed; fingers III–IV–II–I in order of decreasing length.

Small heel tubercles sometimes present, none on outer edge of tarsus; metatarsal tubercles moderately elevated, inner (oval) twice as large as outer (conical); one supernumerary plantar tubercle sometimes present at base of toe; toes unwebbed, with lateral ridges and moderately expanded tips; toetip rounded or slightly pointed at end; semicircular toepads with “U-shaped”

TABLE 1. VARIATION IN SOME MEASUREMENTS OF *Eleutherodactylus amadeus* (30 RANDOMLY CHOSEN ADULT PARATYPES [15 MALES, 15 FEMALES] AND THE HOLOTYPE [USNM 258676, MALE]). Values are means  $\pm$  1 SE (in mm).

	Males	Females	Holotype
Snout-vent length	18.7 $\pm$ 0.31	23.4 $\pm$ 0.34	18.8
Head length	7.65 $\pm$ 0.123	9.47 $\pm$ 0.133	7.5
Head width	7.19 $\pm$ 0.129	8.79 $\pm$ 0.148	7.4
Tympanum	1.15 $\pm$ 0.019	1.55 $\pm$ 0.038	1.1
Eye diameter	2.73 $\pm$ 0.041	3.22 $\pm$ 0.045	2.6
Eye-naris distance	1.95 $\pm$ 0.038	2.54 $\pm$ 0.047	2.0
Internarial distance	1.88 $\pm$ 0.034	2.23 $\pm$ 0.025	2.0
Interocular distance	2.23 $\pm$ 0.041	2.85 $\pm$ 0.055	2.5
Thigh length	8.41 $\pm$ 0.137	10.6 $\pm$ 0.20	8.5
Shank length	8.89 $\pm$ 0.123	11.1 $\pm$ 0.15	8.9
Tarsal length	5.68 $\pm$ 0.094	7.17 $\pm$ 0.103	5.4
Foot length	8.34 $\pm$ 0.136	10.6 $\pm$ 0.18	8.2
Fingertip (III) width	0.74 $\pm$ 0.021	0.93 $\pm$ 0.036	0.7
Toetip (IV) width	0.71 $\pm$ 0.023	0.81 $\pm$ 0.028	0.7
Number of vomerine odontoids (right row)	7.2 $\pm$ 0.40	10.7 $\pm$ 0.54	8

circumferential groove bordering distal two-thirds; heels just touch when flexed legs are held at right angles to sagittal plane.

In preservative, dorsal ground color is pale yellow, tan, brown, or dark brown, with males tending to have lighter colors; dorsal body markings variable (see pattern polymorphism) and either lighter or darker than ground color; distinct black or dark brown "eye" stripe on side of head, extending posteriorly from narial opening to just above insertion of arm; brown or dark brown markings on upper lip and occasionally on lower lip and below eye; dorsal surface of head (snout) pale yellow or tan and separated from darker body by dark brown (or black) interocular bar, the latter occasionally bordered posteriorly by a dark triangle (apex oriented posteriorly); tympanic membrane usually clear below but with variable amounts of brown pigment on upper edge and center; dorsal surface of lower arm unpatterned, or sometimes with two narrow transverse bands (one on wrist and another between wrist and elbow); anterior dorsal surface of upper arm with distinctive dark brown or black blotch; dorsal surface of thighs with brown mottling, or sometimes with brown transverse bars; dorsal surface of shank and foot unpatterned, or each with single wide tan or brown transverse bar; ventral ground color white or pale yellow (although fine dark stippling is noticeable under magnification); ventral surface of body and hindlimbs with

tan or brown spots (0.5–0.7 mm in diameter), made up of areas of denser microscopic stippling (ca 30–50 dots per spot) or larger flecks of brown pigment; ventral spotting more pronounced in females, although some individuals of both sexes with unpatterned venters; ventral surface of lower arm sometimes brown with narrow light longitudinal stripe extending from wrist to elbow; palmar and plantar surfaces variable, but usually white or yellow with coarse dark brown stippling; glandular areas (if present) orange or yellow; testicular peritoneum dark brown or black.

Live weight of adults, 0.38–0.61 g ( $\bar{x}$  = 0.49, N = 8) in males; 0.73 and 1.08 g (N = 2) in females. Other measurements, including those of the holotype, are presented in Table 1.

*Etymology*.—After the 18th century composer, Wolfgang Amadeus Mozart; for the remarkable resemblance of the wide-band audiospectrogram of this species (Fig. 3) to musical notes.

*Pattern polymorphism*.—*Eleutherodactylus amadeus* is considerably variable in dorsal pattern. Seven basic patterns are present (Fig. 2), either singly, or in combination, forming 17 different pattern types. These pattern types, and their frequency of occurrence (N = 265) are: reverse parentheses (30.6%), unpatterned (26.8%), narrow middorsal stripe/long dorsolateral stripes (14.0%), short dorsolateral stripes (9.1%), "W"

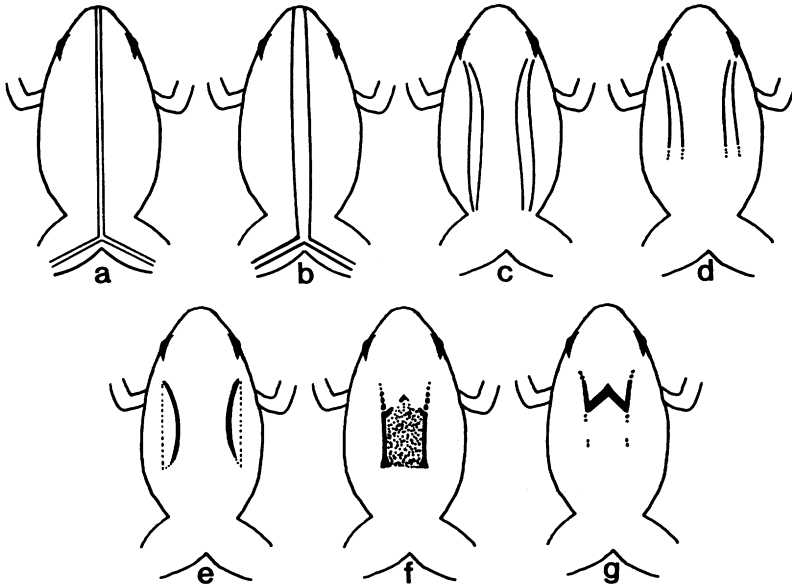


Fig. 2. Dorsal pattern variation in *Eleutherodactylus amadeus*. (a) narrow middorsal stripe, (b) broad middorsal stripe, (c) long dorsolateral stripes, (d) short dorsolateral stripes, (e) reverse parentheses, (f) blotch, and (g) "W." Patterns a-e are light on a darker ground color.

(3.0%), long dorsolateral stripes, (2.6%), narrow middorsal stripe (2.3%), dorsal blotch (2.3%), broad middorsal stripe/long dorolateral stripes (2.3%), reverse parentheses/"W" (1.5%), broad middorsal stripe (0.8%); narrow middorsal stripe/short dorsolateral stripes, reverse parentheses/broad middorsal stripe, narrow middorsal stripe/blotch, narrow middorsal stripe/"W," long dorsolateral stripes/"W," and short dorsolateral stripes/"W" occurred in only one animal (0.4%) each. Some individuals classified as unpatterned, particularly males, had faint traces of pattern but could not be classified with certainty into any of the other pattern types.

*Comparisons.*—*Eleutherodactylus amadeus* occurs in an area of high species diversity of *Eleutherodactylus*. Twenty-six species are known from the Massif de la Hotte and many of those are sympatric (Hedges and Thomas, 1987). Also, several of the pattern types found in *E. amadeus* occur in other species of similar size. Thus, identification of this species may be difficult or impossible with other than live or well-preserved material.

It is unlikely that *E. amadeus* occurs on the North Island, and since it does not closely resemble any North Island species, they will not be considered here. Of the 35 species of *Eleutherodactylus* occurring on the Hispaniolan South

Island, certain members of the *auriculatus*, *ricordii*, and *varleyi* groups (Schwartz, 1958, 1969, 1973; see Frost [1985] for current allocations of species) could be confused with *E. amadeus*. Those are: *E. abbotti*, *E. audanti*, *E. armstrongi*, *E. bakeri*, *E. heminota* (*auriculatus* group); *E. glaphycompus* (*ricordii* group); *E. eunaster* and *E. glanduliferoides* (*varleyi* group).

*Eleutherodactylus abbotti* (SVL = 18 mm [males], 22 mm [females]) and *E. audanti* (SVL = 18 mm [males], 23 mm [females]) are similar in size to *E. amadeus*, and often have a shank bar, an eye stripe, and lower arm markings. Both occur in the Massif de la Hotte and are sympatric with *E. amadeus*, although *E. abbotti* does not occur in the higher elevations. They can be distinguished from most *E. amadeus* by their areolate or granular venter. A scapular "X" marking and dorsolateral folds are usually present in both species; *E. audanti* also has a dark postanal triangle and several diagonally oriented flank bars; all are features not found in *E. amadeus*.

*Eleutherodactylus armstrongi* (SVL = 30 mm [males], 40 mm [females]) is not known from the Massif de la Hotte. However, it has glands (supraxillary, inguinal, and postfemoral), a similar ventral texture, and two pattern types which are both found in *E. amadeus* (short and long dorsolateral stripes). Aside from having a larger adult body size, *E. armstrongi* differs from *E.*

*amadeus* in several subtle pattern features: the dorsal surface of the snout is usually as dark or darker than the body (not lighter), and the eye stripe, and lip markings (if present) are obscured by dark pigmentation. In addition, the testicular peritoneum of *E. armstrongi* is white (black in *E. amadeus*).

*Eleutherodactylus bakeri* and *E. heminota* are perhaps the two most similar species to *E. amadeus* and both are sympatric with it. Each has a single wide shank bar (sometimes faint or absent in *E. heminota*), a dark eye stripe, and a dark interocular bar (sometimes faint or absent in *E. bakeri*); all are characteristics of *E. amadeus*. *Eleutherodactylus bakeri* also shares several different pattern types with *E. amadeus*: long dorsolateral stripes, broad middorsal stripe, and narrow middorsal stripe. As the name suggests, *E. heminota* normally has a pattern of short dorsolateral stripes, although some individuals have long dorsolateral stripes and/or a narrow mid-dorsal stripe. In addition, the ventral texture of *E. heminota* is similar to that of *E. amadeus* (fine indentations or corrugations). However, both *E. bakeri* and *E. heminota* lack the glandular areas present in most preserved specimens of *E. amadeus* (caution: live frogs do not have visible glands). *Eleutherodactylus bakeri* (SVL = 36 mm [males], 38 mm [females]) is a distinctly larger species, has relatively larger digital tips, lacks a dark patch on the anterior dorsal surface of the upper arm, and has an areolate venter. It also has a common dorsal pattern type not found in *E. amadeus*: white spots, outlined in black. *Eleutherodactylus heminota* (SVL = 21 mm [males], 30 mm [females]) is slightly larger than *E. amadeus* and has relatively larger digital tips (never pointed, as in many specimens of *E. amadeus*). It is a bromeliad dwelling species that is also found in the axils of banana plants (*Musa*) but rarely, if ever, found under rocks and logs on the ground (the diurnal retreat of *E. amadeus*).

*Eleutherodactylus glaphycompus* (SVL = 20 mm [males], 32 mm [females]) occurs in the Massif de la Hotte and could be confused with *E. amadeus*. Although it has a single, wide shank bar, the dorsal ground color in life is usually green, a color not found in *E. amadeus*. Also, it has paired external vocal sacs (paired vocal sacs in *E. amadeus* are internal), larger digital tips (never pointed), and lacks glandular areas and a clearly defined eye stripe. It is sympatric with *E. amadeus* near Plaines Formon, usually calling from pockets in limestone rocks at night, but has not been found in the higher elevations of Parc National Macaya.

*Eleutherodactylus eunaster* (SVL = 20 mm [males], 25 mm [females]) and *E. glanduliferoides* (SVL = 15 mm [males], 17 mm [females]) are not known to be sympatric with *E. amadeus* but have several similarities with that species. Both have glandular areas (supraxillary, inguinal, and postfemoral) and a pattern type found in *E. amadeus*: long dorsolateral stripes/narrow middorsal stripe (this is the only pattern known in *E. glanduliferoides*). Male *E. eunaster* can be distinguished by their paired external vocal sacs. Also, *E. eunaster* has a distinctly rugose dorsum and the eye stripe is either lacking or not well developed. *Eleutherodactylus glanduliferoides* is smaller than *E. amadeus*, has very small digital tips, and a more pointed snout. It is presently known only from the Massif de la Selle.

In the key to Hispaniolan *Eleutherodactylus* (Henderson and Schwartz, 1984), male *E. amadeus* key out to *E. abbotti*. Large females (>25 mm SVL) key out to *E. armstrongi*, *E. auriculatoides*, *E. bakeri*, *E. heminota*, or *E. semipalmatus*, depending on pattern type and presence or absence of inguinal glands. Most females (<25 mm SVL) key out as far as step 20 (*haitianus* and *abbotti*).

*Natural history*.—The upper elevations of the Massif de la Hotte (above 1300 m) are characterized by West Indian pine (*Pinus occidentalis*), often in association with woody shrubs, tree ferns, bromeliads, and climbing bamboo (Franz and Cordier, unpubl.). *Eleutherodactylus amadeus* has been taken from 1000 m (Plaines Formon) to 2340 m (the crest of Pic Macaya). It was frequently encountered under rocks and logs during the day, and on the ground or up to 50 cm high (usually 15 cm) in herbaceous vegetation at night. It has a four-note call (Fig. 3). Each note is identical in frequency and duration and they are separated by about 0.5 sec. The interval between calls averaged 32.3 sec (30–34, N = 4) for one individual, and 37.7 sec (36–39, N = 3) for another. Calling sites were usually low on herbaceous vegetation, or on the ground. Similar two-note calls were heard in thick herbaceous vegetation low to the ground in the late afternoon and early evening in areas where *E. amadeus* was abundant. After dark, only the four-note call was heard and it was thus assumed that the two-note “daytime” call was of that species, although no frogs were collected giving two-note calls.

Occasionally, eggs were found under objects on the ground, in association with one (N = 4), two (N = 1), or three (N = 1) adults. The eggs,

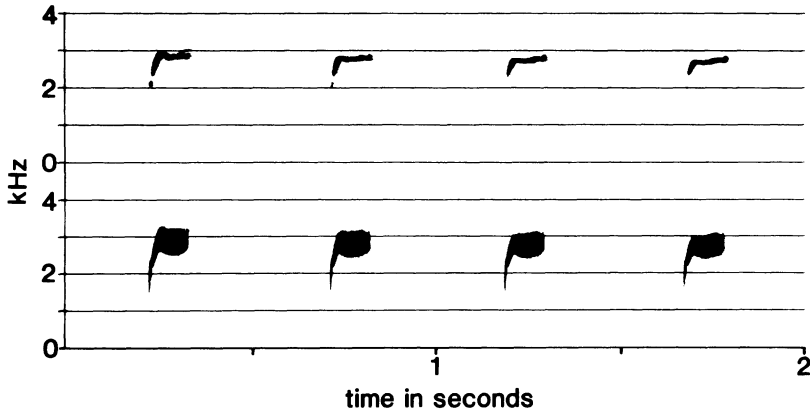


Fig. 3. Audiospectrograms of a single four-note call of *Eleutherodactylus amadeus* (above, 45 Hz filter; below, 300 Hz filter), USNM 258721, paratype.

11–27 in number, were in various stages of development and measured 3.4–5.1 mm in diameter. Hatchlings measured 4.2–4.4 mm SVL and had one egg tooth. Clutch size of gravid females (dissected) averaged 11.4 (11–12,  $N = 5$ ), and thus the larger clusters of eggs found under objects on the ground (i.e., 27 eggs) probably represent clutches from two or more females.

*Remarks.*—*Eleutherodactylus amadeus* does not fit neatly into any of the currently recognized species groups of West Indian *Eleutherodactylus*. Since it most closely resembles *E. heminota*, it could be tentatively placed in the *auriculatus* group (Schwartz, 1969). However, it has smaller digital pads and is less arboreal than most members of that group. Also, it has a relatively smooth venter (usually not areolate or granular) and a paired internal vocal sac, two features not often associated with *auriculatus* group species. Although its species-group allocation remains uncertain, it does appear to show affinities with other South Island *Eleutherodactylus*, as indicated by the many shared pattern features noted above.

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- (SBH) DEPARTMENT OF ZOOLOGY, UNIVERSITY OF MARYLAND, COLLEGE PARK, MARYLAND 20742; (RT) DEPARTMENT OF BIOLOGY, UNIVERSITY OF PUERTO RICO, RIO PIEDRAS, PUERTO RICO 00931; AND (RF) DEPARTMENT OF NATURAL SCIENCES, THE FLORIDA STATE MUSEUM, UNIVERSITY OF FLORIDA, GAINESVILLE, FLORIDA 32611. Accepted 20 March 1987.

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## Trophic Dynamics of a Top Predator, *Ambystoma tigrinum nebulosum* (Caudata: Ambystomatidae), in a Lentic Community

JOSEPH R. HOLOMUZKI AND JAMES P. COLLINS

**We describe the food web dynamics of fishless lentic communities of montane east-central Arizona. We highlight the changing trophic status of a top predator, larval tiger salamanders (*Ambystoma tigrinum nebulosum*), using long-term dietary information on different age classes and populations. Larvae are on the third trophic level when <30 mm snout-vent length (SVL) eating predominantly daphnids and dipteran larvae. This pattern appears to be true regardless of whether larvae will develop into typical or cannibalistic morphs. Beyond 30 mm SVL, *A. t. nebulosum* larvae eat a greater variety and range of sizes of aquatic insects and are on the fourth trophic level with larval predaceous diving beetles, *Dytiscus dauricus* and *D. marginicollis*, and leeches. Interactions between these predators are complex, changing with ontogeny and density. Cannibalistic salamander morphs and adult *Dytiscus* are on the fifth and highest trophic level in the freshwater ecosystem. Conspecifics comprise about 84% of the diet of cannibalistic morphs. Only one typical morph of 418 analyzed in this study ate a conspecific. However, above ≈65 mm SVL, typical salamander morphs are too large to be eaten by cannibalistic morphs and beetles. The food web is species-rich and dominated by relatively small, invertebrate and vertebrate ectotherms.**

**C**HANGES in the abundance of top predators can significantly affect the diversity of species at lower trophic levels in natural communities (Connell, 1975; Paine, 1980; Pimm, 1980). Theoretically, such changes also affect structural properties of food webs, such as food chain length and position of omnivores within a web (Cohen, 1978; Pimm, 1982). These empirical and theoretical results emphasize the importance of understanding the trophic patterns of top predators, since these animals potentially

have such a disproportionate effect on community structure.

Describing trophic relationships is complicated because abundances and behaviors of predators and prey in communities change relative to many factors including age (Rissing, 1981), morphology (Gilbert, 1976), and ontogeny (Ranta and Nuutinen, 1985). For the sake of simplicity, however, these factors are often ignored in describing food webs. Nonetheless, detailed descriptions of local food webs and fac-