

but his recognition of *Aspidoscelis* as a subgenus implies that he would treat the taxa of the *C. lemniscatus* species group as members of a subgenus *Cnemidophorus*. If this is what Axtell is recommending, we note that this would be in violation of Article 23 of the International Code of Zoological Nomenclature (1999), as *Ameiva* would have priority over *Cnemidophorus* as the generic name.

If we have inaccurately assumed Axtell's (2003) intended new subgeneric classification mentioned above, then there are only two other options he might be advocating. The first would be for *Ameiva* and *Kentropyx* to be subgenera within either an expanded genus *Ameiva* (oldest available name) or an expanded genus *Kentropyx*. In both cases, phylogenetic principles would be violated as the species of the subgenus *Kentropyx* (whether considered to be in the genus *Ameiva* or *Kentropyx*) are more closely related to members of the genus *Cnemidophorus* (members of the *C. lemniscatus* species group *sensu stricto* of South America) than to species of *Ameiva*. Alternatively, Axtell (2003) could be recommending the recognition of *Ameiva* and *Kentropyx* as separate genera, each with a single nominate subgenus. If so, not only would this complicate the nomenclatural situation with the erection of redundant taxa (i.e., subgeneric content being equivalent to generic content), but also it would do nothing to correct the paraphyletic nature of *Cnemidophorus sensu lato*.

In Reeder et al. (2002) nomenclatural stability was best served by avoiding additional generic changes (beyond resurrecting *Aspidoscelis*) until future evidence is brought to bear on other parts of the phylogeny, by not lumping all of the taxa into *Ameiva* while awaiting that evidence, and by not erecting formal subgeneric taxa that would be temporary. Stability is not served if the results of Reeder et al. (2002) are rejected or modified without bringing new data or analyses to bear on these issues. New data, however, have been collected recently. With much more mtDNA sequence data (i.e., 2609 bp vs. 876 in Reeder et al. [2002]) and several additional Neotropical teiine taxa (including the type species of *Cnemidophorus*, *C. murinus*), new analyses and results provide additional strong support for the recognition of the North American clade of *Aspidoscelis* (Reeder, Bell, and Cole, unpubl. data). In conclusion, we encourage use of the genus *Aspidoscelis* for North American whiptail lizards as specified by Reeder et al. (2002) and, until further evidence or analyses are brought to bear on this issue, we reject Axtell's (2003) unjustified allocation of *Aspidoscelis* as a subgenus of *Cnemidophorus sensu lato*.

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ARTICLES

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Egg Attendance by Female Frogs in Two Species of *Eleutherodactylus* from Costa Rica

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Eleutherodactylus crassidigitus and *E. fitzingeri* are common inhabitants of the forest floor of humid lowland and premontane forests from Costa Rica through Colombia, occurring from sea level to 1500 m in elevation (Savage 2002). Although relatively common, little information is available on the reproductive biology of these species. Both species, as well as most members of the genus, lay encapsulated eggs out of water and undergo direct development within the egg bypassing the larval stage and hatching out as miniature adults (Savage 1975). The secretive nature of these and many other species of *Eleutherodactylus* makes collection of detailed ecological observations haphazard and fortuitous at best.

In the only report of egg attendance in *E. crassidigitus*, Taylor (1952) reported finding an adult and 26 eggs under a rock. There are two reports of egg attendance in *E. fitzingeri*. Dunn (1931) found 44 eggs attended by an adult frog, which he identified as a male, but based on size alone, 51 mm snout to vent (SVL), Lynch and Myers (1983) suggested it was a female. Mendoza Quijano et al. (2002) reported a female *E. fitzingeri* attending 85 eggs in a small cavity on the ground. These three observations suggest that *E. crassidigitus* and *E. fitzingeri* may provide parental care to their eggs (Townsend 1996). Egg attendance occurs in at least 48 of the more than 525 species of *Eleutherodactylus* and of these, 24 species exhibit female attendance of eggs (Crump 1996, Townsend 1996). Herein I describe female clutch attendance for *E. crassidigitus* and *E. fitzingeri* with notes on egg deposition sites, clutch size and hatchlings.

I made observations along the south central Pacific coast of Costa Rica at the following localities: Hacienda Baru National Wildlife Refuge, Dominical, Puntarenas (09°16'00"N, 83°52'20"W, 10 m

TABLE 1. Summary of attending female snout–vent length (SVL) and eggs per clutch of *Eleutherodactylus crassidigitus*. Means reported as $\bar{x} \pm 1$ SD.

Date	Female SVL (mm)	Eggs Per Clutch
14 May 2000	39	36
3 June 2000	39	25
28 May 2001	41	42
13 June 2001	43	47
3 July 2001	45	45
	$\bar{x} = 41.4 \pm 2.6$	$\bar{x} = 39.0 \pm 8.8$

elev.); Finca Los Arboles, Tres Piedras, Puntarenas (09°19'30"N, 83°52'0"W, 95 m elev.); and Quebrada Grande, Palmar Norte (08°57'95"N, 83°26'60"W, 90 m elev.). This area is tropical moist forest and receives 2500–4000 mm of rainfall annually, and experiences a dry season from late December through April (Campbell 1999).

During a 26-month period from 19 December 1999 through 15 May 2002, I encountered 11 female *E. fitzingeri* attending clutches and five *E. crassidigitus* attending clutches during quadrat and transect sampling. I measured SVL with a 15 cm plastic ruler and egg diameter with dial vernier calipers. I found all 16 clutches under leaf litter. After I removed and counted eggs I replaced them and attending female within 5 cm of the eggs and replaced the leaf litter on top of both. In two additional cases I obtained egg counts by dissection of gravid *E. fitzingeri*. The eggs of both species were non-pigmented, spherical with yellowish yolk, and were clustered in a grape bunch although not connected by a jelly or foam matrix.

I found 5 female *E. crassidigitus* attending clutches in the months of May (N = 2), June (N = 2), and July (N = 1). In all cases the attending frog was sitting on top of the clutch and were covered by leaf litter. One adult female and a clutch were collected and deposited in the collection of the University of Costa Rica (UCR 14759).

Oviposition sites were associated with shady microhabitats within the forest floor. I found three clutches near the buttresses of large trees: two clutches were found in vertical crevices inside the buttresses of *Brosimum utile*, and one clutch was under deep leaf litter near the root mass of a *Ceiba pentandra*. I discovered a fourth clutch in the crack of a large boulder and a fifth in the deep leaf litter of *Scheelea rostrata* fronds. I found 11 female *E. fitzingeri* attending clutches in the months of January, February, April, June, and September (Table 2). I collected one attendant female and two gravid females and deposited them at UCR (UCR 14714, 16031, 16033).

I recorded seven clutches in primary forest and four clutches along streambeds. All were under leaf litter in deep shade, and nine clutches abutted roots, logs, buttress or boulders. All nests were circular inside a depression in the soil with the eggs flush with the surface of the ground. A small, raised, ridge of soil and debris surrounded the edge of each nest. It appeared that females created or modified these basins by clearing them out of all debris. When a female was brooding, her body completely covered the entire clutch. These females became rigid and flattened when disturbed and remained in this position when handled.

From 9 to 18 February 2002 I marked and monitored one attending female twice daily, once in the morning and once at night, for 10 days. During the day the attending female was always sitting on the eggs. The female attended the clutch everyday, and 8 out of 10 nights, until she disappeared. The eggs were not ready to hatch, and I estimated them to be at approximately stage 9 of development based on tail movements (Townsend and Stewart 1985).

Females attended eggs until they hatched. On three occasions I found females attending nests in the process of hatching. Hatchlings were found hopping on and under the leaf litter. The nests contained the remnant egg capsules. From 1 to 4 June 2001 I monitored a nest of new hatchlings dispersing from the nest. A female frog remained next to the clutch for three days until all hatchlings had dispersed. I observed a similar behavior on two other occasions. Hatchlings of *E. fitzingeri* had a visible yellow yolk sac and a mean SVL of 7.2 ± 0.74 mm (N = 36).

The average clutch size of *E. fitzingeri* was 62.1 ± 18.7 eggs with a range of 24 to 81 (N = 8, Table 2). A positive correlation exists between clutch size and female SVL ($r^2 = 0.54$, $df = 7$, N = 8) as has been reported in other *Eleutherodactylus* species (Wake 1978). I dissected two gravid females and counted 84 and 92 eggs, respectively. I excluded these from the analysis because it is unknown whether this species deposits multiple clutches. Egg diameter ranged from 2.80 mm to 5.71 mm for 99 eggs measured of four clutches (Table 2).

TABLE 2. Summary of clutch characteristics of *Eleutherodactylus fitzingeri*. Means reported as $\bar{x} \pm 1$ STD; all measurements are in millimeters.

Date	Female SVL	# Eggs per clutch	# Eggs Measured	Mean Egg Diameter	Nest Dimensions (L x W x H)	# Hatchlings Measured	Mean Hatchling Size	Locality
3 Apr 2000	55	71						Dominical
17 Apr 2000	41	24						Dominical
15 Jun 2000	43	45	9	4.97 ± 0.19	58 x 62 x 18			Dominical
22 Jun 2000	44	69						Dominical
22 Apr 2001	46	62			64 x 70 x 24			Tres Piedras
22 Apr 2001	45	71	72	5.42 ± 0.23	60 x 72 x 23			Tres Piedras
1 Jun 2001						16	7.1 ± 0.65	Tres Piedras
5 Sep 2001	51	74	74	3.10 ± 0.15	63 x 72 x 25			Tres Piedras
15 Sep 2001	57	81	9	3.27 ± 0.18				Palmar Norte
17 Jan 2002						11	7.0 ± 0.74	Tres Piedras
3 Feb 2002						9	7.0 ± 0.88	Tres Piedras
9 Feb 2002	57	84						Tres Piedras
9 Feb 2002	55	92						Tres Piedras
	$\bar{x} = 49.4 \pm 6.2$	$\bar{x} = 67.3 \pm 19.8$						

Non-rattling Defensive Tail Display in the Dusky Pygmy Rattlesnake, *Sistrurus miliarius barbouri*: A Previously Undescribed Behavior

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Eggs attendance is the most common form of anuran parental care (Wells 1981) and can serve many functions including: protection against predators and pathogens, aeration of aquatic eggs, hydration of terrestrial eggs, prevention of developmental abnormalities, and to assist hatchlings as they emerge from the nest (Crump 1994). In the case of terrestrial breeding species the principle function of parental care includes hydration of eggs and protection from invertebrate predators (Townsend 1996), which may be the case in *E. crassidigitus* and *E. fitzingeri*. This paper confirms the anecdotal observations of Dunn (1931), Mendoza Quijano et al. (2002), and Taylor (1952), that females of these two species provide parental care to their clutches by egg attendance. 100% of the clutches I found had an attending female present indicating that clutch attendance is obligatory and not facultative.

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Defensive tail displays are often exhibited by snakes with bright and/or blunt tails in response to a stressor or a tactile stimulus and depending on the species, these displays can vary in speed, duration, frequency and proportion of tail length used (Greene 1973). Tail displays also make the tail visually obvious to a potential predator and may provide survival value to a snake by intimidating the predator, diverting the predator's attack away from the head and toward the tail, or distracting the predator and thus allowing the snake to strike or escape (Greene 1973). While rattling in rattlesnakes is a well-known defensive tail display used in potentially dangerous situations, non-rattling defensive tail displays might also function either as warning, distraction, or disorientation mechanism as they do in non-rattlesnakes (Greene 1973, 1988, 1992, 1997; Klauber 1972). As part of a larger repertoire of defensive behaviors, non-rattling tail displays might be particularly useful for rattlesnakes with inaudible or barely audible rattle chains or for those rattlesnakes possessing an insufficient number of rattle segments to produce a rattling sound. Here, we document a non-rattling defensive tail display for the first time in the dusky pygmy rattlesnake, *Sistrurus miliarius barbouri*.

Sistrurus miliarius barbouri is a small rattlesnake species, seldom exceeding 55 cm, that has a bright yellow tail as a juvenile and a disproportionately small rattle compared to other rattlesnake species. Rowe et al. (2002) reported high rates of rattle loss in this species, with approximately one-half of all snakes examined possessing fewer than two interlocking segments. Because at least two interlocking segments are needed to produce a rattling sound, approximately one-half of all pygmy rattlesnakes are incapable of producing a rattling sound (Rowe et al., 2002). In field observations associated with another study, we noticed that in addition to rattling, this snake undulates its tail when captured. The entire tail is swayed back and forth in large arcs, while the distal half of the tail is wiggled in smaller sinusoidal movements. Both motions occur at a faster speed than those observed when this species caudal lures, and are often interrupted by brief periods of rattling that last approximately one second. Based on these observations and the bright and often rattleless tail of *S. m. barbouri*, we hypothesized that these undulatory (not vibratory) tail movements are a defensive tail display that is part of the typical defensive repertoire in *S. miliarius*. Based on this hypothesis and Greene's (1973) observations, we made two predictions about what we might ex-