



When Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*) in northerly climes hibernate, hundreds of them aggregate in the same hibernaculum. During the winter, this apparently serves to prevent them from freezing and they also have access to each other for breeding in the spring.



A heated conflict between two male Grass Frogs (*Rana temporaria*) and one male Common Toad (*Bufo bufo*). Clutches of frog eggs are visible in the water. See related note on p. 82.



An adult Red Milk Snake (*Lampropeltis triangulum syspila*) constricting and swallowing a large Woodland Vole (*Microtus pinetorum*). See related note on p. 94.



### Front Cover: Vipul Ramanuj

A King Cobra (*Ophiophagus hannah*) eating a Hump-nosed Pit Viper (*Hypnale hynale*) at the Agumbe Rainforest Research Station in the Western Ghats of India. See related article on p. 95.

### Back Cover: Jay Fleming

Yellow-bellied Sea Snakes (*Pelamis platurus*) are the only sea snake in the eastern Pacific Ocean, and the only species that is present on the Pacific Coast of Central America. See related article on p. 69.





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Even when visitors were present, Dr. Fitch was meticulous about recording data.

### REMEMBRANCE

### What's in a Name?

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Photographs by C. Kenneth Dodd, Jr.

Tearly 14 years have passed since I first heard the name "Dr. Henry Fitch," invariably spoken in tones of near-reverence. The name, often abbreviated to simply "Fitch," is always spoken softly, and followed by thoughtful, staring-at-your-shoes silence — even more so since his death. His absence in the herpetological community is sorely felt, even by those who knew him only vicariously through the legacy of his work. For those lucky enough to have had a closer relationship with the man, the scientist, (dare I say) the Legend, his loss leaves an indelible wound on the heart.

When first introduced to the name, I was only a "spouse of," part of a group of perhaps four, maybe six herpetologists and wildlife students, and



A permanent array of drift fences and traps led to many captures and recaptures during the 50-year study of the Reservation's snakes and lizards. Checking the traps was a daily ritual.

brand new to this world of amphibian-and-reptile legend, lore, science, and pioneers. Like the tip of an iceberg, the tone and silence, that inwardturning focus and gentle smile that accompanied the name "Fitch," foretold of a man who I sensed must be a giant among these men of science.

Whenever I asked: "Who is this Dr. Henry Fitch?" the answer came back unvaried: "You'll just have to meet him!" Luckily, I did...

For this occasion, I had again joined my husband, some of his colleagues, and numerous students for a field trip within the University of Kansas Fitch Natural History Reservation<sup>1</sup>. We stood in jittery clumps, shuffling our feet and staring off into the greening woods. We made halting conversation with one another as we waited for our guide to arrive.

My mental image of an iceberg-sized Greek hero assumed its true human form. An aged, frail-looking, stooped-back man came gingerly toward us, leaning on his well-used walking stick. He stood in a beam of morning sunlight, like an ancient turtle basking himself into wakefulness and optimum mobility. My companions and I eased back a bit, yielding him as much of the sun's energy as possible. Yet we remained close enough that our sight and hearing could still perceive every particle of him.

Here was Fitch, at last! The Legend. A frail little man?

Nevertheless, all that I had been led to believe proved true. Meeting him that day, with no exchange of words between us, told me something of the mystery surrounding that particular tone of voice, that air of inner contemplation and silent reverence that surrounded any mention of the name "Fitch." Cumulative, spontaneous honor and respect rippled through and around our little group like an invisible wave.

I don't remember what Dr. Fitch said to us that morning before we set off on our hike through his beloved woods. My ears, I think, went deaf in the midst of marvelous wonder. With the sun backlighting his thin body and his white hair aglow, dozens of butterflies suddenly appeared, lighting on his shirt, at his feet, or hovering around him. As he turned to go, he did so with awareness of this tender entourage, moving gently and carefully so as not to harm or frighten his little friends. Once in motion, however, his winged shroud dissipated as quickly as it had arrived. We loaded into two vans and headed deeper into the Reservation.

Dr. Fitch was the first to disembark. He wasted no time shepherding people, counting heads, or acting the tour guide. Once his feet touched the earth, he moved — and he moved like Gandhi, striding in a long-practiced rhythm that took him almost out of sight before we followers could assemble our thoughts. Across the meadow, up the hill, through the briar patch, over the crest, into the mixed-oak woodlands, and skimming the talus and limestone boulders, he traveled with all the ease of a field mouse on familiar terrain.

Awkwardly, we straggled into the small clearing beneath a copse of trees where Dr. Fitch stood smiling, patiently waiting, observing with some amusement each person's breathless arrival. We gathered around him, anxious to quell our huffing and puffing and miss nothing of what the soft-spoken man had to say. We tottered on the sharp-edged boulders that ringed the tiny clearing, jockeying for a somewhat level place to stand in an effort to disguise our mere-human condition.

<sup>&</sup>lt;sup>1</sup> The University of Kansas renamed its Natural History Reservation in 1986 to honor Henry Fitch.



Dr. Fitch measuring a Common Garter Snake (Thamnophis sirtalis).

"This," Fitch said when all had arrived, "is a good place for Copperheads." Several eyes rolled downward toward feet now frozen and precariously perched atop countless pockets where slender Copperheads might easily coil. I mentally calculated the difficulty I had in getting *down*hill to this scenic glen, and the likelihood of sure failure in getting my now-wearied, oxygen-deprived, flatlander's hide *up-n-out* in the event that such a beastie lay under *my* boulder.

"Here's one," Fitch announced calmly. His eyes were focused on a smallish boulder near his own feet. "I'll get it," he offered, slowly leaning toward the ground. One thin arm stretched out invitingly toward the snake as he leaned his bent frame ever closer to Mother Earth and Eden's scourge, his hand, arm, and face coming incrementally nearer to his deadly goal.

An audible, collective gasp rose from the circle of on-lookers. "Dr. Fitch," someone squeaked, "let one of us get it."

"No," replied the unperturbed leaning man. "I'll get it."

And so he did. As calmly and gently as a mother with a newborn, Fitch made his acquaintance with the Copperhead by the rock, picked it up without the use of hook or staff, and revealed his prize, face beaming with pure joy. He held it firmly behind the head in a well-practiced, strong, and confident hand. We all breathed again, but the frowns of concern for his safety did not relax.

"Oh," he said, and my heart skipped a beat (as I'm sure many others did), fearing that he had been bitten. But, no, his exclamation had simply been one of mild self-admonishment. "I forgot my snake bag," he said. "I'll have to take this old girl back to the van to get her stats."

Copperhead securely in hand and without further adieu, Dr. Fitch set to again with his Gandhi-stride. Skimming over the talus, he led us another merry chase ... up the slope, beneath the trees, through the briars, over the crest, down across the meadow. By the time we all had reassembled on the road by the two vans, Dr. Fitch had found his snake bag and had half the stats recorded.

"Done," he announced, beaming at us all with his smile. "I'll take her back now."

"Let one of us," someone offered, perhaps concerned for the thin legs that would have to traverse the route back ... and likely Copperhead cousins camouflaged in the dappled light beneath the trees.

"I'll do it," Fitch stated gently, but with a firmness that broached no discussion. "She and I are old friends," he added, in that same tone of reverence for the snake with which I'd heard his own name spoken. And off he went, across the meadow, over the crest into the briars, and out of sight. A few heartbeats later, his hoary head again topped the horizon. His mission accomplished, I saw him pause briefly on the crest amidst the briars, his face turned skyward with a look of love that encompassed the whole earth.

Dr. Henry Fitch. The name echoes in my memory with a tone of honor and a kind of love that I can't explain. Words cannot describe what I (and doubtless so many others) continue to feel for the man, the scientist, and (Yes!) the Legend. Every butterfly reminds me of that grand adventure in the Kansas woods on a summer day in 1996. Those lucky enough to have met him understand my inability to describe him. No one can put Henry Fitch into mere words; he had to be *experienced*.

Those who will only meet him through reading his biography, his lifetime of scientific writings, or others' memoirs will not begin to understand even half the man behind the name — but those who take the time to hear the subtext within the stories of this remarkable giant among men will doubtless be blessed for the effort. They and future generations may only make a tip-of-the-iceberg, second-hand acquaintance with the marvelous Henry Fitch, but oh what a discovery that will be! That sort of experience will still your heart, turn your thoughts inward, and broaden your vision to encompass the whole earth. It will make you smile into the sky, call all the little living things "old friend," and cause you to stare at your own two feet in silent wonder, hoping that you too can learn to walk with a Gandhi-stride and make a Fitch-difference in a world mostly unseen and un-experienced by the "civilized" masses.

Could there be any better way to honor the man than to walk in his legendary footsteps?



An "old friend." Dr. Fitch came to know many of the residents of the Fitch Natural History Reservation.



### New Perspectives on the Ecology and Natural History of the Yellow-bellied Sea Snake (Pelamis platurus) in Costa Rica: Does Precipitation Influence Distribution?

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"... narrative accounts of rarely observed events in species' life histories sometimes have much merit and value. Even a single observation may constitute a valuable contribution and may be a break-through in understanding the species' ecology."

Henry S. Fitch, 1987

Tore than 60 species of sea snakes have evolved and radiated to occupy tropical oceanic habitats. The majority of these (50+ species) are entirely marine and do not intentionally leave seawater (Heatwole 1999). Nonetheless, fewer than 2.5% of all snake species live in marine environments, and the evolutionary transition from terrestrial to marine

habitats is considered to be particularly difficult (Lillywhite et al. 2008a). Osmoregulatory challenges are paramount, and all marine species of snakes (indeed all marine reptiles) have evolved salt glands to assist with elimination of excess salt that is ingested with diet or incidental drinking. Water balance is a related but different issue, and the body water that is lost pas-



Fig. 1. Pelamis platurus on a Costa Rican beach. These snakes are sometimes stranded on beaches due to strong offshore winds that cause the snakes to drift toward the shore.

sively to the sea or in feces and secretions must be replenished either from freshwater sources or indirectly from food or seawater. The indirect sources involve further loading of salts and/or metabolites that must be eliminated with further losses of some water.

Recently, Lillywhite et al. (2008b) demonstrated that three species of Sea Kraits (*Laticauda* spp.) require fresh drinking water to replace body water deficits, as these snakes dehydrate in seawater in spite of the fact that they possess salt glands. Evidently, in these species, salt glands are important to ion balance but are insufficient to maintain water balance in marine environments. Based on current literature, representative species belonging to four out of five major lineages of marine snakes have been shown to require fresh water (or very dilute brackish water) for the maintenance of normal water balance (Lillywhite et al. 2008b). Therefore, changes in patterns of precipitation related to global warming may have important implications for the survival and distribution of marine snakes.

Whether so-called "true sea snakes," which are fully marine species, require fresh water for water balance remains to be determined. We are currently investigating this question, and we have some evidence for a freshwater requirement in the Yellow-bellied Sea Snake, *Pelamis platurus* (Figs. 1 & 2). Based on laboratory investigations of water and sodium fluxes in this species, Dunson and Robinson (1976) found that fasting *Pelamis* dehydrate in seawater (–0.4% body mass per day), and they documented drinking of fresh water when it was offered to dehydrated snakes. Snakes kept in seawater survive for long periods if fed on freshwater fish (Dunson and Robinson 1976; AS, pers. obs.), but whether these snakes can survive for long periods if kept in full seawater and fed on marine fish remains unclear.

### Yellow-bellied Sea Snakes (Pelamis platurus)

This species of sea snake has the broadest distribution of any snake. It ranges from the coastal waters of eastern Africa along the southern Asian coasts to Japan, southward and eastward to Australia and islands of the western Pacific, thence eastward to the Americas. It is the only sea snake that has reached the eastern Pacific Ocean, and is the only species that is present on the Pacific Coast of Central America. This snake is entirely marine, gives birth to living young at sea, and is pelagic in habits. It is a species of small to moderate size, reaching a maximum length of about 1 m (Solórzano 2004). *Pelamis* has been regarded as a "passive surface drifter" that is often wafted by currents to latitudes at which it is not a breeding resident (Dunson and Ehlert 1971). Because of its cosmopolitan distribution and pelagic habits, this species of sea snake is of central importance to testing the hypothesis that fresh water is required for physiological water balance in marine habitats.

Observations of others and our own collecting experiences in Costa Rica indicate that Pelamis are found in greatest numbers in association with oceanic "slicks" (Kropach 1971, 1975; Dunson and Ehlert 1971). Slicks are smooth glassy streaks forming drift lines in the ocean resulting from the accumulation of foam, floating plant parts, and other debris (flotsam; Fig. 3). They occur in convergence zones where organic material accumulates, flattens the water, and creates zones of concentrated biological activity. Slicks may contain contaminate films of organic oils probably derived from diatoms, and they become discernible because of their damping effect on small wavelets. The convergence zones are created by a variety of physical processes and currents such as internal waves and eddies (Ewing 1950). Slicks are biologically important because plankton become concentrated in the convergence zones and create good places for zooplankton and fishes to find food. Indeed, slicks have been regarded as biological communities. They can also be harmful to sea life, however, because they also concentrate noxious debris and pollutants. Slicks can be relatively small and shortlived, but they can also form drift lines extending for hundreds of meters or kilometers. They are likely agents favoring dispersal of sea snakes, but their dynamics in this context are very poorly understood. We propose three hypotheses for why sea snakes associate with oceanic slicks. First, a very popular notion in the literature is that slicks provide improved feeding opportunities due to occurrence of fishes seeking shelter beneath the floating debris (Kropach 1975, Heatwole 1999). A second hypothesis is that convergence of waters concentrates floating sea snakes just as it does floating debris, which would be a purely passive phenomenon. In support of this idea, others have conjectured that *Pelamis* probably does not actively seek out slicks (Dunson and Ehlert 1971). A third hypothesis is camouflage, for the sea snakes resemble some of the floating parts of plants both in color and in form, often mimicking floating sticks to which fish are attracted (Hunter and Mitchell 1968). This could reduce predation on sea snakes as well as facilitate their feeding opportunities. Kropach (1975) also suggested that gathering at slicks increased mating opportunities for sea snakes, but this would seem dependent on one of the other reasons for the primary association of snakes with slicks.

### The Coastal Distribution of Pelamis in Costa Rica

Yellow-bellied Sea Snakes are generally distributed along the entire Pacific coast of Costa Rica, and are usually found within 1–20 km of the coast (Voris 1983, Solórzano 2004). Especially dense populations have been noted at several locations in relatively close proximity to the coastline. These include Golfo de Papagayo and associated bays (Bahía Culebra and several playas immediately to its south), Cabo Blanco at the south end of the Nicoya Peninsula, waters between Bahía de Coronado and the northern end of the Osa Peninsula (Punta San Jose), and within the Golfo Dulce near the southern end of the country. These populations are known to us from the experiences of one of us (AS) or from literature. Other dense populations almost certainly occur elsewhere, but have not been brought to our attention.

We are presently exploring the hypothesis that the coastal distribution of *Pelamis* is partly dependent on the availability of fresh water. This was suggested for the euryhaline marine snake Acrochordus granulatus (Lillywhite and Ellis 1994) and was demonstrated to be the case where species of Laticauda, or "Sea Kraits," have been studied on a local scale at Orchid Island, Taiwan (Lillywhite et al. 2008b). Three species of Laticauda are abundant at sites with access to a freshwater spring or estuary, whereas few or no snakes are found at strictly seawater sites. Moreover, the abundance of these snakes also varies with rainfall, and fewer snakes are found during periods of drought or low rainfall. As discussed elsewhere (Lillywhite et al. 2008b), Laticauda spp. exhibit a patchy distribution that correlates with low-salinity tropical waters in the western Pacific and Indian Oceans. Also, a preliminary assessment of sea snake distribution in tropical south Asia and the Indo-Australian region reveals that the species diversity of all sea snake species correlates with mean annual rainfall (Lillywhite et al. 2008b).

Several sources of fresh water are potentially available to sea snakes. In addition to precipitation, these include springs, estuaries, or temporary outflows from the coast. Heavy rainfall forms a temporary freshwater lens at the ocean surface due to the density difference from seawater, and such lenses are the only source of fresh drinking water in the open sea away from the immediate coastline. The fact that Pelamis in Costa Rica can be found nearer to the coast during the dry season (AS, unpubl. obs.) is potentially relevant; and in Mexico, even more pronounced seasonal changes in distribution are evident (HL and CS, unpubl. obs.; see also Duellman 1961). These snakes might be moving to closer associations with coastal estuaries during periodic droughts, based on knowledge of sites with which we are familiar from our own fieldwork. Pelamis are occasionally reported from estuaries (Shuntov 1966). Indeed, various species of sea snakes are observed in estuaries, and they sometimes move considerable distances into rivers (Dunson 1975). Alternatively, Pelamis might appear to be more abundant nearer the coast due to prevailing stronger winds during the dry season, which could wash these snakes onto the shore at times (Solórzano 2004). Numerous reputable observers have described strandings of *Pelamis* on beaches, usually in association with storms (Dunson and Ehlert 1971). Slicks also might form in greater number near the coastal bays during the



Fig. 2. Pelamis platurus illustrating some of the variation of color pattern, which varies from mostly black to black and white or yellow to all yellow.

dry season. These hypotheses remain to be tested with the alternative explanations in mind.

#### Conclusion

Some marine snakes, including certain sea snakes, have been shown to be dependent on access to fresh water for water balance and occur in greater abundance near freshwater sources (Lillywhite et al. 2008b). We do not know whether the majority of sea snake species, which are entirely aquatic,







**Fig. 3.** Slicks seen near Playa del Coco, Costa Rica. (A) A narrow slick identified by foamy driftline. (B) Flotsam and debris associated with a slick. (C) A broader slick without debris; note the calm water in the center of the photograph.

also require fresh water. Physiological studies suggest that the pelagic species Pelamis platurus dehydrates in seawater and will drink fresh water in the laboratory (Dunson and Robinson 1976). Thus, one might infer that Pelamis requires fresh water for water balance, but this aspect of its physiology remains to be properly tested and documented. The movements of this pelagic species are largely unknown, but some features of its distribution in Costa Rica suggest that it might associate more closely with coastal sources of fresh water, such as estuaries, during times of periodic drought. The potential influence of fresh water on movements of this species might affect metapopulation dynamics in important ways that remain to be explored. We are currently investigating the physiology, distribution, and genetic structure of Pelamis populations in these contexts. Knowledge of the water requirements of sea snakes — and Pelamis in particular — will enhance our understanding of the distribution of these marine reptiles and how they might respond to future changes in the distribution, intensity, and periodicity of precipitation.

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### Observations and Comments on the Diet of the Many-banded Krait (Bungarus multicinctus multicinctus) in Taiwan

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The Many-banded Krait (Bungarus multicinctus multicinctus, Fig. 1) **1** occurs naturally in Burma, the Indo-Chinese Peninsula, southern China, Hainan, Hong Kong, and Taiwan (U.S. Department of the Navy 1991, Zhao and Adler 1993). We found a dead-on-road (DOR) male on 2 November 2007 on the Northern Cross Road (Route No. 7) close to Minchi (elevation 1,021 m; TWD 97, N 24.614164°, E 121.482272°), Yilan County, northern Taiwan. Snout-vent length (SVL in mm), taillength (TL in mm), and body mass (BM in g) were 740 mm, 100 mm, and 98.9 g (excluding stomach contents), respectively. We immediately noticed that an undigested snake's tail and the krait's own heart were protruding from the damaged part of the upper throat region (Fig. 2). Dissection revealed two ophidian prey items in the digestive tract, a juvenile male

Mountain Wolf Snake (Lycodon ruhstrati ruhstrati; SVL 260 mm, TL 82 mm, BM 6 g) and an adult female Mountain Keelback (Pseudoxenodon stejnegeri stejnegeri; SVL 490 mm, TL 88 mm, BM 41.1 g). The anteriormost portions of both prey items were partly digested, which indicated they had been ingested in headfirst positions (Fig. 3).

Lue et al. (2002) suggested that the coloration of L. r. ruhstrati is a form of Batesian mimicry, causing it to resemble B. m. multicinctus, although these two species differ in their defensive behavior (Norcal [sic] and Mao 2006). Mao (1970) reported cannibalism in B. m. multicinctus in Taiwan. Therefore, the krait-resembling coloration of L. r. ruhstrati may provide a degree of protection in most predator encounters, but not against predation by B. m. multicinctus.



Fig. 1. The Many-banded Krait (Bungarus multicinctus multicinctus) in Taiwan occurs in a variety of habitats, many of which (e.g., low grassy areas, rice paddies, irrigation ditches) are associated with water.

Pseudoxenodon s. stejnegeri occurs mainly in mountainous regions at elevations of about 1,000 m above sea level, but B. m. multicinctus usually occurs at lower elevations. Pope (1935) reported B. m. multicinctus at 700 m in Kuatun, mainland China, and assumed that that was the species' maximum elevational distribution. Kuntz (1963) stated that they occur primarily at low elevations (below 600 m) in Taiwan, and Lue et al. (2002) surmised that this snake species occurs mainly at altitudes below 500 m, and that they only rarely can be found at 500–1,000 m. Our observation, however, can not conclusively prove that B. m. multicinctus occurs naturally in Minchi, because some snakes, especially the Chinese Cobra (Naja atra), Many-banded Krait, and Oriental Ratsnake (Ptyas mucosa) are released by certain religious groups along Route No. 7, especially between Sze-lan and Minchi (Mao, pers. obs.; Yo and Wong 2007). However, our observation does show that snakes can be exploited by B. m. multicinctus in mountainous areas.

Kuntz (1963) indicated that *B. m. multicinctus* in Taiwan occurs in a variety of habitats (e.g., lowland wooded areas, bamboo thickets, grassy areas associated with water, rice paddies, irrigation ditches), whereas Mao (1970) simply stated that *B. m. multicinctus* prefers habitats near water. Many-banded Kraits reportedly feed primarily on loaches, frogs, skinks, snakes, and mice (Mao 1993, Zhao et al. 1998). Slowinski (1994) noted that, compared to the other kraits in the genus *Bungarus* (e.g., *B. ceylonicus*, *B. fasciatus*, and *B. caeruleus*), *B. m. multicinctus* appears to be more piscivorous (63.16%) than



**Fig. 2.** The road-killed Many-banded Krait, with its heart and the tail of a *Pseudoxenodon stejnegeri stejnegeri* protruding from the damaged section of its body.



**Fig. 3.** From left to right: The road-killed *Bungarus multicinctus multicinctus* and its prey: *Lycodon ruhstrati ruhstrati* and *Pseudoxenodon stejnegeri stejnegeri*. Note the partly digested head regions of the snakes that were consumed.

ophiophagous (34.21%). This conclusion was based on the results of Mao (1970), who also reported that larger individuals tend to be more ophiophagous than smaller ones, and that prey correlated closely with habitat, although he failed to provide habitat descriptions, and listed only Taoyuan County as a collection site. Lin et al. (1995), on the other hand, reported B. m. multicinctus to be more ophiophagous, and attributed piscivory to ontogenetic changes in diet or to low-elevation wetland pollution and/or habitat destruction for industrial and community development. Based on the prey items reported and the collection site description in Mao (1970), we determined that all prey types described were species restricted to low-elevation rice paddies, ponds, and adjacent areas. Our conclusion is further supported by descriptions of the dominant land utilization of the Taoyuan area at that time (Yang 1994), which were ideal for wetland fauna and flora. The report of Lin (1995), in contrast, was based on specimens collected by road sampling, especially in mountainous areas. We thus concluded that the apparently contradictory dietary preferences reported by Mao (1970) and Lin (1995) may merely reflect sampling of different habitats, leading to the question whether habitat heterogeneity could account for unusual prey exploitation by B. m. multicinctus.

In 1997–2009, we conducted ecological studies on snakes in wetland (e.g., rice paddies, drainage ditches, ponds, streams, etc.) and non-wetland

**Table 1.** Prey of Many-banded Kraits (*Bungarus multicinctus multicinctus*) collected from wetland (e.g., ponds and rice paddies) and non-wetland (e.g., secondary forests and dry cultivated areas) habitats in Taiwan. An asterisk (\*) indicates that a species occurs in both habitat types, but, in this case, it was recorded from a Betel Nut Palm plantation, which is classified as dry cultivated land. References: ¹this study; ²Mao 1970; ³Day et al. 1994; ⁴Lin et al. 1995; ⁵Mao et al. 2006; ⁶Lin 2008; ⁶Mao, unpubl. data; ⁵Norval, unpubl. data; °Ji-Shou Yang, pers comm.

	Wetlands	Non-wetlands
Snakes	Enhydris plumbea (n = 9)²	Ramphotyphlops braminus (n = 1) <sup>4</sup>
	Bungarus m. multicinctus (n = 1) <sup>2</sup>	Amphiesma stolatum* $(n = 1)^7$
	<i>Xenochrophis piscator</i> $(n = 3)^7$	Cyclophiops major $(n = 2)^{3,7}$
		Orthriophis taeniura friesei $(n = 1)^8$
		Lycodon r. ruhstrati $(n = 1)^1$
		Pseudoxenodon s. stejnegeri $(n = 1)^1$
		Protobothrops mucrosquamatus $(n = 1)^5$
		Viridovipera s. stejnegeri (n = 2) <sup>7, 9</sup>
Lizards	Plestiodon chinensis formosensis (n = 1) <sup>2</sup>	Plestiodon elegans (n = 2) <sup>4</sup>
	Eutropis multifasciata (n = 1) <sup>6</sup>	Sphenomorphus indicus (n = 1) <sup>4</sup>
Fish	Misgurnus anguillicaudatus (n = 10) <sup>2</sup>	
	Fulta alba $(n = 14)^2$	



Fig. 4. A Many-banded Krait catching and consuming a Taiwan Habu (Protobothrops mucrosquamatus).

areas (e.g., dry cultivated lands, betel nut palm plantations, mountainous and foothill secondary forests, bamboo thickets, etc.) of Taiwan. Apart from chance encounters, we also made use of traps to collect snakes. In wetland habitats, we employed floating funnel traps, baited with loaches to collect semi-aquatic snakes, and, except for these water snakes (i.e., Chinese Water Snake, Enhydris chinensis; Plumbeous Water Snake, E. plumbea; Ringed Water Snake, Sinonatrix annularis, Olive Keelback, S. percarinata suriki; and Chequered Keelback, Xenochrophis piscator), B. m. multicinctus was the most frequently collected species and always ate all of the bait in the trap. A short drift-fence/funnel-trap unit was utilized in non-wetland areas. Again, some B. m. multicinctus were collected, although the nearest permanent water sources (e.g., stream, wetland, pond, etc.) were as far as 1 km away. We compared the prey items of all B. m. multicinctus encountered in these habitats and those recorded in the literature (Table 1).

Except for species such as the Five-lined Blue-tailed Skink (Plestiodon elegans), Indian Forest Skink (Sphenomorphus indicus), Chinese Green Snake (Cyclophiops major), L. r. ruhstrati, P. s. stejnegeri, and Chinese Green Treeviper (Viridovipera stejnegeri stejnegeri), which occur to moderate elevations (~1,000 m) in Taiwan, most of the reptilian prey of B. m. multicinctus are species that occur in the lowlands (Lue et al. 2002). We also found that B. m. multicinctus from wetland habitats prey more frequently on loaches, eels, and semi-aquatic snakes in that order of frequency, whereas B. m. multicinctus from non-wetland or mountainous forest habitats prey primarily on terrestrial or semi-arboreal snakes (e.g., C. major, V. s. stejnegeri, Taiwan Habu, Protobothrops mucrosquamatus, Fig. 4) and terrestrial skinks (e.g., P. elegans, S. indicus).

Pope (1935) reported predation on mice and frogs by B. m. multicinctus, but neither of these prey types were recorded from B. m. multicinctus in nature. Consumption of mice and frogs appears to be based on observations under captive conditions; at best, they are rare dietary items of B. m.

multicinctus, despite references to the contrary (e.g., Maki, 1935). Under captive conditions, we have observed that a few B. m. multicinctus accept newborn mice as prey, which suggests individual variation in accepting various prey. As for frogs, even though Maki (1935), Kuntz (1963), and Mao (1970, 1993) listed frogs as prey items of B. m. multicinctus, we were unable to confirm that possibility. While working at the Wildlife Animal Shelter, National Pingtung University of Science and Technology in 2001, the first author never observed B. m. multicinctus attempting to prey on two sympatric wetland frogs (Cricket Frog, Fejervarya limnocharis and Taiwanese Frog, Hoplobatrachus rugulosus) that were offered as food. Frogs recorded in stomach contents of B. m. multicinctus might have been prey of other snakes, such as the Buff-striped Keelback (Amphiesma stolatum), E. plumbea, or X. piscator, which had been eaten by kraits. However, regardless of prey type (snakes, loaches, eels, or skinks), all share one feature — a cylindrical body shape. This would indicate that B. m. multicinctus exhibits a preference for cylindrical prey items, as do some sea snakes (e.g., Voris and Voris 1983).

In conclusion, prey availability in different habitat types appears to be reflected in the diet of B. m. multicinctus, with only cylindrical body shape as a common denominator. Consequently, studies describing prey taken by kraits should consider the type of habitat from which the animals in question were taken.

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### Blocked-flight Aggressive Behavior in Snakes

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Every naturalist accumulates field observations and experiences worthy of Eexpanding into full-blown research projects. More often than not, however, the information languishes undeveloped in memory, paper piles, and these days, computer files. Some interesting observations on snake behavior I have made over the years are among my many unfinished projects.

Experienced naturalists know that most snakes flee when encountered in nature. More sedentary, slow-moving, or cryptic snakes will remain still or coiled in order to go unnoticed. Rattlesnakes, when disturbed, coil and rattle. After a while, they also may move away from the intruder, perhaps continuing to rattle as they break out of their coil and flee. A few snakes, however, do something different.



**Fig. 1.** A Cottonmouth (*Agkistrodon piscivorus*) "chasing" the author while engaged in aggressive behavior during blocked flight with head raised, striking, flattening its body, vibrating its tail, and moving directly toward the author. This snake did not follow the author when he stepped aside, but raced to safety into the water beyond.



Fig. 2. A Cottonmouth mouth-gaping as it crawls toward the author.

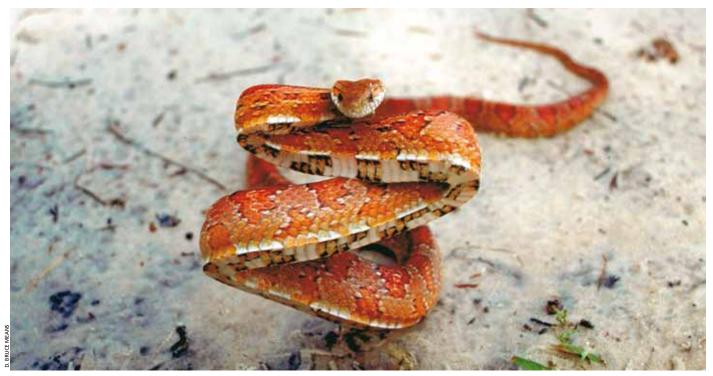


Fig. 3. An Eastern Cornsnake (Pantherophis guttatus) crawling toward the author, striking forward, as he blocks its escape from a dirt road.

That different behavior was first displayed to me when an adult Eastern Cottonmouth (Agkistrodon piscivorus conanti) rose up like a cobra and menacingly crawled toward me in front of a dozen students (Fig. 1). I had just guaranteed my field class that Cottonmouths do not chase people. In those few moments, as I rapidly backed up from the approaching snake, a potential behavioral study was born (see Chapter 8 in Means 2008).

We had encountered the snake one warm late afternoon in May, when snakes — and Cottonmouths especially — are most likely to move. It was crossing a wide, sandy road in the Apalachicola National Forest of the Florida panhandle The adjacent swamp from which the Cottonmouth had emerged was drying up from a severe drought, and the snake probably was looking for new aquatic habitat or a drying waterhole from which to gorge on the concentrated aquatic animals.

As so often happens with snakes, it stopped crawling as my vehicle approached and was fully stretched out in a "frozen" posture. I lined up the students on the road shoulder from which the snake had come and I took a position on the other side, blocking its forward motion. Our movements stimulated it to coil up and do its "Cottonmouth" display, with its attention focused on me, who was closest to the snake and gesticulating to the group. After a few minutes, the snake suddenly rose up cobra-like and began crawling rapidly at me with the forward one-fourth of its body raised.

With its neck spread slightly, the snake continued to advance as I backpedaled, making a few striking parries as it neared my feet. When I stepped sideways from the snake's trajectory (which was directly toward a swamp on the other side of the road), I was gratified that the snake maintained its original direction and did not turn to follow (or "chase") me. Its "aggressive" behavior obviously was a bluff to assist the snake in making its getaway into the safety of the swamp.

Realizing that this poorly trafficked, wide sandy road between two swamps offered an ideal site to study this behavior, my wife, Kathy Steinheimer, and I road-cruised this 0.5-km stretch ten times in the next two years. She videotaped 16 episodes of me interacting with Cottonmouths. Cottonmouths "chased" me 10 of 17 times that I blocked their movement. It simply appears to be bluffing behavior, but aggressive nevertheless. I call it shammed (bluffed) aggression during blocked flight.

Cottonmouths engaged in such aggressive flight exhibited several characteristic behaviors, including crawling rapidly toward me, raising the head and neck off the ground, expanding the jaws, flattening the body, vibrating the tail, tongue-flicking, lunging and striking forward, and rarely, musk-squirting. A great deal of variation exists in the intensity of these behaviors. A few displayed the behavior as they dashed toward the cover of the roadside vegetation. Some assumed the classic coil-up and mouth-gape defense first and then broke into aggressive flight within a few minutes.

I was able to initiate flight behavior in a coiled Cottonmouth simply by flipping it over on its back by means of my snake hook. Upon righting itself, the snake ended up lying in a straight position. It then either coiled again and mouth-gaped, or fled, at which time I could step in front of it. Other Cottonmouths were relatively placid, coiling repeatedly and refusing to flee. Of the 17, one hid its head under its body when coiled and refused to break out of that posture. Another mouth-gaped as it crawled rapidly toward me (Fig. 2). Another interesting behavior we noted is that when fleeing Cottonmouths crawled out of the sandy roadbed and entered the roadside vegetation, they sped up their forward motion and became even more animated in their aggressive bluffing.

Allen and Swindell (1948) were the first to describe aggressive flight in the Cottonmouth: "One three footer, when approached, struck upward so hard that he lifted his body off the ground. He advanced, coiling and striking repeatedly, following the retreat of the observer. Others have been seen to charge deliberately with open mouth. Most attackers seem to do so in a bluffing manner rather than in vicious pursuit."

More recently, studies have analyzed Cottonmouth defensive behaviors in response to being stepped on or approached closely, and to being picked up with an artificial arm (Gibbons and Dorcas 2002, Glaudas and Winne 2007). In these studies, caged snakes or those with unrestricted opportunities to flee were less likely to display aggressive flight behavior. Apparently, the behavior is most likely to be triggered when free-ranging snakes are blocked along a chosen trajectory after they are already in flight.

My intention in videotaping these "chase" episodes was to do a study of Cottonmouth behavior during blocked flight by analyzing the filmed sequences. Alas, when I returned from an overseas trip, I discovered that the



Fig. 4. An Eastern Brownsnake (*Pseudonaja textilis*) coming straight for the author as he backs away.

tape containing the episodes had been accidentally overwritten with soap operas, so the project has not been resurrected. Because the two of us were busy videotaping the short-lasting behavior, we took few still photos, which only show "snapshots" of the full behavior.

Over the years, I have encountered similar shammed aggression during blocked flight by several species of snakes. The behavior is induced only when one places one's body in front of a moving snake, blocking its escape. Many snakes, especially colubrids, will turn and flee in another direction, but some do not. In snakes as small as Pigmy Rattlesnakes (*Sistrurus miliarius barbouri*), I stimulated similar bluffed aggression episodes in two of seven individuals. I even encountered an Eastern Corn Snake (*Pantherophis guttatus*) crossing a road that rose up and tried to bluff me out of its way (Fig. 3).



Fig. 5. A Southern Banded Watersnake (*Nerodia fasciata*) mimicking the aggressive flight behavior of the Cottonmouth, sham-striking forward with head raised, body inflated, and jaws widened.

In Victoria State, Australia, I deliberately stepped in front of a crawling Eastern Brownsnake (*Pseudonaja textilis*) and got another surprise (Fig. 4). Not only did it rise cobra-like and move threateningly towards me, but it also seemed purposefully to exaggerate the undulations of its body in the loose gravel of the road. This fast-moving snake is extremely venomous and responsible for more snakebite deaths in Australia than any other species (Whitaker et al. 2000). Fortunately, as I stepped out of its trajectory, it did not turn toward me but attempted to make good its escape in the direction it was fleeing. Whittaker and Shine (1999) described 455 defen-

sive responses of free-ranging Eastern Brownsnakes to experimental close encounters with humans, but scored only 12 of these in which the snake advanced towards the observer. Of these, only three advances were judged to be offensive. In their study, however, they did not report attempts to block the path of the snake once it began to flee. Researchers have observed that many other large Australian elapids react to an intruder by rising up, flattening the neck, opening the mouth, and continuing in the direction of the intruder (Johnson 1975, Greer 1997).

My most interesting encounter with a bluffing snake has to be an example of behavioral mimicry. One morning in June 2002, I was walking along the sparsely vegetated floodplain of the Escambia River in western Florida when, suddenly, a snake rose up cobra-like and crawled rapidly upright while I walked at a safe distance alongside it taking photos of what I assumed was another Cottonmouth engaged in aggressive bluffing. Its body proportions, pattern, and behavior were so like a Cottonmouth that I didn't discover its true identity until I looked at my digital readout. It was a perfect Cottonmouth mimic, a Southern Banded Watersnake, *Nerodia fasciata* (Fig. 5).

Diverting many species of snakes from the beeline trajectory of their intended direction is often difficult. This has been particularly evident to me during attempts to photograph moving snakes. Many seem fixated on the original direction of their movement so that one cannot easily make a snake reverse its heading. Drag the snake backwards and it will repeatedly crawl forward along its previous track.

I believe that the "aggressive bluffing" behavior I have witnessed in the Cottonmouth, Pigmy Rattlesnake, Corn Snake, Eastern Brownsnake, and Banded Water Snake were elicited under the special circumstances of encountering the snakes in habitats familiar to them and by blocking their escape along a direction they had chosen. Future studies of aggressive behaviors exhibited during blocked flight should take these *a priori* conditions into account.

I probably do not have time in my life to travel the world looking for opportunities to block the escape path of wild snakes, but maybe by reporting these observations — about which I feel sure Henry Fitch would have enjoyed reading — will stimulate other naturalists to watch for "bluffed aggression during blocked flight" in snakes everywhere. I suspect that most experienced field herpetologists have had similar encounters with snakes, and the list of snake species that do this may be long. I cannot help but wonder if shammed aggression behaviors are more prevalent in venomous snakes, since they are more likely to survive an attack by envenomating the intruder if the bluff doesn't work. Maybe someone will conduct in-depth studies and a more complete review of this interesting behavioral phenomenon in snakes, although I urge snake-lovers not to try these potentially dangerous experiments, and professional herpetologists who might do so should wear proper snake boots and other snakebite-prevention apparel, unlike me in Figures 1 and 4.

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### Terrestrial Burrowing in Nesting Softshell Turtles (Apalone mutica and A. spinifera)

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Photographs by the senior author.

After nesting, female Softshells have been observed to burrow for variable distances under the sand surface in close proximity to the just-completed nest. We describe terrestrial burrowing behavior in Apalone mutica and A. spinifera from Kansas, Arkansas, and Louisiana and discuss possible reasons for the behavior.

Tost nesting freshwater turtles minimize their time spent terrestrially, ost nesting treshwater turies minimize clear leaving the water to nest and returning immediately following nesting (Burke et al. 1994). Exceptions to this include some turtles that migrate long distances to nest (e.g., Emydoidea blandingi; Rowe and Moll 1991) and species that bury themselves after nesting (e.g., Kinosternon flavescens and K. subrubrum; Iverson 1990, Burke et al. 1994). Putative reasons for burrowing in Kinosternon include nest attendance/defense and awaiting conditions that would reduce stress or increase survival during the turtles' return to water (Iverson 1990, Burke et al. 1994).





Fig. 1. Male Apalone spinifera (top) and male A. mutica (bottom).





Fig. 2. Softshell habitat on sandbars of the Kaw River in Kansas (top) and nesting habitat along the White River in Arkansas (bottom).

North American Softshells (Apalone spp.; Fig. 1) are well known for their characteristic behavior of burrowing into sand and other soft substrates under water (Webb 1962, Graham and Graham 1991); however, little is known regarding their propensity to burrow terrestrially after nesting. We have observed shallow terrestrial "troughs" in association with nesting crawls of A. mutica and A. spinifera on sandbars that result from females crawling just underneath the surface of the sand and resurfacing some dis-





**Fig. 3.** (A) A curved trough (dashed outline) of *Apalone spinifera* on the Comite River in Louisiana. (B) A straight trough (dashed outline) of *A. mutica* on the White River in Arkansas. The researcher is probing to find the exact location of the nest.

tance away. We also have observed the process of trough excavation in one *A. mutica*.

Collectively, we have observed a total of 8 troughs of *A. mutica* on sandbars of the Kansas River in Kansas (Plummer 1976, unpubl. data, 7 troughs of *A. mutica* on the White River in Arkansas (Plummer, unpubl. data), and 7 troughs of *A. spinifera* and 4 unidentified *Apalone* troughs on the Comite River in Louisiana (Doody 1995). Troughs varied in length from 0.5–4.0 m (mean 2.2 ± 1.24 m SD in Louisiana) and about 20–30 cm in width. Troughs (Fig. 3) varied in shape from straight to curved to sinuous to figure-eight shaped. One trough that appeared to be made by one female *A. mutica* consisted of three separate segments in close proximity, each approximately 2–3 m in length.

Most nesting crawls of *A. mutica* and *A. spinifera* did not exhibit troughs (72 of 77; 93.5% nests of *A. mutica* and 198 of 209; 94.7% nests of *A. spinifera*). However, 5 of 8 (63%) troughs contained nests in Kansas and 11 of 15 (73%) troughs contained nests in Louisiana. Troughs were found only during the nesting season (late May–mid July for both species). Except for basking, this period is generally the only time the highly aquatic softshells are found in terrestrial situations (Webb 1962). We have found both preand post-nesting adult females (Fig. 4) burrowed typically at the exit end of the trough, but we have not found hatchlings, juveniles, adult males, or subadult females in troughs. Nests may occur anywhere in the trough, but usually were toward one end, most often at the entrance (Fig. 3B).

Few literature references address nesting troughs or their function. Harper (1926) noted that nesting softshells (probably *A. ferox*) sometimes burrowed before returning to water. *Apalone* spp. generally nest on open sandbars on sunny days (Webb 1962, Plummer 1976, Doody 1995), when extended exposure to high temperatures could presumably be lethal. One hypothesis for the function of troughs is that mothers burrow to temporarily escape high surface temperatures and await optimal conditions for return to water. This behavior is similar to that of Mud Turtles (*Kinosternon*), which nest long distances from their aquatic habitats (Burke et al. 1994).

Alternatively, burrowing turtles may exhibit cryptic behavior in response to disturbance or predation risk. In support, one *A. mutica* burrowed terrestrially after being disturbed by MVP while she was nesting. Burrowing by *Apalone* is common in aquatic situations (Graham and Graham 1991). For example, when approached from some distance, individual turtles will readily bury themselves under the sand in shallow water (Graham and Graham 1991; JSD, pers. obs.; MVP, pers. obs.).

Another possible function is that nesting turtles bury themselves to more closely assess the suitability of substrate characteristics such as temperature. However, only 5% of 68 *A. spinifera* nests in one study were associated with the behavior (Doody 1995). Finally, mothers may simply respond to a physical constraint. Extended hot weather conditions or coarse-grained sand may render surface sand not cohesive, causing the sand to cave in on itself when a turtle attempts to excavate a chamber (Doody et al. 2004; Fig. 5) or when hatchlings try to emerge from the nest chamber (Mortimer 1990; Fig. 6). As a consequence, the closely related Pig-nosed Turtle (*Carettochelys insculpta*) may nest at lower elevations on sandbars due to the friable sand at higher elevations (Doody et al. 2004); however, lower elevations increase the risk of flood mortality. By burrowing, softshell



Fig. 4. Female Softshells, such as this *Apalone spinifera* from Gin Creek, Arkansas, can be quite large.

mothers could excavate a nest in cohesive sand by removing the uppermost loose sand. This putative behavior is perhaps a simpler version of bodypitting displayed by sea turtles and the Amazonian Giant River Turtle, Podocnemis expansa (Schauble et al. 2006, Vogt 2008). Body-pitting may aid turtles attempting to nest on sandbars that have a layer of loose, dry sand. In support of this hypothesis, Apalone nests associated with troughs were deeper than those without troughs (Doody 1995).

Although we have generated hypotheses for the unusual "troughing" behavior exhibited by softshells, current evidence does not allow us to favor any particular one. Focal observations of nesting turtles would be particularly useful but difficult given the relatively low frequency of the behavior. Accordingly, the thermoregulation hypothesis would be difficult to test. However, the other two hypotheses may be more easily testable. First, mock predators or some other disturbance could be introduced to nesting turtles to test the predation risk hypothesis. Second, the cohesive sand hypothesis could be addressed by attempting to excavate an artificial nest chamber next to the trough. Failure to create a chamber would lend support to this idea (Doody et al. 2004).

### Acknowledgments

After informing Henry Fitch about the unusual behavior of a nesting female Apalone mutica that MVP had observed on the Kansas River during the 1973 nesting season, Henry said, "You ought to look into that." Well Henry, here it is — thanks for the suggestion.



Fig 5. A female Apalone mutica excavating a nest along the White River, Arkansas.



Fig. 6. Hatchling Apalone mutica ready to emerge from a nest (the top 5 cm of sand has been brushed back) along the Comite River, Louisiana.

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### Apparent Competition by Grass Frogs (Rana temporaria) and Common Toads (Bufo bufo) for Breeding Sites

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Photographs by the author.

The Grass Frog (*Rana temporaria*; Fig. 1) is widespread throughout most of Europe, ranging from northern Spain to the Urals (absent from southern and central Iberia, much of southern Italy, and the Caucasus) and east to western Siberia and northern Kazakhstan through northern Greece and Bulgaria. The species has a patchy distribution in mountainous parts of the Balkans. It has been recorded from sea level to elevations approaching 2,700 m above sea level (asl) in the Pyrenees.

The Common Toad (*Bufo bufo*; Fig. 2) is widespread in Europe (excluding Ireland and most Mediterranean islands, although present on Sicily) and northern Eurasia, with populations in parts of western



 $\textbf{Fig. 1.} \ \, \textbf{An adult male Grass Frog } \textit{(Rana temporaria)} \ \, \textbf{approaching the breeding pond.}$ 



Fig. 2. An adult female Common Toad (Bufo bufo).



Fig. 3. The Bohemian forest pond where frogs and toads apparently competed for calling and mating sites.

Asia (Turkey, Syrian Arab Republic, and Lebanon) and northern Africa (Morocco, Algeria, and Tunisia). In Europe, the species is present in most areas (including the United Kingdom and Scandinavia), ranging as far east as northern Kazakhstan and eastern Siberia. In the Middle East, it is found through much of Turkey, northwestern Syrian Arab Republic, and has recently been recorded from two mountainous locations in Lebanon. In Africa, it has a very fragmented range in the more mountainous regions. The species has an altitudinal range of sea level to 3,000 m asl; however, in northern portions of the range the species occurs only at lower elevations.

I observed reproductive activity of Grass Frogs at a forest pond on the southeastern edge of the Middle Bohemian Region at an altitude of ~410 m asl (49° 48' N, 15° 21' E; Fig. 3). Once quite common in the region, populations of these frogs have recently been declining, with extended dry periods through the spring and summer of recent years playing a major role. Drought conditions leave frog broods with a low probability of surviving until metamorphosis.

Reproductive activity for local amphibians begins with spring warming trends. On 3 April 2009, large numbers of male Common Toads (*Bufo bufo*) appeared at the pond, and I observed egg-laying and fertilization during the following two days. The first vocalizing male Grass Frogs began to congregate on 6 April. Ovipositing began that evening and continued through the following day (Fig. 4).

On the morning of 7 April, a group of about 15 male Grass Frogs were interspersed with a rowdy collection of about 10 Common Toads. Males of both species were actively vocalizing. A skirmish ensued among the males of both species, leaving individual toads and frogs limping and injured. One battle between two Grass Frogs and one Common Toad (Fig. 5) was particularly heated, as these males apparently competed for prime calling and mating sites.



Fig. 4. Congregating Grass Frogs and egg masses.



Fig. 5. A heated conflict between two male Grass Frogs and one male Common Toad. Clutches of frog eggs are visible in the water.

### Submerged Calling by Oregon Spotted Frogs (Rana pretiosa) Remote from Breeding Aggregations

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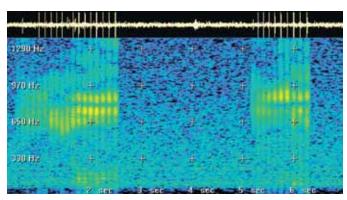
Frog calls, largely associated with reproduction (i.e., advertisement and release calls), have been the subject of much interest and study (Schiötz 1973, Rosen and Lemon 1974, Wells 1977, Fellers 1979, Duellman and Trueb 1986, Kelley 2004). Although we mostly hear frog calls and choruses coming from the surfaces of ponds, a number of species call while submerged. *Xenopus* and other pipids, all highly aquatic frogs, call while submerged (Elepfandt 1996, Christensen-Dalsgaard and Elepfandt 2004). Platz (1993) described a new species of leopard frog (*Rana subaquavocalis*; but see Goldberg et al. 2004) that exclusively emits mating calls while submerged that are inaudible at the surface. Ranids from the western United States, taxonomically distinct from their kin in the eastern U.S. (CNAH, 2009), have relatively weak calls that do not carry far from breeding locations. Several of these western ranids call both at the surface and while submerged when in or near breeding aggregations (Storm 1960, Licht 1969, Briggs 1986, MacTague and Northern 1993).

The Oregon Spotted Frog (*Rana pretiosa*) is a highly aquatic explosive breeder that overwinters under ice in much of its extant range and spawns soon after ice leaves the ponds (Hayes 1994). Eggs are deposited in communal aggregations of a few to sometimes more than a hundred egg masses. In the Sunriver area in central Oregon (elevation 1,320 m), breeding begins sometime between early March and early April, depending on conditions. Although the breeding season may last up to a month, breeding activity at individual oviposition sites typically spans a period of two to five days (pers. obs.). During breeding events, males gather at oviposition sites, calling actively at the surface with breeding taking place mostly during the day.

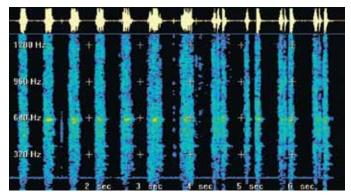
Recorded advertisement calls of *R. pretiosa* consist of a string of low "clucks" or knocks, emitted at a rate of 3–7/sec, with peak intensity between 600–900 Hz. Release calls, emitted by both males and females, were more of a single or double "squawk" given at a rate of 1–2 squawks/sec and with a frequency spectrum similar to advertisement calls. Release calls



Adult Oregon Spotted Frog (Rana pretiosa).



Sonogram of the male advertisement call of Rana pretiosa.



Sonogram of the release call of Rana pretiosa.

can be elicited almost any time by picking up a frog with the thumb and index fingers placed directly behind the forelimbs. Recordings of *R. pretiosa* advertisement and release calls at the Sunriver Nature Center are available at www.sunrivernaturecenter.org.

Here, I report for the first time that *R. pretiosa* also calls actively from submerged locations tens to hundreds of meters away from and several days prior to the formation of breeding aggregations.

### Methods

Sub-surface listening was conducted using a DolphinEAR  $^{\rm TM}$  hydrophone (model DE100-6-112), with a 6-m cable and preamp or DolphinEAR PRO hydrophone connected directly to a ZOOM H-4 digital recorder. Listening was conducted by casting the hydrophone from shore to the length of the 6-m cable, allowing it so sink, listening for 1 min, retrieving approximately 1 m, and listening again. Recordings were taken when good quality calling signals were detected.

Two sites were utilized for submerged calling surveys. Bullfrog Pond (BFP, 43°51'01"N x 121°26'50"W) is a 0.3-ha isolated (no hydrologic



Communal oviposition site showing ~18 newly laid egg masses adjacent to and on 12 egg masses laid several days earlier. Green algae are developing within older egg



Author holding pre-amp and cable of a DolphinEAR hydrophone on the shore of Lake Aspen.

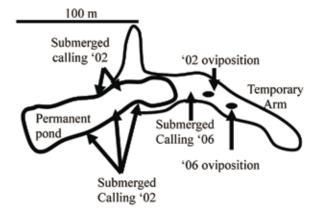
connections to nearby water bodies), excavated pond, somewhat irregular in shape, approximately 100 m long, and 10-25 m wide. Maximum depth is 2.5-3 m. Spring runoff raises the water level as much as 1 m, creating a shallow arm that extends up to 150 m from one end of the permanent portion of the pond. Breeding takes place in the distal portion of this temporary arm. The maximum distance from any point within the permanent pond to the oviposition site is approximately 200 m. Egg-mass counts over the past 10 years ranged from 21-200+ (median 24). Mark and recapture studies suggest only limited migration into or out of BFP (unpubl. pers. obs.). Oviposition generally takes place over 1-3 days.

Lake Aspen (LA, 43°53'10"N x 121°26'47"W) is a 2.5-ha excavated pond with year-round connections to other water bodies, including the Deschutes River. Water levels are controlled by weirs and fluctuate by no more than 30 cm. A long-term mark and recapture study (unpubl. data) has documented that several hundred adult R. pretiosa move to LA in the fall to overwinter, entering via a shallow outlet channel. In March and April, frogs migrate out of LA to spawn at a communal oviposition site known as Duck Pond Marsh (DP, 43°53'28"N x 121°26'52"W) approximately 1 km away. At DP, egg masses are deposited in several collective clusters over an area of approximately 10 x 80 m. Spawning at DP spans 2-4 weeks, usually in bursts of 2–5 days at any one collective aggregation (unpubl. pers. obs.). Due to the larger size of LA, no attempt was made to systematically survey the entire shoreline. Instead, the hydrophone was deployed at locations along about 200 m of shoreline on either side of the outlet channel used by frogs to move to the oviposition site.

BFP was ice-covered during surveys on 14 March 2002, except for open water at a seep at the south end. By 21 March, the spring thaw had provided numerous openings around the edges of the pond, although 5-8 cm of ice remained over much of the pond. The only sounds detected by hydrophone on 14 and 21 March were bubbles escaping from the ice. At approximately 1100 h on 28 March, advertisement calls of male R. pretiosa were detected at a depth of approximately 0.5 m near the edge of a patch of Cattails (Typhus sp.) within the permanent pond. Three males appeared to be calling at that location. Additional small groups of calling males were subsequently detected at four additional locations scattered around the perimeter of the pond. I found detectable calls only in a narrow zone 2-3 m from shore at depths of 0.5-1 m. Moving the hydrophone more than 2-3 m away from a calling individual was sufficient to lose the call because of sound attenuation. No frog calls were audible at the surface, and all frogs appeared to be concealed in submerged grass or sedge on the bottom. The weather on 28 March was cool (~12 °C) with a heavy overcast. I saw one frog at the surface of the pond during 2 h of surveying, a mature female that remained at the surface for approximately 5 min after detection, then submerged and was not seen again.

On 30 March, a high pressure weather system arrived, bringing warm sunny weather. On 31 March, a breeding aggregation of males formed at the historic breeding location and breeding commenced. A total of 21 egg masses were deposited over the course of approximately 24-36 h, with breeding completed some time on 1 April. Eighteen egg masses were clustered together, with three satellite masses deposited <3 m from the main aggregation. The distance from the breeding site to the various submerged calling locations was 80-150 m. During oviposition, 10-20 males were observed calling from the surface in the vicinity of the egg masses. Calling was audible up to 30 m away. Some males also were observed calling from the bottom in 10-15 cm of water, and their calls were audible but muffled. No calling was detected away from the breeding site on 30 March.

Hydrophone listening at BFP in 2003 and 2005 failed to detect any submerged calling prior to or remote from the formation of a surface aggregation and subsequent oviposition. At 1000 h on 15 March 2004, a single male was detected calling from a submerged position ~10 m from the eventual oviposition site. By 1330 h, several males had emerged at the oviposition site and were calling intermittently. That evening, from 2030–2130 h, all surface activity at the oviposition site had ceased, but a number of males were calling actively at the afternoon calling location and at two additional locations in the permanent portion of the pond approximately 80 m from



Schematic of Bullfrog Pond showing 2002 and 2006 locations of submerged calling and subsequent breeding.

the oviposition site. The following day, all detectable activity had shifted to the oviposition site and breeding commenced.

In 2006, ice remained on the ponds until late March and water stood at record high levels. On 3 April 2006, I detected several males calling from a 20-m zone in the middle section of the temporary arm of the pond. This calling zone was 20–40 m from the oviposition site used in prior years, and 40–60 m from the site that would be used in 2006. After dark, at 2100 h, several dozen males were detected calling at depths of 30–60 cm within this same narrow band, about 20 m long. Multiple calling males created a continuous chorus. At this time, no surface activity was detectable. From 1000–1130 h on 4 April, I detected submerged calling at this same location, but no more than two or three frogs were heard. No calling was detected from within the permanent pond. By 1400 h, a few males had surfaced and were calling near the historic oviposition site. On 5 April, surface activity had shifted about 20 m farther up the temporary arm and spawning commenced. Over the next three days, 46 egg masses were deposited in one major cluster and five satellite masses 2–5 m away.

Lake Aspen, a very different site, yielded somewhat different results. At 1130 h on 4 April 2002, one frog was detected calling about 4 m offshore near the pond outlet at a depth of about 1.5–2.0 m. Calling was sporadic, with pauses often lasting several minutes. A second individual was detected at a similar depth about 30 m to the west. No further calling was detected that year and no submerged calling was detected during several daytime surveys in 2006. At 1300 h on 28 March 2007, individual males were detected at two of six locations where the hydrophone was deployed. At 2100 h that evening, however, 1–3 males could be heard at four of six listening locations. At 1100 h the following day, a single frog was detected calling at one of the locations. These calling locations are approximately 1 km from the main oviposition site.

#### Discussion

Advertisement calls of male *Rana pretiosa*, a highly aquatic frog, were detected coming from submerged locations separated from oviposition sites by tens to hundreds of meters and sometimes preceding the formation of breeding aggregations by several days. Submerged calling activity was considerably greater after dark, even though most breeding activity occurs during the day. Once breeding aggregations formed at oviposition locations, males were detected only in the vicinity of the breeding aggregation, with calling restricted to the surface or at depths shallow enough for the calls to be audible above water.

Platz (1993) suggested four possible selective advantages for submerged calling: Avoiding predators, avoiding temperature extremes, extending the breeding and/or developmental season, and increasing sound



Common Garter Snake (*Thamnophis sirtalis*) swallowing a Spotted Frog (*Rana pretiosa*).

transmission range. In central Oregon, the principal predators on *R. pretiosa* include Garter Snakes (*Thamnophis sirtalis*), Great Blue Herons (*Ardea herodias*), Mink (*Neovison* [=*Mustella*] *vison*), and Raccoons (*Procyon lotor*). Most of these predators are visual, daytime hunters. Calling while submerged, especially at night and at depths greater than 30 cm, would help *R. pretiosa* avoid these predators, except for raccoons.

In central Oregon and indeed throughout much of the range of *R. pretiosa*, temperatures on clear nights during the breeding season fall rapidly after sunset, and overnight temperatures from -10—5 °C are common, although water temperatures a few centimeters below the surface typically remain at 8–14 °C. Submerged calling would thus avoid the cold temperatures at the surface. Increasing the larval developmental period is probably not important for *R. pretiosa* at Sunriver, where metamorphosis is normally completed in late July or August, but might be important at some high elevations sites where snow and ice can dramatically shorten the active season. Despite the density of water, submerged calling does not appear to increase sound transmission range at the depths and in the environment used by *R. pretiosa*. Ladich and Bass (2003) stated that "…in shallow waters, sound propagation is very much limited…." Indeed, I found submerged calling was often undetectable at distances greater than 1–3 m from the source when the frogs were hidden in submerged vegetation.

Many if not all of the species of Rana found in the western United States apparently call both at the surface and while submerged near breeding aggregations (Storm 1960, Licht 1969, Briggs 1986). This appears to be the first report of submerged calling by any of these species that is separated from breeding aggregations both spatially and temporally. Anecdotal reports place amplectic pairs of R. pretiosa at varying distances from breeding sites. However, whether remote pairing is simply opportunistic as frogs move toward breeding sites or if active mate selection may be taking place remotely from breeding sites and related to submerged calling is unclear. Several important questions remain to be answered. Is active mate selection taking place prior to arrival at breeding aggregations? If so, then what is the function of large aggregations of unpaired males found calling at the surface at oviposition sites? Conversely, if mate selection is principally accomplished in the breeding aggregations at oviposition sites, then what function does submerged calling serve? Does the presence of both surface and submerged calling in several species of western ranids suggest that this clade is evolutionarily in transition from one strategy toward the other or that competing selective pressures help maintain dual strategies? Do other western species that emit advertisement calls both at the surface and submerged (i.e., R. cascadae, R. boylii, and R. luteiventris) engage in submerged calling prior to and at some distance from the formation of breeding aggregations? Answering these questions will provide a better understanding of the ecology of this entire group of anurans.

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## Suburbanization of a Central Texas Herpetofauna

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Photographs by the author. All were taken at the study site.

Reptiles and amphibians were surveyed on the Balcones Escarpment in central Texas as the area was transformed into suburbia. Of four habitats, oak-juniper savanna was totally destroyed and a quarter of the adjacent oak-juniper woodland was eliminated, but two creeks and most deciduous riparian forest remained. Extirpation of 12 of 30 species (40%) included 55% of nine amphibian species, 50% of two turtles, 33% of six lizards, and 30% of 13 snakes. Herpetofaunal richness declined exponentially from 1965 to 1990 with increased house building, then stabilized through 2005 as building slowed and stopped. Species survival was related to use of cultural and remaining natural habitats, secretive behavior, and human interest.

Tuburban development in Woodway (a suburb of Waco), McLennan Ocounty, Texas had begun in 1964, when I started a 46-year project to record the area's natural and unnatural herpetofaunal history (Gehlbach 2002). The 80-ha savanna was part of a ranch totally erased by suburbia during the study, and about 20% of adjacent woodland was lost. One earth-dammed stock pond was kept for fishing; the other was demolished by floods. Habitat protection was inadvertently affected by city building codes that saved forested ravines with steep slopes, creeks and their terraces, and by a planned-unit development's 6-ha private nature preserve of creek, forest, and woodland in 1984.

This study presents features of extirpation, survival, and general abundance of each species of amphibian and reptile and describes herpetofaunal change during the study site's suburban development. I hope it will stimulate other studies that support conservation and educational use of nature preserves in our ever-growing U.S. cities.



A mating pair of Cope's Gray Treefrogs (Hyla chrysoscelis).



Strecker's Chorus Frog (Pseudacris streckeri).

### Methods

Fieldwork covered the 120-ha study site (elevation 165–196 m) on the Balcones Escarpment in all months in 1964–2009. Original habitats were mature evergreen oak-juniper savanna, a livestock pasture with tree "islands" (locally called motts), two permanent creeks (each with a stock pond in a 12-m deep ravine with deciduous riparian forest), and deciduous oak-juniper woodland on limestone slopes with rock outcrops above the forested ravines. Observational and catch and release surveys in March–October included a 3.3-km transect (gradually reduced by house building to 1.2 km) in all habitats 2–4 times/week, 20 covered pitfall traps arranged



Great Plains Narrowmouth Toad (Gastrophryne olivacea).

randomly in  $200 \text{ m}^2$  of protected riparian forest and checked daily in April–June 1984–1989, and daily dead-on-road (DOR) records on 3–5 km of city streets bordering natural habitats and among houses in the study site and 1 km beyond it on all sides.

Species are grouped as follows: (1) Extirpated (no evidence for five consecutive years), (2) uncommon surviving (noted less frequently than weekly), or (3) common surviving (noted daily to weekly). Proportional herpetofaunal changes were analyzed, as was the cumulative number of extirpated species per five-year period in 1965–2005 relative to the concurrent rate of house building.



Smallmouth Salamander (Ambystoma texanum).



Texas Spotted Whiptail (Aspidoscelis [Cnemidophorus] gularis gularis).

Scientific names follow Collins and Taggart (2009) or subsequent updates on the website of the Center for North American Herpetology (www.cnah.org); if recently changed, previous names are in brackets to assist recognition.

### **RESULTS Extirpated Species:**

Woodhouse's Toad (Anaxyrus [Bufo] woodhousii woodhousii). Uncommon; disappeared by 1970 without evidence of local reproduction.

Cope's Gray Treefrog (Hyla chrysoscelis). Uncommon March-April breeder in a stock pond and adjacent creek pools in riparian forest until game fish were stocked in the pond and some escaped into the creek in 1980; this frog disappeared in 1982.

Strecker's Chorus Frog (Pseudacris streckeri). Common November-February breeder in the savanna's rain pools further formed as livestock wallows in natural depressions until eliminated by 1975.

Great Plains Narrowmouth Toad (Gastrophryne olivacea). Uncommon breeder in savanna rain pools during April-June until 1975, but did not disappear until 1979.

Smallmouth Salamander (Ambystoma texanum). Common in the riparian forest; bred during October-December rains in creek pools and the stock pond that became a fishing pond. The second-most frequent DOR amphibian; gone by 1982.

Ornate Box Turtle (Terrapene ornata). Only two records in the savanna; none after 1975.

Texas Horned Lizard (Phrynosoma cornutum). Common in the savanna until 1975; subsequently uncommon in suburban vacant lots



Texas Patchnose Snake (Salvadora grahamiae lineata).



Broad-banded Copperhead (Agkistrodon contortrix laticinctus).



Ground Snake (Sonora semiannulata).



An adult Yellowbelly Racer (Coluber constrictor flaviventris).



A juvenile Yellowbelly Racer (Coluber constrictor flaviventris).

until 1978. A pronounced decline throughout central and eastern Texas coincided with insecticide spraying from airplanes in the 1970s to eradicate populations of imported Fire Ants that expanded during suburbanization.

Texas Spotted Whiptail (Aspidoscelis [Cnemidophorus] gularis gularis). Common in the savanna until 1975 and later uncommon in vacant lots among houses; gone by 1986.

Texas Patchnose Snake (*Salvadora grahamiae lineata*). This rarest of the 13 original snake species was found only twice in oak-juniper woodland; not seen after 1988.

Broad-banded Copperhead (*Agkistrodon contortrix laticinctus*). Uncommon in the two natural wooded habitats and occasionally in wooded suburban yards until 1970. A winter den 5 m above a creek in a limestone crevice had 19 sunning adults in October 1967; the den was apparently destroyed by dynamite and later bulldozed during development of planned-unit housing; extirpated by 1971.

Lined Snake (*Tropidoclonion lineatum*). Only three individuals were found under ground surface cover in the savanna, all before 1975, making this the second rarest snake in the original herpetofauna.

Ground Snake (*Sonora semiannulata*). Uncommon; 1–2 found annually under surface cover in evergreen woodland until 1983. Both plain brown-colored individuals and snakes with black heads and neck spots on a dull orange-brown ground color were present.

### **Uncommon Surviving Species**

Southern Leopard Frog (*Lithobates sphenocephalus utricularius [Rana sphenocephala*]). Once a common breeder in creek pools in March–May, and still common in creeks and ponds outside the study site. Gradually less abundant in the study plot; not recorded in 2007–2009, hence extirpation is possible.

Northern Cricket Frog (*Acris crepitans*). Inhabits creek sides and breeds in creek pools in April–May, but, like the other anurans, eggs and tadpoles are washed downstream by floods enhanced by street drainage. Effective reproduction seems increasingly less infrequent for this and all of the suburban creek breeders that remain common to abundant elsewhere in local rural areas.

Three-toed Box Turtle (*Terrapene carolina triunguis*). Originally uncommon in riparian forest and rare in evergreen woodland. Since 1991, only one marked adult male has been found annually (but not in 2009), so the present status is unknown. A few liberated pets from outside the region were known before 2000, but extirpation is now quite possible.

Yellowbelly Racer (*Coluber constrictor flaviventris*). Moderately abundant in the original savanna and woodland, but gradually more uncommon in remaining woodland and woodland-yard edges, where it hunts lizards such as Northern Green Anoles and Texas Spiny Lizards. Originally 1–3 DOR records per year, but only one since 2000, reflecting reduced numbers.

Flathead Snake (*Tantilla gracilis*). This fossorial species is secretive but persists in remaining forest and woodland. Equal to Rough Earth Snakes, Flathead Snakes were the least frequent catch in pitfall traps and are the only surviving snake not yet found on developed property. This is the third



An adult Eastern Hognose Snake (*Heterodon platirhinos*) exhibiting a defensive display against a predator.



Coastal Plain Toad (Ollotis nebulifer [Bufo valliceps]).



Mediterranean Gecko (Hemidactylus turcicus) on the brick wall of a house.

most frequent DOR snake, most often on roads bordering or less than 75 m from remaining natural habitat.

Texas Garter Snake (*Thamnophis sirtalis annectens*). Always uncommon, although it persists in riparian forest near creeks and occasionally appears in suburban yards and gardens that adjoin remaining natural habitat.

Eastern Hognose Snake (*Heterodon platirhinos*). Another snake originally uncommon and rare today. Because of its initial aggressive, neck-flattening, defensive behavior, it is commonly thought to be dangerous and is sometimes confused with the Copperhead, hence summarily killed. Coastal Plain Toads are known food. A 48-cm (total length) adult was active at 16 °C in early December. One DOR was recorded in 2007.



Texas Spiny Lizard (Sceloporus olivaceus).

### Common Surviving Species:

Coastal Plain Toad (Ollotis nebulifer [Bufo valliceps]). The most abundant anuran and most frequent DOR in all years, apparently because individuals congregate on streets to feed on insects below streetlights. Lays eggs in creek pools and backyard ponds during April-August rains, the longest breeding season among anurans. It is the only amphibian that utilizes artificial ponds at suburban residences. Whether an individual breeds more than once annually is unknown. Suburbanites do not mind toads on their property.

Rio Grand Leopard Frog (Lithobates [Rana] berlandieri). Breeds in creek pools during August-October. Increasingly less common, although, as noted for other anurans, abundant in ponds outside the study area. Street and yard water drains into creeks, so flooded eggs and tadpoles and/or dissolved toxins may be detriments to continued existence.

Mediterranean Gecko (Hemidactylus turcicus). Introduced to Waco, Texas in the early 1950s (B. Brown, pers. comm.) and to the study site by 1982. Lives on brick and stone walls and inside houses and other buildings; hatchlings appear anytime except December-February. Adults are active



Northern Green Anole (Anolis carolinensis carolinensis) on a potted porch plant.



Western Rat Snakes (Scotophis obsoletus [Elaphe obsoleta]) readily climb trees.



Rough Green Snake (Opheodrys aestivus).

throughout the year during nights with temperatures above ~15 °C, but in winter only if bricks have been sun-heated. One DOR.

Texas Spiny Lizard (*Sceloporus olivaceus*). In open forest, woodland, and wooded suburban yards on the ground and rocks and in trees (see also Blair 1960). Rarely climbs herbaceous vegetation. Gardens and backyard refuse piles are nest sites, also for Green Anoles, Ground Skinks, Western Rat Snakes, and probably other species. The most frequent DOR lizard.

Northern Green Anole (*Anolis carolinensis carolinensis*). Common around houses, less so in forest and woodland edges. Lives in planted herbaceous vegetation, shrubs, and trees in gardens, and climbs potted patio and porch plants and house walls. This species increased dramatically during suburbanization, benefiting from human interest and plantings that attract its insect food. Two—three broods per year in June—September. Adults are active throughout the year in sunny weather at temperatures above ~15 °C. The third most frequent DOR lizard.

Ground Skink (*Scincella lateralis* [*Lygosoma laterale*]). Only slightly less abundant than the Green Anole, but rarely noticed by suburbanites because of its secretive terrestrial habits in and under ground cover in wooded yards and gardens, especially at forest and woodland edges; 2–3 broods per year in July–September (see also Fitch and Greene 1965). This is the most frequent reptile in pitfall traps, and the only abundant species without a DOR record.

Rough Green Snake (*Opheodrys aestivus*). Moderately common in open riparian forest and brushy edges along creeks and in yards and gardens, where it is unnoticed lying lengthwise on low foliage while sit-andwait foraging for insects. Its green coloration and behavior hide it so effectively that I never heard of one killed by people. One DOR record.

Western Rat Snake (*Scotophis obsoletus* [*Elaphe obsoleta*]). This largest of local snakes (to 2 m total length) is common in forest and woodland, less so on wooded suburban property. It is the snake I am most frequently asked to remove; for example, a 1.5-m adult coiled inside a cooking pot in a kitchen cabinet. Active in March–November; eggs hatch in August–September. Hatchlings and adults eat lizards, including Mediterranean Geckos on brick-walled houses to second-floor heights. A nest predator



Rough Earth Snake (Virginia striatula) in pre-shedding condition (note the "cloudy" eye).



Texas Blind Snake (Rena [Leptotyphlops] dulcis) emerging from the soil.

of open and cavity-nesting birds, including small owls (Gehlbach 1994). Fourth most frequent DOR snake.

Texas Blind Snake (Rena [Leptotyphlops] dulcis). Abundant in suburbia, mostly during April-June under flat ground cover objects such as pathway stepping stones; also dug up in flower beds, found alive in swimming pools, on garage floors, in Eastern Screech-Owl nests (Gehlbach and Baldridge 1987) and Fire Ant mounds (Baldridge and Wivagg 1992). The second most frequently recorded DOR snake, and tied with the Texas Brown Snake for second most frequent pitfall catch.

Texas Brown Snake (Storeria dekayi texana). Like other small invertebrate-eating snakes, encountered mostly during the spring under ground cover after rains. Lives largely in riparian forest but also in suburban yards, although less commonly than Blind and Rough Earth snakes. It is the second most frequent pitfall catch and third most abundant DOR snake.

Rough Earth Snake (Virginia striatula). The most abundant suburban snake and DOR reptile of any species. Lawn and garden watering might promote its earthworm food, while small size, burrowing behavior, brown coloration, and use of ground-surface cover contribute to its existence in suburbia. Active in March-November.

### Discussion

Survival was nil for species that depended mostly on the erased savanna. Strecker's Chorus Frogs, Great Plains Narrowmouth Toads, and Ornate Box Turtles did not survive, while Texas Horned Lizards and Texas Spotted Whiptails remained only temporarily on large vacant grassy suburban lots in the former savanna area. Other amphibians bred in declining numbers in creek pools or were extirpated by stocked game fish. However, one toad, three lizards, and four snakes began to live partly in suburban yards and gardens. Most people did not mind toads, but two of the lizards and all of the snakes survived in suburban habitats by being inconspicuous.

Native species most commonly encountered in suburbia were, in order of frequency, Northern Green Anole, Coastal Plain Toad, Rough Earth Snake, Texas Spiny Lizard, Ground Skink, Texas Blind Snake, and Rough Green Snake. They and other survivors benefited from the study site's heat-island (Landsberg 1981), which averaged 1.5 °C higher than a corresponding rural value in March-October (Gehlbach 1994), and suburb-forest edge habitat that supplied 40% more potential insect prey than 12 m away in the forest interior in September-October (D. Quigley, pers.

Human attitudes were negative toward the largest snakes and contributed to the extirpation of Copperheads and declines in Yellowbelly Racers and Eastern Hognose Snakes. Homeowners sometimes asked me to remove large snakes, but not those less than ~15 cm in total length, which many believed were "worms." Small size, brown color, soil or ground-litter habitat, and green color combined with sit-and-wait foraging hid some lizards and snakes in suburbia. Conversely, the Northern Green Anole's red dewlap displays, body color changes coordinated with perch color, and prominent use of cultivated plants drew human interest and protection that might have enhanced the obvious increase in the numbers of this species in suburbia.

Creek-breeding anurans were negatively affected by water runoff from city streets and private properties. These unnatural sources probably contain petroleum and pesticide toxins, and street drains concentrate rain into flash floods that wash eggs and tadpoles out of the creeks. Thus, Southern Leopard, Rio Grande Leopard, and Northern Cricket frogs declined — but not Coastal Plain Toads, perhaps because their breeding season is 1.7 times longer than those of the other anurans, and hence are more likely to avoid floods. Also, only this toad bred in and might have benefited from artificial ponds in suburban yards.

Twelve (40%) of the study site's 30 original species of amphibians and reptiles disappeared during suburbanization. This fraction is significantly less than the 67% extirpation of 21 species surveyed by Minton (1968) in an older suburb of Indianapolis, Indiana ( $\chi^2 = 7.2$ , P = 0.007). Amphibian losses were coincident with degraded aquatic habitats in both suburbs and proportionately higher than those of reptiles: 75% versus 61% of species in Indiana and 55% versus 38% in Texas without intra- or inter-site differences ( $\chi^2$  < 0.23, P > 0.63).

The rate of herpetofaunal decline in this Texas study was 1-5 species per five-year period of exponentially increasing suburban growth during 1965-1995. Subsequently, no additional species were lost as suburban growth became progressively slower through 2005. During nine five-year periods through 2005, the changing and then stable herpetofauna was strongly correlated with the cumulative number of city building permits for the study site and surrounding 1-km wide suburban area (3° polynomial regression,  $r^2 = 0.95$ , P = 0.001).

### Acknowledgements

Colleagues, family, friends, and students joined hunts; Nancy Gehlbach was present most frequently and made helpful comments on the manuscript. Dena Quigley provided insect abundance data from Malaise traps. Henry S. Fitch participated in a transect survey in the 1970s, and I am honored to dedicate this study to his memory in recognition of his friendship and exemplary professional career in herpetology and ecology.

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### Red Milk Snake Taking Large Prey Late in the Season

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Photographs by the author.

Red Milk Snakes (*Lampropeltis triangulum syspila*) are secretive and little is known about their behavior when compared to many other North American snakes (Ernst and Ernst 2003). They are dietary generalists and are known to prey on mammals, birds, lizards, snakes, reptilian eggs, amphibians, fish, earthworms, slugs, and insects (see review in Ernst and Ernst 2003).

Milk Snakes have relatively small heads and mouths and narrow bodies, and they generally appear to prefer small, narrow prey (Fitch and Fleet 1970, Ernst and Ernst 2003). Lampropeltis t. syspila (total length [TL] 144–812 mm) is smaller than L. t. triangulum (TL 175–1140 mm; Williams 1988) and presumably eats smaller prey. Among the mammalian prey recorded for L. triangulum are voles (Clethrionomys gapperi, Microtus ochrogaster, M. pennsylvanicus, M. pinetorum; see review in Ernst and Ernst 2003). Fitch (1999) reported 36 prey items from 19 L. t. syspila and 8 scats. Nine of the prey items were Microtus ochrogaster, 8 of those were specifically identified as nestlings and size was not specified for the other.

On 28 September 2007 at 1433 h, I investigated a rodent distress call in Union County, Illinois. The call came from beneath leaf litter in a wooded area next to a gravel road between limestone bluffs and swamp. I saw a leaf move and lifted it, revealing an adult *L. t. syspila* with three coils around an adult Woodland Vole (*Microtus pinetorum*). The head of the vole protruded from the coils, but the snake's head was not visible. At 1436 h, the snake started searching for the head of the vole and, at 1439 h, it grasped the rostrum of the vole and began swallowing. Four people quietly observed the event and took flash photographs as unobtrusively as possible. The snake remained intent on consuming its meal despite the disturbance.

The snake finished swallowing the vole at 1519 h (40 min swallowing time) and before the prey had reached the snake's midbody, it started crawling out of sight into the leaf litter. During the event, we noted that the snake had a shriveled, blind left eye. The weather was sunny with an ambient air temperature of approximately 30 °C.

The snake was not restrained in order to allow it to finish its meal, and so the length and weight of the snake and the vole were not recorded. The vole was identified using features visible in the photographs. *Microtus pinetorum* has a uniform reddish-black dorsum and a short tail (18–24 mm) relative to its hind feet (approximately 16 mm). The habitat (leaf litter in oak, hickory, and maple forests) also was consistent with that used by *M. pinetorum* (Hoffmeister 2002).

This feeding event was notably late in the year for a *L. t. syspila* to be consuming prey. Fitch and Fleet (1970) recorded 20 natural food items for *L. t. syspila* in northeastern Kansas. All were consumed in late April, May, or early June, with the exception of one *Plestiodon fasciatus* in a snake captured on 25 September 1964. To my knowledge the present account is the first unambiguous report of *L. t. syspila* consuming an adult *M. pinetorum*.

### Acknowledgements

I thank Michael Dloogatch for reviewing this note and Amy Sullivan for identifying the vole.

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Adult Red Milk Snake (*Lampropeltis triangulum syspila*) constricting and swallowing a large Woodland Vole (*Microtus pinetorum*).

# Observations on a Wild King Cobra (Ophiophagus hannah), with Emphasis on Foraging and Diet

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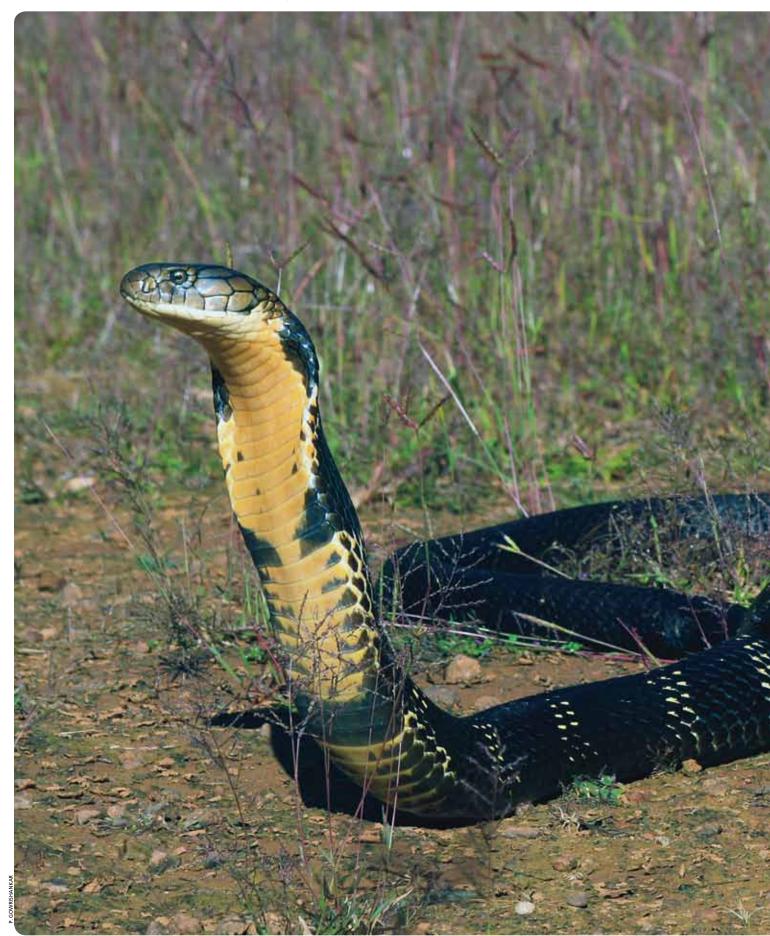
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Since 2005, we have conducted research on King Cobras (Ophiophagus hannah) in the forests and plantations surrounding Agumbe Rainforest Research Station (ARRS) located in the Western Ghats of southern India. In March 2008, we started a radiotelemetry project and to date we have tracked four adult King Cobras (three males, one female) for varying periods. Although we have documented a number of interesting facets of King Cobra biology, this note is confined to observations made on a single male (M2) from June-November 2009. During this time, we observed M2 capturing and consuming 26 pit vipers (two Hump-nosed Pit Vipers, Hypnale hynale, and 24 Malabar Pit Vipers, Trimeresurus malabaricus). We provide details of these remarkable observations, and briefly discuss them in the context of our ongoing efforts to understand and conserve these charismatic serpents.

ring Cobras in southern India are distributed along the length of the  $oldsymbol{\Lambda}$ Western Ghats (the chain of hills just inland from the western coastline of peninsular India), from the southernmost tip, called Kanyakumari (Black Rock Estate), north to Goa (Bondla Wildlife Sanctuary). The range of King Cobras in this part of India coincides with areas of extremely high rainfall and corresponding wet deciduous, riparian, and evergreen rainforest (Smith 1943). The King Cobra is uncommon throughout its range, and most of its original habitat has been destroyed. In addition, King Cobras are



Radio tracking in the rainforest is challenging, with vegetation, hillocks, and even heavy rain interfering with signals.



M2, an adult male King Cobra of "average" size (3.21  $\,$ 



n total length) in the Western Ghats of southern India.



M2 strikes and catches an adult female Malabar Pit Viper at midbody; the viper is trying to sink its fangs into the cobra.

typically killed on sight throughout most of their range. However, Hindus living in the Malnad region of Karnataka State, including our study area, the villages and Reserve Forests around Agumbe, actually worship King Cobras and the snakes are rarely harmed, even if they enter a residence. This tolerant attitude for the largest venomous snake in the world has not only facilitated our research and educational efforts, but also has provided us with over 100 opportunities to "rescue" King Cobras from human habitations (Shankar, in prep.).

As inferred by their scientific name, King Cobras feed primarily on snakes, including their own species (we have observed intraspecific predation in both captive and wild individuals). The only other prey reliably reported from the wild were two species of Monitor Lizards (Varanus spp.), the Common Indian Monitor (V. bengalensis, Smith 1943) and the Water Monitor (Varanus salvator, C. Traeholt, pers. comm.). Two of us (RW and PGS) have observed King Cobras over the past several decades, and we have found that adult snakes (mean total length [TL] of males ~300-400 cm; females ~225-275 cm TL) in the Western Ghats prey mainly on the ubiquitous Indian Rat Snake (Ptyas mucosa; mean TL ~175 cm, maximum TL ~350 cm, mean mass ~1,250 g). Although we commonly observe Indian Rat Snakes in open and swampy areas of both cultivated and wild land, we rarely observe them in deep forest. Unusually large male King Cobras (> 400 cm TL) are known to prey on Indian Pythons (Python molurus); one of us (RW) was shown photos of a male King Cobra killing and swallowing a mediumsized python (~210-240 cm TL), and a 366-cm individual killed and swallowed a 280-cm Reticulated Python (Python reticulatus, Shebbeare 1947).

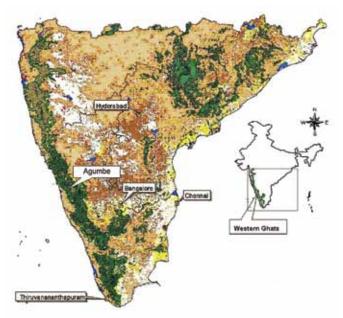
Some speculation (B.G. Fry, pers. comm.) suggests that King Cobras may be immune to the venom of viperids and elapids, and that they may

take special "precautions" when feeding on prey species with long fangs. Zoos around the world that exhibit King Cobras either condition them to eat dead rodents that have been prepared with odors from snakes and/ or feed them snakes that have died on exhibit. This has resulted in a long list of venomous and non-venomous snakes, some as exotic as African Gaboon Vipers (*Bitis gabonica*), that have been fed to captive King Cobras (S. Pfaff, pers. comm.). However, an understanding of trophic ecology based on captive feeding records is less than satisfactory. King Cobras have been observed feeding on Banded Kraits (*Bungarus fasciatus*) in the wild (Saravanakumar, pers. comm.), and herein we describe what appears to be selective hunting of venomous pit vipers.

#### Methods

We obtained all feeding observations reported here while radiotracking "M2," a male (TL = 321 cm, mass = 4,900 g), into the coelomic cavity of which we implanted a 25-g temperature-sensitive radio transmitter (Model AI-2T, Holohil Ltd., Ontario, Canada). We released the snake one day after the surgery on 28 March 2009 at its exact point of capture (~1 km from the Agumbe Rainforest Research Station [ARRS]). Over the next two days, the snake moved 2.3 km, climbing down a steep escarpment that rendered radiotracking impossible. The signal was lost on 31 March, but recovered ten weeks later on 7 June after incredible perseverance by the tracking team. The snake had moved ~6 km straight-line distance from where it was lost, and we have tracked him every day since 10 June.

We radiotracked M2 each morning, staying with him throughout the day until nightfall. On days when the snake did not move (i.e., 20 consecutive days when shedding), we still obtained a fix every hour. At each fix, we recorded a suite of environmental parameters (e.g., ambient and body temperature, relative humidity, cloud cover), GPS coordinates, and habitat variables (e.g., canopy cover, dominant plant species, shelter type). If the snake was moving or visible when located, we made every effort to observe its behavior. Although our initial protocol was not to get too close to the snake for fear of influencing natural behavior or causing it to move or hide, we quickly learned that M2 did not seem to be disturbed by observers within a few meters, as long as trackers remained fairly still. The ability to



Agumbe, South India

Map of southern India showing the location of the Western Ghats and the Agumbe Rainforest Research Station.



M2 catches a Hump-nosed Pit Viper at midbody and proceeds to swallow it alive, doubled over, in a few short minutes.

closely approach the snake has enabled us to make the detailed observations reported on in this paper.

Our data indicate that King Cobras are primarily diurnal, although, on a few occasions, we tracked animals after dark and recorded some movements, once until 2200 h, but that was exceptional. M2 almost always found a shelter site well before sunset and sometimes as early as 1400 h. Depending on weather, such as rainfall, ambient temperature, and availability of sunlight, M2 typically emerged from his resting place around 0900 h (range = 0830-1200 h). We always stayed within the range of the radiotransmitter signal, because even short movements could result in losing the signal in the dense rainforest environment. In addition, this allowed us to infer changes in behavior of the snake by monitoring variations in signal intensity and rate. When feasible, we kept the snake under sporadic line-of-sight observation using binoculars. We took detailed notes describing all movement and behaviors observed, including what appeared to be obvious foraging behavior as revealed by increased tongue-flicking and apparent scent-tracking, presumably in response to prey odors.

#### Results and Discussion

During 2008, we tracked our first adult male King Cobra (M1) for more than 100 km over a nine-month period through a wide range of landscapes, much of it human-dominated (e.g., arecanut [betelnut] plantations, rice fields, and community forests). Unfortunately, we subsequently lost him. However, those data and others from over 100 "rescued" snakes suggests that at least some King Cobras "prefer" human-dominated landscapes. Perhaps King Cobras are drawn to man-made features because they attract rodents, which in turn provide for an increased relative abundance of Indian Rat Snakes.

During the first two months, we tracked M2 through a mix of dense intact forest, degraded community forests, and rarely plantations. However, at the onset of the monsoon in June, M2 moved into deep forest not far from ARRS, where he has remained, except for one brief period of 22 days when he retreated into a termite mound near farmlands on 20 September, emerging newly shed on 12 October. Between 7 June and 22 November, M2 moved 35.6 km through an area (which we are tentatively referring to as his "home range") totaling 6.3 km<sup>2</sup>.

We naively assumed that M2 would not be very active during the monsoon, because annual rainfall in Agumbe averages over 7,000 mm and has peaked at over 11,000 mm during the four-month monsoon season in June-September. We assumed that heavy and persistent rainfall would cause feeding to taper off until the return of warmer, dryer weather. However, M2 was first observed finding, killing, and eating a Malabar Pit Viper (Trimeresurus malabaricus) on 6 July at the height of the rainy season. Over the following four and a half months, we observed M2 eating a total of 26 pit vipers, two of which were diminutive Hump-nosed Pit Vipers (Hypnale hynale).

Whether or not M2 moved on any given day usually depended on whether or not it was raining, rainfall intensity, and presence or absence of direct sunlight. On drier, sunnier days, M2 typically basked for 15-45 min before beginning to hunt. Foraging activity consisted of apparently purposeful searching, characterized by constant tongue-flicking and active probing of crevices, burrows, tree buttresses, and vegetative debris. Data from days on which we observed M2 feeding on one or more pit vipers (n = 23), he spent from 37 min to >7 h per day foraging (mean = 3.5 h/day).

When M2 apparently detected an odor trail of a pit viper, his foraging activity became visibly more intense, sometimes inducing "head jerking," followed by sustained tongue-flicking along the presumed odor trail up to a height of 20 m in the canopy. On several occasions, pit vipers seemed alarmed by the close approach of M2, causing them to fall or launch from their perch (Malabar Pit Vipers are primarily arboreal, pers. obs.). A considerable amount of time spent foraging by M2 consisted of climbing in lower and mid-canopy. Of the 24 Malabar Pit Vipers consumed by M2, 17 (70.8%) were found and captured in trees, shrubs, vines, or dead branches, and seven (29.2%) were found and captured on the ground.

Our observations suggest that King Cobras are able to detect movement from relatively long range, perhaps as far as 50-100 m. We have observed King Cobras intently watching us as we moved through dense forest thickets. We also have observed a King Cobra that appeared to be watching a flock of herons flying overhead. However, their visual acuity may be poor, as they do not seem to easily recognize stationary objects, be they prey animals or potential threats (such as ourselves). India's forest pit vipers are typically nocturnal ambush predators, remaining sedentary by day (pers. obs.). Indeed, we have observed pit vipers in the exact same location and even position for as many as seven days. King Cobras are unlikely to see a motionless pit viper. In fact, we observed M2 directly pursue and subdue pit vipers that he had disturbed, causing them to move. When unsuccessful at capturing the pit viper, M2 relied on chemosensory searching to follow the odor trail. We observed M2 lose the odor trail, such as when the pit viper fell into or crossed over water, but he persisted in his search until he picked up the trail again. Remarkably, he even seemed able to successfully find and follow odor trails in heavy rain. Although pit vipers would often remain motionless, they would invariably move when M2 got too close, thereby causing him to strike immediately.

In one startling two-hour episode recorded on video, we observed the King Cobra locating a large gravid female Malabar Pit Viper, causing it to fall from its perch about 15 m above the ground and try to evade capture.



Riparian habitat at the Agumbe Rainforest Research Station in southern India.



Adult female Malabar Pit Viper.

M2 promptly descended and followed the pit viper odor trail three times around and across a large, swift stream before finally catching and killing it. Although the pit viper was easily visible to us, M2 passed close to his prey several times, apparently so intent on picking up olfactory cues that he failed to see the snake. At one point, the odor trail was strong enough to induce M2 to bite a stone twice, providing further evidence of the prominence of olfaction over vision under some circumstances.

We also documented interesting prey handling behavior. In 16 of the observed prey captures, once M2 saw the pit viper, he approached the head end (Malabar Pit Vipers have a narrow neck and wide, triangular head characteristic of viperids) and grasped the smaller snake either just behind or directly on the head. Our observations of King Cobras feeding on Indian Rat Snakes indicate that they are not particular about which part of the body they grab, even though retaliatory bites from Indian Rat Snakes, including on the head of the King Cobra, commonly occur. Perhaps M2 was trying to avoid being bitten by the pit vipers. In nine of the predation events we observed, the King Cobra received what appeared to be a penetrating retaliatory bite. While the scales of a King Cobra probably prevent penetration, a pit viper presumably could pierce the interstitial skin between scales. When bitten by pit vipers, M2 invariably dropped his prey, waiting an average of 10 min until the pit viper was immobilized from being envenomated. Although Malabar Pit Viper venom has relatively low toxicity (Dhananjaya, pers. comm.), the bite of the Hump-nosed Pit Viper has caused kidney failure and occasional deaths in humans in Sri Lanka (de Silva 1990).

We observed M2 capturing a large, gravid female pit viper, grasping it at midbody, only to receive what appeared to be a penetrating bite on the side of the head. M2 immediately released the pit viper and, with head and neck erect up to approximately 50 cm, appeared to watch the envenomated prey climb a nearby branch to a height of about 6 m. M2 remained motionless in this position for the next half hour, mouth partly open, without tongue flicking or reacting in any way. Even the pit viper, falling dead from a branch after 20 min, approximately 1 m away, and the approach of the tracker within approximately 3 m to check for swelling at the site of the bite (none was evident), did not elicit a response. After 30 min in this upright position, M2 came out of his apparent "trance" and immediately started searching for the pit viper, ignoring the dead snake in front of him and instead climbing (all the while vigorously tongue flicking) to the point where the snake fell. He then returned to the ground to eventually find and swallow the dead snake.

The maximum time for a pit viper to be consumed, starting with the point at which it was bitten and ending when it was swallowed, was 67 min and the minimum time was 4 min (mean = 14 min). In 16 predation events, M2 grasped the prey by the head or neck and, in a few cases, immediately swallowed it alive, completing the task within a few minutes. In the case of a small Hump-nosed Pit Viper (mean adult TL ~25 cm, mean mass <40 g), M2 simply grasped the snake at midbody and swallowed it while it was doubled over, without bothering to "jaw-walk" towards the head. Four pit vipers were grasped at midbody, three by the tail, and we failed to observe three other captures. Eleven of the snakes were still moving or clearly alive when swallowed, 12 were immobile and three we failed to see clearly.

We estimated 12 of the pit vipers to be ~60 cm TL (these were probably all females, several appeared gravid), five were approximately 45 cm TL (average adult male size), and seven were roughly 30 cm TL. We observed M2 eating two pit vipers per day on three separate days. The cobra frequently defecated after a swallowing episode.

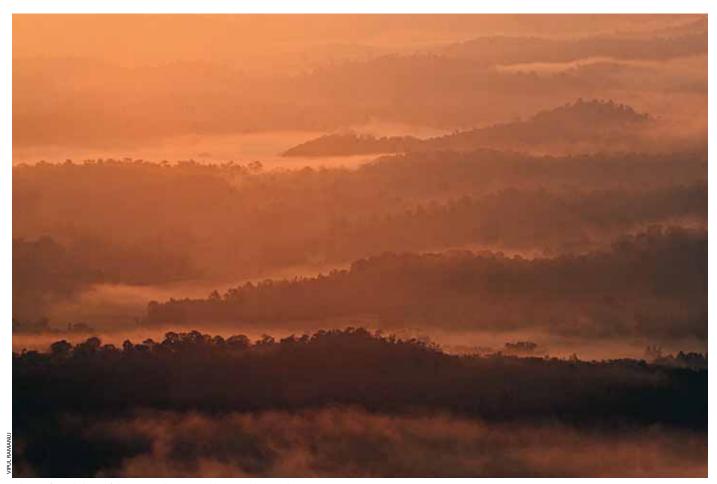
During this study, M2 spent approximately 50% of his active hours foraging/hunting for prey, in this case pit vipers. On one occasion, he spent over five hours continuously foraging before he located a pit viper to eat. He was not observed searching for, pursuing, or capturing any other species of snake during this time, despite the presence of other species similar in body mass to smaller pit vipers (see below). Since we followed M2 every day throughout his entire diurnal activity period, we almost certainly recorded the vast majority of predation events over the full 140-day period. During that time, our field team was with M2 for about 8 h per day for a total of 1,120 h. During this time, we observed M2 a total of 74.89 hours engaged in obvious foraging behavior that led to an actual predation event. On average, M2 consumed a pit viper every 5.38 days, and spent an average of 2.88 h foraging for each of the 26 pit vipers he caught and consumed.

In July-November, M2 primarily restricted his activity to deep forest. This period of time coincided with heavy rainfall in the Agumbe area. During rainy periods, we rarely observe snakes species that are known to be typical prey of King Cobras (e.g., Indian Rat Snakes). In addition, we have observed Indian Rat Snakes far more frequently in open meadows and agricultural lands, presumably with high prey densities, than in dense forest. In contrast, pit vipers are apparently more active during the monsoon season, as evidenced by our increased observations. Other snake species, which are typically visible during the rainy season in the vicinity of Agumbe, are Beddome's Keelback (Amphiesma beddomei), Large-eyed Bronzeback (Dendrelaphis grandoculis), and the Common Vine Snake (Ahaetulla nasuta); however, we did not observe M2 eating any of these species during the time in which he consumed the 26 pit vipers. Although pure speculation, perhaps King Cobras as a species (or M2 as an individual)

prefer pit vipers, or the odor trail of pit vipers is somehow easier to follow than those of other sympatric species.

Also interesting to consider is whether or not the pit vipers that M2 consumed could provide him with enough energy to maintain his health. When we captured M2 in early March, he weighed 4,900 g, which is an average mass for a healthy 321-cm King Cobra. If M2 consumed an average-sized adult Indian Rat Snake (~175 cm TL, ~ 1,250 g) his body mass to prey size would be approximately 4:1. A small sample of ten Malabar Pit Vipers captured in the vicinity of ARRS yielded an average TL of 45 cm and an average mass of 35 g. Although we were unable to obtain masses on the pit vipers consumed by M2, we estimated the range of their masses to be 30-60 g, which correlates to an average mass of approximately 50 g. Using this 50-g estimate, the mass ratio of predator to prey is roughly 98:1. If we add together the average approximated weights of all 26 pit vipers consumed, the predator-prey mass ratio is 3.77:1, which is approximately equal to that of a single Indian Rat Snake. One obvious question arising from this exercise is whether a total pit viper mass of 1,300 g is sufficient nutrition for a very active 5-kg King Cobra over a period of 18 weeks, not to mention a presumed increase in predation risk while moving.

Based on our observations, M2 apparently expended a great deal of energy searching, climbing (observed almost every day), and persistently and repeatedly following pit viper odor trails for what seemed to be a meager reward. However, M2 did not appear to have lost a significant amount of mass, nor did his body condition appear to suffer. Nevertheless, small snakes such as pit vipers, with the attendant need for large energy expenditure to find them, are unlikely to fulfill the nutritional requirements of such a large, active snake.



The rainforest habitat of the King Cobra at Agumbe in southern India.



Google Earth® image showing sites at which M2 was relocated. ARRS = Agumbe Rainforest Research Station.

Whether or not M2 will alter his foraging tactics during the upcoming mating season, when King Cobras of both sexes become much more active (judging from the dramatic increase in "rescue" calls received during the period of January–May), remains to be seen. Perhaps M2 will move into human-dominated landscapes, such as plantations and crop fields, where relative abundance of Indian Rat Snakes is apparently much higher.

#### Acknowledgements

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### TRAVELOGUE

# The Backdoor Turtles of Tortuguero

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Photographs by the author.

Casa Verde, the weathered, palm-sheltered former field headquarters of the Caribbean Conservation Corporation's venerable Green Turtle research program, and now its modernized successor, the John H. Phipps Biological Field Station, stand squarely between two great biological worlds. To the fore stretches the Caribbean Sea with all its teeming marine life. Its edge here is the black sand beach of Tortuguero, named for the small coastal village adjacent to the station, and the most important sea turtle nesting site in the entire western Caribbean. To the rear lie the rich Costa Rican lowland rainforest and a complex network of freshwater canals, rivers, and swamps threaded through its verdure.

For the biologist, few if any other places on earth offer so many opportunities, the nature of which depends simply upon the door from which one emerges. Archie Carr and the legion of biologists upon whom the reputation of Tortuguero has been built went out the front door to the dark beaches and their droves of nesting Greens and Leatherbacks. Instead, I go out the back to study an equally fascinating but poorly known assemblage of smaller turtles resident in Tortuguero's freshwater and forest

habitats. Long ignored and overshadowed by the huge, spectacularly abundant sea turtles, these non-marine species have unobtrusively gone about the business of living without much attention from biologists. However, recent investigations that I have conducted on their ecology have revealed much of interest in these small packages. Their natural history, unique and worthy of record for its own sake, also provides insight into the origin of the Neotropical non-marine turtle fauna and the evolutionary strategies that allow its survival. One of the freshwater species has led me through a proverbial revolving door. In spite of my original intentions to stay in the jungle, it took me back to the beach to observe a critical phase of its life history in the Tortuguero ecosystem.

Studying the turtles of Tortuguero is a singular experience in itself. Cruising the green-walled streams while four-foot iguanas launch themselves from overhanging branches, and parrots, toucans, and howler monkeys scold, gurgle, and roar overhead adds a dimension to turtle trapping that can't be matched in the Temperate Zone. The presence of caimans, Bull Sharks, and stingrays in the rivers, and Jaguars, fer-de-lances, and rov-



Adult male Meso-American Slider (Trachemys venusta), with a carapace length of about 40 cm, on the beach at Tortuguero.



A hatchling slider at a nesting site in cocoplum scrub along the beach at Tortuguero.

ing herds of White-lipped Peccaries in the forest also contribute spice to the ambience.

Our efforts to date have yielded data concerning five of the six species inhabiting the Tortuguero area. The rare Narrow-bridged Mud Turtle (Kinosternon angustipons) occasionally turns up at Tortuguero, but we have not yet located its apparently rather specialized habitat. The observed species range across the niche spectrum from the almost totally aquatic South American Snapping Turtles (Chelydra acutirostris) and Meso-American Sliders (Trachemys venusta), which emerge from water only for egg-laying, occasional movement into other aquatic habitats and, in the latter, for sunbathing on emergent logs, to the semiaquatic White-lipped Mud Turtle (Kinosternon leucostomum) and Black River Turtle (Rhinoclemmys funerea), which spend significant amounts of time both in water and wandering on the forest floor, to the fully terrestrial Brown Wood Turtle (Rhinoclemmys annulata), which enters water only to drink or soak in forest puddles.

Besides these more traditional taxonomic and habitat approaches to classifying Tortuguero's turtles, ecological information may help to categorize them according to their respective biogeographic histories. While all of Tortuguero's turtles are certainly tropical in terms of their current geography, their survival here depends upon strikingly different adaptive approaches to coping with the tropical environment. These varying strategies provide clues to their past. From this perspective, two of Tortuguero's turtles seem out of place indeed.

Reproductive patterns are especially diagnostic in this regard. The two mud turtles and the Black River and Brown Wood turtles lay one or only a small clutch of small (mud turtles) to relatively very large eggs (Black River and Brown Wood turtles) on the forest floor, either asynchronously throughout the year or over extended periods during the rainy season. They characteristically make little or no effort to bury the eggs other than scraping a little leaf litter over them before they permanently leave the scene. This reproductive pattern has been observed in small to medium-sized rainforest-dwelling turtles in both the New and Old World tropics and is considered to be indicative of long-term tropical residency — perhaps an adaptive response to the myriad egg and hatchling predators that roam the rainforest floor. Unpredictability in laying time and location discourages predators from ganging up on the turtles' reproductive effort as they can, for example, on the nearby Green Sea Turtle nesting beach.

All the sea turtles, and the world's Temperate Zone freshwater and terrestrial species, practice a very different nesting strategy. These turtles typically lay one or more large clutches of relatively small eggs in carefully constructed subterranean nests that are sealed after egg deposition. Nesting takes place within a distinct season and nests often are concentrated in suitable areas that provide both easy access for nesting females and the proper micro-environment for the developing embryos. As predators often home

in on these nesting areas with great efficiency, these species are more likely to survive as a result of their ability to "swamp" predators through their high annual fecundity and the long reproductive life of adult females. The snapping turtles and sliders of Tortuguero reproduce in this typical Temperate Zone pattern.

Tortuguero's crazy-quilt amalgam of species with such divergent nesting strategies is best explained by the relatively recent invasion of the closely related ancestors of the latter two species into the Neotropics from temperate North America. With closure of the Central American isthmus during the Pliocene and the subsequent climatic turmoil of the Pleistocene, the time was ripe for faunal exchanges between the two continents. During drier periods when the forest shrank and rainforest specialists were at a disadvantage, the opportunistic snapping turtles and sliders probably colonized Central and South America. Today, the snappers range as far south as Ecuador and the sliders' range extends into temperate Argentina. During wetter periods, as in the current interglacial, however, these Johnny-comelatelies are apparently at a distinct disadvantage in the re-coalescent rainforest, as their distributions are extremely disjunct through this vast area and their present population sizes often are low compared to the temperate habitats in which they often dominate the turtle fauna. Characteristically, both species are relatively uncommon at Tortuguero. One focus of my work was to determine how these species live at Tortuguero, which, with the exception of the area around the village, is still characterized by primary rainforest as dense as that anywhere in the Neotropics.

Currently, two tropical species in the genus *Chelydra* and as many as nine mainland Latin American species in the genus *Trachemys* are recognized — all very closely related to their Temperate Zone ancestors, the Common Snapping Turtle (*Chelydra serpentina*) and the Slider (*Trachemys scripta*), respectively.

Although little comparative information was available concerning the ecology of snapping turtles in other tropical locations (i.e., limited natural history observations in Chiapas by Miguel Alvarez del Toro and in Colombia by the late Federico Medem are available), the collective data from several studies of sliders in tropical Mexico, Belize, Colombia, Venezuela, and especially Panama indicated a remarkably similar ecology to that of populations in temperate North America. Observed ecological differences in the tropics (e.g., greater size, annual egg production, longer nesting seasons, etc.) were more a matter of degree, largely related to greater opportunities for foraging, growth, and reproduction in the year-long warmth rather than substantive change in lifestyle. While I found essentially the same patterns at Tortuguero, the sliders here were unique in two characteristics that warranted further study. First, they are huge, even by tropical slider standards, with some females attaining carapace lengths of 44 cm and weights up to 10 kg. Second, circumstantial evidence had accumulated that sliders used Caribbean Sea beaches for nesting — a very unslider-like trait, and



A slider nesting track on Tortuguero Beach.



An adult South American Snapping Turtle (Chelydra acutirostris) at Tortuguero

known in only a handful of other non-marine turtles. Turtle biologist Peter Pritchard had previously observed that non-marine turtle tracks observed on Tortuguero beaches were always those of adult slider females (which are much larger than males) and that the discarded carcasses of sliders that had been collected on beaches for food by Tortuguero residents were also adult females. These observations suggested that beached sliders were not just waifs washed out of the Tortuguero Estuary during flood periods. In addition, in June 1989, Jim Spotila, Tom Yocky, and I were searching for Leatherback nests along Tortuguero Beach when we encountered a small strange track that we followed to a single slider hatchling on the lower beach near the surf line. We backtracked it to its probable nesting site in the cocoplum scrub of the upper beach berm. These observations intrigued me, and I resolved to study the ecology of sea-beach nesting and its adaptive significance for sliders in the Tortuguero ecosystem. I was particularly interested in why, of all the slider populations across the vast range of these species, sea-beach nesting had evolved only here, and whether the huge size characteristic of Tortuguero females was somehow linked to this phenomenon.

Peter Pritchard, who has thought about most things "turtle" at some time or another, had previously suggested that beach nesting was probably a response to the need for open nesting sites, always in short supply in virgin rainforest, and that large size provided physiological advantages during the period of sea travel required to reach appropriate nesting sites. A study of the ecology of Panamanian sliders by my brother Edward Moll and John Legler in the 1960s had established that golf courses, plantations, and other more open sites were used to the exclusion of rainforest for nesting in their



Snapper habitat near Tortuguero.

Canal Zone study area, so this first idea made sense. As all sea turtles and those other freshwater species known to venture into the sea, such as the Asian river terrapins and Asiatic Giant and Nile softshells, are very large animals by turtle standards, the association of large size and seaworthiness also held merit. My sabbatical leave from teaching responsibilities during a spring semester several years ago allowed me the freedom to walk the Tortuguero beaches from January through March, the peak of the slider nesting season, to acquire more information.

Fringed by Coconut Palm and Seagrape, the black sand beach of Tortuguero extends unbroken for 35 km from the Tortuguero Canal Estuary in the north to the Parismina River Estuary in the south. Always beautiful, it nevertheless can be a difficult place to work. By day, it quickly became lethally hot, with sand surface temperatures approaching 70 °C. Upon returning from early morning surveys, I usually entered the cool gloom of the adjacent forest for a respite - often entertained by wingsnapping mating displays of White-collared Manakins and slowly foraging troops of Black Howler Monkeys in the tree tops. On moonless nights, the beach could be so black as to lose its features altogether, and I was regularly upended by beach litter and by stepping off newly wave-cut benches that changed position nightly — but, if there were hardships, they were more than offset by the lure of discovery and the beauty of the wild tropical beach. One bright moonlit night, for example, I sat watching a nesting



Eggs excavated from a snapper nest near Tortuguero.

slider in the cocoplum scrub while an early-season Leatherback, spangled with phosphorescence and moonglow, hauled out of the surf to nest just thirty meters down the beach. On another night, as I returned to Casa Verde after reaching the southern terminus of my survey route, I noticed Jaguar tracks paralleling my own footprints for more than three kilometers. It was a big animal, apparently watching me curiously (I prefer not to think hungrily) from the darkness as I trekked down the beach. Without doubt, experiences such as these were the "adventures of a naturalist on remote Caribbean shores" that Archie Carr had in mind when he wrote *The* Windward Road nearly 50 years earlier.

Gradually, through observation and radiotelemetric monitoring of sliders in the rivers, in the sea, and on the beach, a characteristically clockwise, albeit variable, nesting pattern emerged. Sliders generally moved north with river currents into the sea via the Tortuguero Estuary or by crossing a narrow strip of land that separated the river from the sea north of Tortuguero Village. They then moved south in the longshore current just beyond the surf line until they hauled up to nest in the cocoplum scrub of the upper beach a few kilometers south of the village in Tortuguero National Park. Spent females would usually return to the sea, moving down-coast for a brief period before emerging again to trek overland across



Brown Wood Turtles (Rhinoclemmys annulata) are fully terrestrial.



Brown Wood Turtle habitat in secondary growth near Tortuguero.

the peninsula to the Tortuguero Canal. Once in the canal, they moved north again with the current to suitable feeding and basking areas. The pattern conserved energy by utilizing the prevailing canal and sea currents, and got the turtles to the appropriate nesting sites with little time spent on land, an important point that I'll address below. The upper beach cocoplum scrub nesting sites provided a moderate thermal environment for egg development well away from the highest tides, as well as protective cover for the laying female and emerging hatchlings. Sliders, like most turtles, have temperature-dependent sex determination, in which warmer nests or nest depths produce females and cooler sites males. Substrate-temperature monitoring indicated that open beach temperatures were too hot and probably lethal to developing eggs while forest soils were root strewn, soggy, and probably too cool for adequate female production. The cocoplum, however, provided few obstructions, proper drainage, and the right thermal regime for the production of both sexes. The latter probably results from a combination of single-sex and mixed-sex nests scattered through the cocoplum scrub. Due to the relative proximity of these suitable beach nesting sites to freshwater habitats, a straight-line distance of a kilometer or less of forested peninsula in between, the sliders can survive at Tortuguero. Without it, as is often the case in more inland rainforests, they probably cannot, and are therefore usually absent from the rainforest turtle fauna.

The question remains, however, why the female sliders simply don't walk across the peninsula to deposit their eggs on the beach? Sliders are fully capable of walking a kilometer or more to lay eggs or moving from pond

to pond in temperate habitats. Why is it better to risk travel over a substantially longer distance by sea in a physiologically difficult environment with a formidable set of predators in order to reach the beach nest site? The answer may be linked to both the size of the Tortuguero sliders and to the vulnerability of their relatively small eggs to a diverse array of terrestrial predators. I think sliders here have resorted to sea travel to avoid leading terrestrial predators to their nest sites. This could occur if predators followed a female wandering overland to the nesting site (or her scent trail) or back-trailed her to the site as she moved directly toward the canal through the forest after nesting. From this perspective, both the long sea travel phase in reaching the nest site and the return to the sea after nesting for a brief period before down-coast emergence and overland movement to the canal make sense. I also think that great size has evolved as a consequence of the sea-travel phase. While it may well confer osmoregulatory advantages by lowering the body-surface-to-mass ratio, work by Bill Dunson of Pennsylvania State University has shown that even smaller turtles have a relatively low rate of sodium influx. I think the large size here has evolved principally to provide the sea-going females with insurance against the predation risks that have been increased by their relatively long nesting migrations and en-route exposure to marine predators. The occasional mutilated carcasses of slider females I've observed washed up on the beach underscore the reality of the dangers. Whit Gibbons has advanced the general hypothesis that large size would confer an advantage in reducing predatory and environmental risks to turtles that must travel from the relative safety of their aquatic home



White-lipped Mud Turtle (Kinosternon leucostomum) from Tortuguero.



White-lipped Mud Turtle habitat at Tortuguero.



Black River Turtles (*Rhinoclemmys funerea*) spend time both in water and wandering on the forest floor.

range for nesting or other reasons. A side benefit of decreased travel risks would be that more time could be expended and more distance traveled in seeking the most optimal nesting sites available. If strong selection reduces terrestrial travel to minimize egg predation, then travel time in the sea must increase accordingly. The evolution of gigantism at Tortuguero is probably a response to these factors.

If the beaches provide the relatively open sites necessary for slider nesting, I wondered what sites might be used for nesting by resident snapping turtles. My studies of their ecology at Tortuguero indicated no substantive changes from the ecology of temperate populations. They were surviving at Tortuguero by living their usual generalist lifestyle characterized by habitat flexibility and omnivory. Reproductive studies by Ron Brooks in Ontario and Justin Congdon in Michigan indicated that northern snappers, like sliders, require relatively open nesting sites. I suspected that they would need such nesting sites at Tortuguero as well, but I never encountered any

on the sea beaches during my slider surveys. By accident, however, I stumbled across a nesting snapper early one February morning on an abandoned milpa, an area cleared and planted for one or more years, then abandoned and allowed to return to forest. These areas remain relatively unshaded for several seasons and provide a key habitat for the survival of Tortuguero's snappers. By focusing my search in these areas adjacent to caños (small streams), I was able to discover several additional snapper nests over an extended period of the spring dry season. These were essentially identical in form and egg characteristics to temperate nests. At Tortuguero, a loose sort of mutualism existed between humans and snappers where the big Tortugas Lagartos ("Alligator Turtles") occasionally were caught for food by local residents, and, in turn, were provided with nest sites via milpa agriculture. Perhaps snapper survival in the modern Neotropics is dependent upon such human activities elsewhere in rainforested areas as well. Tree falls near waterways may provide similar nesting opportunities by letting more sunlight reach the ground, but I never encountered any nesting snappers in natural forest openings at Tortuguero.

I think of the sliders and snappers of the Neotropics as the "Beverly Hillbillies" of the turtle world — true misfits, but gamely trying to make a go of it in an alien culture. The collective ecological evidence from Tortuguero and elsewhere indicates that they have not yet blended into the rainforest community during their brief residence here. Their generalized ecology and need for non-forested nesting sites clearly evolved to cope with a different environment far from their current home. The other turtles here have become highly adapted for life in the rainforest. Reproducing and regularly foraging on the forest floor and even, as our research indicates, being involved in symbiotic seed-dispersing relationships with many local plants, these species have truly become part of the fabric of the rainforest ecosystem. In contrast, the newcomers have extended their characteristic flexibility to the extreme to survive here in spite of the all-encompassing forest. By using such tricks as beach and milpa nesting they have managed to hang on, barely, by the skin of their jaws, as the forest has reclaimed its former domain during these wetter times since the last ice age. From this perspective, the sliders and the snappers of the Neotropics may be among the few species to benefit from the continued destruction of the rainforest.



Tortuguero Beach.



The Tortuguero River provided slider and Black River Turtle habitat.



A JJAEP student and a hatchling Ornate Box Turtle with radio transmitter attached.

# Turtles in the Dust: Effects of Hands-on Scientific Training on a Group of Behaviorally At-risk Students' Knowledge and Empathy

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Photographs by the senior author.

**Abstract.**—We taught a group of behaviorally at-risk students lessons on box-turtle biology and natural history before translocating hatchling Ornate Box Turtles (*Terrapene ornata ornata*) to a nature area adjacent to their school. The students then assisted with data collection and ultimately used telemetry to re-locate the turtles and independently collect data. Each student in the experimental group was given a questionnaire prior to beginning and again after completion of the program, with questions covering box-turtle biology, natural history, and empathy toward animals. Students in a control group were given the same questionnaire at similar times. Students in the experimental group felt they improved their knowledge concerning box-turtle biology and natural history after training, whereas control group students did not. Neither group, however, showed a change in empathy between the pre- and post-questionnaires. Incorporating behaviorally at-risk students in research projects may enable researchers to complete projects while at the same time involving an often-neglected portion of the population.

#### Introduction

Interactions with animals at a young age improve social development and attitudes toward nature in children (Myers and Saunder 2002). In addition, companion animals in the classroom are known to increase sensitivity toward humans and possibly decrease aggression (Hergovich et al. 2002). Gender, animal ownership, and attitudes toward animals also affect empathy toward humans (Taylor and Signal 2005). However, no consensus links interactions with animals and increased empathy toward humans (Paul 2000, Taylor and Signal 2005). We also are unsure whether involving students in intensive, hands-on science programs with animals might also increase empathy toward nature.

The goals of this study were to increase scientific knowledge and foster empathy toward animals in a group of behaviorally at-risk students by engaging students in a hands-on research project. We predicted that as a result of personal involvement in box-turtle research, the experimental group of students would show increased knowledge and empathy when compared to a control group that received neither classroom lessons nor an opportunity to participate in field research.

#### Study System

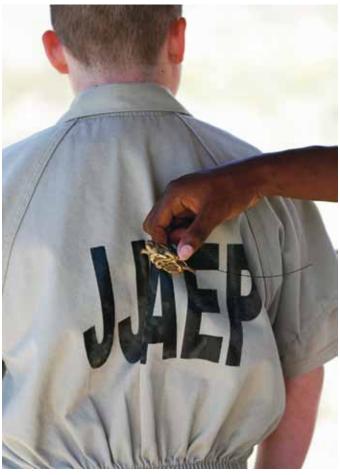
The Juvenile Justice Alternative Education Program (JJAEP) is an alternative education program for students who have been expelled from any of the eight school districts in Lubbock County, Texas. The program focuses on discipline and attempts to bring students' knowledge up to their current grade level. More information can be found at www.lubbockisd.org/ JJAEP/. A 0.6-ha nature area is adjacent to the school and is bisected by a nature walk.

The Ornate Box Turtle (*Terrapene ornata ornata*) ranges from southern Texas to South Dakota and from Colorado to Indiana. It is the state reptile of Kansas (Dodd 2001) and is often well-liked wherever it is found near people. Like most members of the genus, the Ornate Box Turtle has declined throughout much of its former range. However, urban Lubbock holds large populations that have received some attention in recent years (Sosa 2009).





Hatchling Ornate Box Turtle (Terrapene ornata ornata).



JJAEP students and a hatchling Ornate Box Turtles.

#### Methods

We worked with students enrolled in the JJAEP from April 2008 to October 2009. One of us, the acting principal of JJAEP (OR), selected male students between the ages of 13 and 17 who met minimum requirements (good attendance and behavior) to participate in the hands-on experiment. Before training, the selected students were given a short questionnaire with questions on box-turtle biology, natural history, and attitudes towards animals. Upon completion of the questionnaire, one of us (JAS) met with the students twice weekly for 45 minutes each time. During the initial three weeks, we lectured the students on box-turtle biology and natural history with the assistance of books and articles. We also demonstrated the proper techniques employed by scientists in the study of box turtles, such as radio telemetry and thread trailing, to the experimental group of students. Beginning on the fourth week, we translocated hatchling Ornate Box Turtles, which had been given to the South Plains Wildlife Rehabilitation Center, to the nature area adjacent to the JJAEP campus. Two hatchlings in 2008 and three hatchlings in 2009 were translocated to the nature area. The experimental group of students aided in the attachment of radio transmitters and measurements of each turtle prior to translocation.

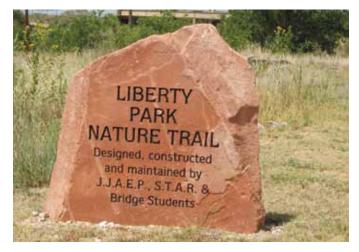
We relocated each hatchling two to five times a week for the remainder of the active season. The students assisted with relocations biweekly during the school year. For each relocation, we recorded date, time, GPS coordinates, weather data, habitat, and activity of the turtles. Before students were dismissed for summer break (approximately six weeks following administration of the initial questionnaire), each student completed the questionnaire again. A control group of students was given the questionnaire twice during 2009, with a six-week interval, but received no training. The questionnaire consisted of factual questions, as well as some about

individual attitudes. For questions 1–11, which focused on students' perceptions of their knowledge (e.g., "how much do you know about box turtles?") answers ranged from 1 ("nothing") to 5 ("everything"). Questions 13–15 offered a range of answers (e.g., for the question "the best place for a box turtle is?" answers were "in nature"; "in a zoo"; "in a cage as a pet"; "there is no good place"; and "none of the above").

We used an analysis of variance to test for changes in knowledge between the answers on pre- and post-questionnaires for the two groups (experimental and control). Significant differences between pre- and post-surveys were then explored further with an independent samples t-test for each group. We tested for differences between qualitative pre- and post-survey questions (13–15) with a chi-square analysis. Results were considered significant at  $\alpha=0.05$ .

#### Results

Five students in 2008 and five in 2009 began in the experimental group. At the recommendation of the JJAEP principal, however, two students did not complete the entire training program in 2009. In addition, 12 students in 2009 were part of the control group and received no training. After training, all students in the experimental group had seen a turtle, whereas no difference in box-turtle sightings existed between pre- and post-questionnaires for the control group. We found a significant difference between control and experimental groups for questions 1–9 and question 11 (p < 0.05), all of them box-turtle specific, but not question 10, which involved factors responsible for environmental degradation. Within the experimental group, we found a significant improvement between pre- and post-responses on questions 1–11 (p < 0.05 in all cases). In contrast, we detected no improvement for the control group for questions 1–11 (p > 0.05 in all cases). No





JJAEP nature trail marker and representative habitat.





JJAEP students using radio-telemetry to relocate translocated turtles.

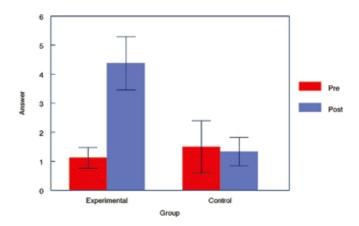
statistically significant differences existed between the pre- and post-answers for questions 13-15 (p > 0.05) for either group.

#### Discussion

Our results indicate that students in the experimental group improved their knowledge on box-turtle biology and natural history. Questions 13–15, however, were an attempt to determine if training impacted students' empathy toward box turtles. The answer choices might have been at the extremes, either a positive or negative response with no neutral choices. If students had a more diverse array of answer choices and we worked with a larger sample of students, we believe the resolution of whether students' empathy changed would improve because empathy is expected to increase when direct contact with animals is provided (Thompson and Gullone 2003).

At-risk students are capable of independently collecting scientific data when given training, despite the fact that some procedures were complex (radio-telemetry) and others required meticulous attention to detail (data recording). The experimental group of students is now trained in advanced scientific procedures that most high school students do not have the opportunity to learn.

In conclusion, our training program was effective in teaching at-risk students biology and natural history of box turtles as well as scientific skills.



Asked "What is your knowledge on how big a box turtle can grow?" experimental-group students showed significantly greater improvement after working with turtles than did control-group students. Similar patterns were seen on all natural history questions (questions 1–11 on the pre- and post-surveys).

Future studies should focus on framing questions on empathy in order to improve resolution. Studies also should examine whether students who participate in training have increased confidence compared to students who do not receive specialized training. Because JJAEP is a school for students expelled from traditional schools, the extra attention could provide students with more confidence and increase their marketability later in life. At a minimum, students were exposed to novel ideas and a potential career path.

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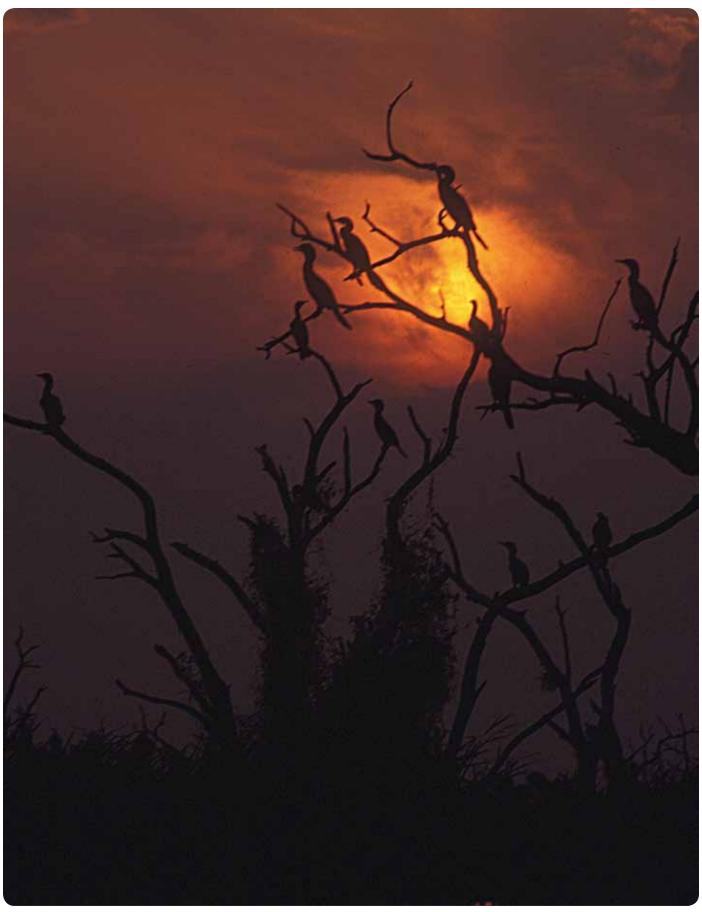
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Management of habitats for target species, such as the Yellow Anaconda (*Eunectes notaeus*) in Argentina, can be beneficial to many other species, such as these Neotropical Cormorants (*Phalacrocorax brasilianus*) at Banyado la Estrella.

#### COMMENTARY

# Is Wildlife Management Business or Conservation — A Question of Ideology

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Photographs by the author (except where noted).

#### Macroeconomics and Conservation Approaches

Tpublished an article in 2007 about anaconda conservation and how it can be affected by macroeconomics (Rivas 2007a). I identified poverty as the ultimate threat to conservation in Latin America and how conservation efforts were bound to meet with little success as long as poverty remains the rule in rural areas. I also identified neoliberal policies¹ as one of the main causes of poverty and highlighted how well intended conservation efforts, based on neoliberal measures, fail to solve the poverty problems of rural regions — and thus also fail in their conservation goals. Instead, they work as a "painkiller," creating the illusion of a solution, providing at best temporary relief, but in fact distracting from seeking real solutions.

#### What is True Conservation?

At the core of any disagreement regarding conservation programs in Latin America is the notion, widely held among many conservation biologists, that any plan for wildlife management, including ecotourism, is by definition a conservation plan. This notion has been promoted for the last few decades in order to capitalize on people's increasing environmental awareness (e.g., Mansfied 2009). However, considerable evidence suggests that wildlife management is not de facto conservation. Consider a bird-watching operation located in an area inhabited by a very shy and rare species. Bird watchers flock to the site during the nesting season to see this rare species, which can produce an economic surge in the local economy. Although such an example might be considered an effective conservation plan, if this rare bird is so shy that the steady parade of tourists compromises nesting success, this population could literally be "watched into extinction." A true conservation program must have conservation as its primary goal and not just as a byproduct. If only a byproduct, the system can easily stray into a regular business regulated solely by the bottom line — and one that might not even be sustainable.

Wildlife harvesting programs fall into one of three categories: (1) Businesses that exploit an environmental commodity until it is depleted. (2) Businesses that use an environmental resource in a sustainable manner but without providing enough economic incentives to the stewards of the land. (3) Programs that use a resource sustainably but also provide substantive economic incentives for local citizens who then have good reasons to protect the environment from other uses that might not be sustainable. When the bulk of the economic incentive benefits the local communities, they will have both reasons and resources to prevent external enterprises from threatening the environment. I would argue that the first example is not conservation at all and that only the third is true conservation. The second example can — and should — take credit for being sustainable, but just because it does not destroy the environment is not enough to construe

it as a conservation program. As a matter of ideology, the goal of a conservation program must be conservation. Economic gain can be a byproduct or a means to do conservation but it must not be the goal. Also, the main beneficiaries of a true conservation program must be the local communities. They are tightly linked to the land and will more likely try to protect an ecosystem that supports them — if they have the resources. External businesses can easily move their operation elsewhere and are not truly committed to the maintenance of the system.

#### Management of Anacondas in Formosa, Argentina

In my 2007 article (Rivas 2007a), I never intended to provide a comprehensive review of the Argentinean Yellow Anaconda management program and I do not intend to do so now. My concern then and now is that management programs that allocate most of the profit to an economic elite provide only superficial relief to the problems of the local people, do not protect the system against external influences, and do not constitute true conservation. In fact, they have the potential for distracting us from seeking real solutions.

Micucci and Waller (2007), and Waller and Micucci (2008) high-lighted a number of positive elements in the Formosa program. In addition, the program has doubtlessly increased the economic status of the local population. From interviews with local people, I learned that the anaconda harvest could increase their yearly income by as much as 50%. I also learned from law enforcement officials that the rate of cattle robbery and common crimes had dropped to historic levels since the program began, which they attributed to the local people having legal means of earning an income. While all these are desirable traits in a management program, they do not



For more than two decades, the Venezuelan Spectacled Caiman (*Caiman crocodilus*) program generated a continuous profit and was often cited as an example of sustainable management in a free-market economy. However, the system collapsed as a consequence of over-hunting, and tanners moved their operations to other sites.

<sup>&</sup>lt;sup>1</sup> In essence, neoliberal policies seeks to transfer much of the control of the economy from public to the private sector under the belief that it will produce a more efficient government and improve the economic health of the nation.



I started to study Green Anacondas (*Eunectes murinus*) in Venezuela in 1992 in order to explore the possibilities for sustainable use. Due to the collapse of the caiman program in the mid-1990s, the Venezuelan government halted other harvesting programs. Consequently, no attempt to harvest anacondas ever materialized in Venezuela. Conservation biologists often believe that their approach to conservation is *pure* conservation, strictly scientific, or somehow devoid of politics or ideology. However, management programs based on a free-market economy rely on constant growth, which is intrinsically at odds with conservation principles. Scientists who fail to realize this are at risk of becoming unwitting tools of economic agendas that they do not understand or with which they might not even agree.

differ from any other business moving into an area and they might fail to protect the ecosystem against non-sustainable uses — because the incentive offered by the anaconda program, as described in Micucci et al. (2006), is not enough to empower the local people, nor does it provide them with the means to oppose a corporate takeover in search of greater profits.

Wildlife management programs around the world are not asked to meet these high standards to qualify as conservation. I would also argue that this is the reason conservation programs more often than not show poor results. This and my earlier 2007 papers are intended to raise awareness about economics and politics among conservation biologists, to design management programs that not only use resources in a sustainable manner with conservation as a byproduct, but to design them with conservation as the principal goal and to include in them means of providing local communities with the resources to withstand pressures from external sources that promote non-sustainable uses in favor of short-term profits<sup>2</sup>.

We should not use the term "conservation" for programs with goals that are not primarily conservation-oriented. For example, catching fish to supply high-end restaurants is called *fishing*, not fish conservation. Fishing operations around the world are first and foremost commercial businesses — and fishing operations have on many occasions over-fished their stocks (e.g., Hutchings and Myers 1994, Larkin 1977, Myers et al. 1997). Furthermore, even sustainable fishing operations do not try to disguise their business as conservation programs. The anaconda management program in Formosa may well be a legitimate, sustainable business that helps the local economy (like any business) and relieves pressure on the natural environment by providing jobs (as businesses often do) — but, if conservation is merely a byproduct, such a program should not be presented as conservation.

#### Globalization or No Globalization? That is the Question

Conservation efforts based on globalization and the free market are risky because they are not time-tested models and fall within a narrow context of economic principles. We cannot trust our precious diversity to such untested economic models. Free-market economies have largely failed in the one task they purportedly are designed to do well: Production of wealth. The United States is one of very few countries (basically the G8³) that have benefited from a free market system — but that is not the case for the majority of the countries that have tried it. Furthermore, the countries that have succeeded under free-market economies are countries that have destroyed most of their pristine natural habitats, as a free market relies on constant economic growth. Using globalization and free-market measures for conservation policies is a response to ideological agendas, and it is not data-driven or supported by facts (e.g., Mansfield 2009).

I do not intend to turn this commentary into a debate on economics or politics, but when we apply a conservation strategy that is tightly linked to an economic ideology we are supporting that ideology, whether we realize it or not. Insisting on free-market measures for conservation despite their repeated failures to protect biodiversity is not only ineffective but shows adherence — conscious or not — to ideological positions that are intrinsically at odds with conservation principles.

#### **Tylenol Conservation**

As I argued in my 2007 articles, temporary measures can and should be developed to address and relieve short-term problems. To differentiate them from real solutions, I labeled them "Tylenol Conservation," as they work like a painkiller, ameliorating symptoms of a disease they are not intended to cure. A management program that relieves local poverty while we search for real solutions is a welcome tool as part of a conservation program, but it is it not conservation by itself — and it should not replace the search for a real solution anymore than a painkiller should replace the search for a real cure.

Many of the conservation solutions we seek in today's world are destined to fail because they rely on the same neoliberal framework responsible for the poverty that is largely responsible for the failure of conservation programs, and they provide only temporary and superficial relief. This is

<sup>&</sup>lt;sup>3</sup> A forum for the world's major industrialized democracies (Canada, France, Germany, Italy, Japan, Russia, United Kingdom, United States) to discuss issues of mutual or global concern.



Large, non-aquatic animals have been unable to flourish in most Capybara (*Hydrochoerus hydrochaeris*) habitats (Hoogesteijn et al. 1997). In fact, Capybara are, for the most part, the lone large herbivore in most of their natural habitats. As such, the normal large prey predator has not evolved, and capybara can be farmed in an almost completely natural setting. Consequently, many conservationists have strongly pushed for governmentally subsidized Capybara farming.

<sup>&</sup>lt;sup>2</sup> Imagine that a corporation wanted to drain large portions of the swamp from which anacondas are being harvested to, for example, plant oil palms for the production of agro-fuels. This operation will destroy the habitat, but would also offer permanent employment with comparable or superior income to what the locals make from wildlife harvesting. Will the locals be willing to oppose this operation to protect the habitat? Will they have the resources to oppose the corporation? I contend that it is only conservation if the answer to these questions is yes.

why I seek to redefine what we do in conservation by promoting a greater awareness of the political and economic framework in which we function. Not doing so can render us unwitting tools of economic and political ideologies that compromise the success of conservation efforts.

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## Always Opportunistic



Not one to question its luck, this Great Egret (*Ardea alba*) readily exploits the human-mediated introduction of Green Iguanas (*Iguana iguana*) onto Grand Cayman.

## IN VASIVE SPECIES

# Island Invaders: Introduced Amphibians and Reptiles in the Turks and Caicos Islands

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The term "invasive" usually refers to non-native species that are having at least some negative impact on local floral or faunal communities. Invasive species are among the top three causes of global biodiversity decline (Lockwood et al. 2007), and understanding their distributions and avenues of introduction is important for regional conservation and management. Moreover, an understanding of the biology and natural history of invaders might help to suggest methods for their control and also predict effects on native wildlife.

Recently, much attention has been paid to invasive reptiles and amphibians (Kraus 2009). Reptiles and amphibians may be especially good colonizers, as evidenced by the nearly circumtropical distribution of certain species, such as the Brahminy Blind Snake (*Ramphotyphlops braminus*) and the Cane Toad (*Rhinella marina*).

Islands seem to be particularly vulnerable to invasive species, as these species often are freed from the pressures of natural enemies (predators and parasites) and competition (Whittaker and Fernández-Palacios 2007). Many tropical and subtropical islands contain unique herpetofaunal assemblages that are vulnerable to disruption by the introduction of nonnative predators and competitors. The West Indies is considered one of the world's most important biodiversity hotspots and the region's native reptiles and amphibians are of particular conservation concern (Myers et al. 2000, Smith et al. 2005). Centuries of habitat modification and the introduction of damaging mammalian predators such as feral cats (*Felis catus*), Indian Mongoose (*Urva auropunctata*), and Black Rats (*Rattus rattus*) have negatively affected many reptilian and amphibian populations (e.g., Iverson 1978, Corke 1992, Smith et al. 2005, Tolson and Henderson 2006). As such, documenting and reporting the spread and impact of introduced herpetofauna remains an important task.

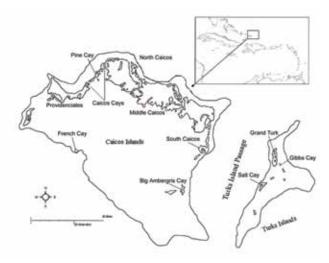


Fig. 1. The Turks and Caicos Islands are located at the southern terminus of the Bahamian Archipelago ~130 km from Hispaniola. Major islands and islands mentioned in the text are labeled.









Fig. 2. Native reptiles of the Turks and Caicos: (A) Turks and Caicos Rock Iguana (Cyclura carinata), (B) Turks and Caicos Curly-tailed Lizard (Leiocephalus psammodromus), (C) Caicos Blind Snake (Typhlops platycephalus), (D) Caicos Dwarf Boa (Tropidophis greenwayi), (E) Antillean Skink (Mabuya sp.), (F) Turks Dwarf Gecko (Sphaerodactylus underwoodi; female, left; male, right), (G) Caicos Dwarf Gecko (Sphaerodactylus caicosensis, male, bottom; female, top), (H) Caicos (Hecht's) Barking Gecko (Aristelliger hechti), (I) Turks Island Boa (Epicrates chrysogaster chrysogaster), (J) Southern Bahamas Anole (Anolis scriptus scriptus).



We have spent the last four years working in the Turks and Caicos Islands (Fig. 1) and have made an effort to document the presence and distribution of non-native species of this archipelago. The Turks and Caicos Islands, located at the southern terminus of the Bahamian Archipelago, contain ten species of native reptiles, eight of which are endemic at the species or subspecies level (Fig. 2). The remaining two species (Anolis scriptus and Mabuya sp.) are widely distributed in the southern Bahamas and throughout the West Indies. No amphibian species is native to the Turks and Caicos. As of October 2009, seven non-native reptilian and two amphibian species have been discovered in the Turks and Caicos, nearly doubling the number of reptiles and adding amphibians in a region where previously they had not been documented. Tourism and large international investments have resulted in explosive development of these islands and a surge in the number of immigrants filling jobs in the construction and service industries. Combined with the rapid increase in imports, the list of invaders might continue to grow. Below we discuss the distribution and abundance of the known invasive reptiles and amphibians in the Turks and Caicos, and encourage other researchers to document similar invasions in other regions that support a unique native herpetofauna.

#### Cuban Treefrog, Osteopilus septentrionalis. Established.

Cuban Treefrogs (Fig. 3) are widely introduced in the Caribbean and southeastern United States, with populations on Puerto Rico, in the Virgin Islands, upper Lesser Antilles, Florida, and elsewhere (Henderson and Powell 2009). These frogs appear able to tolerate xeric conditions that would prevent most other amphibian colonists from becoming established. As long as they have access to ephemeral or permanent sources of freshwater, these frogs can breed prolifically and become abundant. Cuban



Fig. 3. Cuban Treefrog (Osteopilus septentrionalis) from North Caicos.

Treefrogs are of particular concern because of their voracious appetites, high densities, and noxious skin secretions. Although this species is native to the Little and Great Bahama banks, it is generally considered a recent arrival to the Turks and Caicos, where it is firmly established on the islands of Providenciales, Grand Turk, North Caicos, and Middle Caicos, and will likely be found on several other islands with the expansion of irrigation for development. On North and Middle Caicos, these frogs reach exceptional densities, often covering the road after a heavy autumn rain. Endemic Caicos Dwarf Boas (*Tropidophis greenwayi*) have even shifted their behavior to feed on these frogs, occupying the interior walls of old stone water wells to capture metamorphs as they climb up the sides from the water below (RGR, C. Deal, and N. Manco, unpubl. data). Color photo vouchers, Austin Peay State University (APSU) 19024, 19027.

#### Greenhouse Frog, Eleutherodactylus planirostris. Established.

Greenhouse Frogs (Fig. 4) are small terrestrial frogs that stow away in soil and plants, and have been introduced to Jamaica, Florida, and the Turks and Caicos Islands from their native range in Cuba, the Caymans, and the Bahamas (Henderson and Powell 2009). This species is a direct-developer, meaning that the larval stage is completed in the egg. Eggs are laid in moist leaf litter, and hatchlings emerge as miniature adults. Greenhouse Frogs occur in the Turks and Caicos on the islands of Providenciales, Grand Turk, North Caicos, and Middle Caicos, and will likely be discovered on other islands. Color photo voucher, APSU 19023.



Fig. 4. Greenhouse Frog (Eleutherodactylus planirostris) from North Caicos.

#### Red-Eared Slider, Trachemys scripta elegans. Not established.

Red-Eared Sliders (Fig. 5) are popular pets with long lifespans, and often are released when owners grow tired of them. Native to the eastern and midwestern United States, these freshwater aquatic turtles have been introduced to many islands in the West Indies, from Puerto Rico and Hispaniola to Guadeloupe and Martinique (Henderson and Powell 2009). They require a consistent source of freshwater and, although this type of habitat is rare in the Turks and Caicos, several ponds built for the Leeward golf course on Providenciales likely provide the main refuge for this species. Only a few adult Red-Eared Sliders have been captured and removed, although a few more probably occur in these manmade ponds. No hatchlings or juveniles have been observed; hence we do not consider this species to be reproducing. Color photo voucher, APSU 19021.

#### Antillean Slider, Trachemys stejnegeri malonei. Established?

A single Antillean Slider was collected in 1975 from Pine Cay on the Caicos Bank (W. Auffenberg, UF 49423), although several other individuals were reported in 1997 from a freshwater pond on the same island (Seidel 1986,



**Fig. 5.** Red-Eared Slider (*Trachemys scripta elegans*) captured near the Provo Golf Club on Providenciales, Turks and Caicos Islands and being held at the National Environmental Centre.

1988; Lee and Ross 2001). This species is believed to be a human introduction to the Caicos Cays (Seidel 1988, 1996) from Great Inagua. We are unaware of any specimens reported since 1997, although persistence of this population from 1973 to 1997 would indicate that reproduction might be occurring, unless the species is being recurrently introduced, a situation that seems unlikely on this privately owned resort island.

#### Wood Slave, Hemidactylus mabouia. Established.

Wood Slaves (Fig. 6) are rapidly expanding their range in the Western Hemisphere, and are firmly established in the Turks and Caicos Islands. These lizards are exceptionally good colonizers and, as human commensals, are afforded frequent opportunities to stow away in cargo, which is probably how they arrived in the Turks and Caicos. They are widely distributed in the Turks and Caicos and are currently known from six large islands: Providenciales, North and Middle Caicos, South Caicos, Grand Turk, and Salt Cay (Reynolds and Niemiller 2009), although they likely occur on many more. We have discovered nests on Salt Cay (Fig. 7) and have recorded juveniles and hatchlings on all six islands. These geckos probably do not represent a great threat to most of the local herpetofauna, except on the islands of North Caicos, French Cay, and Big Ambergris, where the endemic Hecht's (or Caicos) Barking Gecko (*Aristelliger hechti*) occurs. These native geckos are ecologically similar to the introduced Wood Slave,



Fig 6. Wood Slave (Hemidactylus mabouia) from Salt Cay, Turks and Caicos Islands.



Fig. 7. Hatched nest of the Wood Slave (*Hemidactylus mabouia*) under a rock on Salt Cay, Turks and Caicos Islands.

occupying vertical surfaces of trees, rock walls, and buildings and feeding on small flying or climbing insects. Color photo vouchers, APSU 18047, 18945, 18946, and 18949.

#### Mayaguana Dwarf Gecko, Sphaerodactylus mariguanae. Established?

Mayaguana Dwarf Geckos are native to the Bahamian islands of Mayaguana and Booby Cay, located about 65 km to the northwest of the Turks and Caicos. Although small (SVL to 41 mm; Schwartz and Henderson 1991), they are much larger than the native *S. caicosensis* (SVL to 32 mm) and *S. underwoodi* (SVL to 32 mm). Dwarf geckos likely move between islands quite easily because of their small size, high fecundity, and proclivity for inhabiting stacks of building supplies, such as cinder blocks and lumber, as well as potted plants, soil, and mulch. Molecular data suggest that native *S. underwoodi* move between the islands of Grand Turk and Salt Cay on cargo (Reynolds and Koneczny, in review).

Schwartz (1968) and Schwartz and Henderson (1991) reported S. mariguanae from Grand Turk. To our knowledge, this species has not been seen there in quite some time, but the record stands in Henderson and Powell (2009). This record likely does not represent a misidentification, as 40 individuals were collected (Albert Schwartz Field Series [ASFS] 10766) and compared to other populations and to S. underwoodi (Schwartz 1968); however, whether these S. mariguanae individuals represent a human introduction or an extension of the species' native distribution is unclear. Also, that this species has apparently not been recorded since Schwartz (1968) and was never found on other islands on the Turks Bank is notable. Schwartz (1968) speculated that these Grand Turk S. mariguanae represented an introduced population, and evidence currently available certainly weighs in favor of this postulate, hence we include this species here as an introduced species. Grand Turk is a heavily developed island, yet endemic S. underwoodi appears to be fairly common, and thus S. mariguanae may yet persist there.

#### Green Iguana, Iguana iguana. Established?

As popular pets, Green Iguanas (Fig. 8) have become established in many areas outside of their native range in Central and South America, perhaps most notably in southern Florida, where they occur in very high densities near residential areas. In the Turks and Caicos, a few Green Iguanas have been found on Grand Turk and Providenciales. They likely represent released or escaped pets. Reproduction has not been documented, but this seems a likely possibility if several mature adults occur in the same area. Color photo voucher, APSU 19019.



Fig. 8. Green Iguana (*Iguana iguana*) captured near Long Bay on Providenciales and being held at the National Environmental Centre.

#### Cuban Knight Anole, Anolis equestris. Not established.

Likely released pets, four Cuban Knight Anoles have been collected and several more sighted at a Grace Bay resort on Providenciales Island. Like Green Iguanas, these large arboreal lizards appear to thrive in appropriate habitat, as they also are quite common where they have been introduced in southern Florida (Meshaka et al. 2004). They apparently are not reproducing in the Turks and Caicos, although that cannot yet be ruled out, given the abundance of lush and irrigated vegetation in the Grace Bay resort complexes. Color photo vouchers, APSU 19025, 19026.

#### Brahminy Blind Snake, Ramphotyphlops braminus. Established.

Essentially a circumtropical species, the Brahminy Blind Snake, which is native to the Indian Subcontinent, has proven to be an exceptional colonizer because of its habit of sequestering itself in potted plants and its parthenogenetic mode of reproduction. This species has been found on both Providenciales and Grand Turk and is likely to find its way to many of the other islands in the archipelago. We currently do not know whether Brahminy Blind Snakes compete with the ecologically similar native blind snakes (*Typhlops* sp., *sensu* S.B. Hedges, *in litt.*), which are more abundant on islands other than Grand Turk and Providenciales. Color photo voucher, APSU 19022.

#### Eastern Corn Snake, Pantherophis [Elaphe] guttatus. Not established.

The Corn Snake (Fig. 9) is native to the southeastern United States and has been introduced elsewhere in the Caribbean, although it is successfully established only on the islands of Grand Cayman (Schwartz and Henderson 1991) and St. Thomas (U.S.V.I., Henderson and Powell 2009). These snakes might have arrived on islands as eggs laid in the soil of large potted trees from Florida; however, escaped pets also are a possible means of conveyance. Thus far, three adults have been found on Grand Turk, one of which laid a clutch of non-viable eggs after capture (B.N. Manco and B. Riggs, pers. comm.). Color photo voucher, APSU 19020.

#### Conclusions

The Turks and Caicos contain a unique assemblage of native reptile species. Threats from habitat modification and direct persecution (i.e., killing snakes) are taking a toll on species such as the Turks Island Boa (*Epicrates chrysogaster*) and the Turks and Caicos Rock Iguana (*Cyclura carinata*)(G. Gerber, unpubl. data; Reynolds and Gerber, in review). Threats from invasive mammalian species, such as cats, are well established, and local reptilian populations have suffered tremendously from their introduction (Iverson 1978, Mitchell et al. 2000). The degree of threat to local wildlife posed



Fig. 9. Eastern Corn Snake (*Pantherophis guttatus*) captured on Grand Turk, Turks and Caicos Islands, and being held at the National Environmental Centre.

by introduced reptiles and amphibians is largely unknown at this time, However, the first step is to document successful invasions. We encourage fellow biologists and amateur herpetologists in the West Indies to take note of introduced species and report them to local authorities.

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## Cuban Brown Anoles (Anolis sagrei) in St. Maarten

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Photographs by the author.

Cuban Brown Anoles (*Anolis sagrei*) are native to the Bahama Islands (Cay Sal, Conception, Crooked, Acklins, Grand Bahama, Little Bahama, Rum Cay, and San Salvador island banks), Cuba and associated cays, Isla de La Juventud, and Little Cayman, including most satellites and cays with even rudimentary vegetation. The species also has become established in Jamaica, either naturally or through human mediation. More recently introduced populations are known in Grand Cayman, Swan Island, Grenada, St. Vincent, the Grenadines (Canouan), Barbados, the Atlantic Coast of México as far as Belize, the Islas de la Bahía (off Honduras), Aruba, Hawaii (Oahu and Coconut Island, Kauai), Taiwan, the southeastern United States, and California (Orange County; Henderson and Powell 2009 and references therein). At least some introduced populations originated in the southeastern United States.

Within a 30-minute period on 2 March 2010, I observed three male and two female *Anolis sagrei* in and around the Philipsburg harbor in St. Maarten. St. Maarten is a major commercial center in the eastern Caribbean; a number of exotic species have been recorded there, and several (e.g., Cuban Treefrogs, *Osteopilus septentrionalis*; Green Iguanas, *Iguana iguana*) have become established (Powell et al. 2005).

Although I did not observe any juveniles, the abundance of observations in such a short period is suggestive of a breeding population. I did observe native Anguilla Bank Anoles (*Anolis gingivinus*) associated with ornamental vegetation in and around the harbor. I saw no evidence of competitive interactions, but the apparently restricted range of *A. sagrei* is suggestive of a recent arrival. Whether the newly established population remains largely restricted to severely altered habitats, as has been described on Grenada (Greene et al. 2002, Germano et al. 2003) and St. Vincent (Henderson and Powell 2005, Treglia 2006, Treglia et al. 2008) remains to be determined. The origin of the population on St. Maarten is unknown.

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Male (top) and female Cuban Brown Anoles (*Anolis sagrei*) from the Philipsburg harbor on St. Maarten. Photographic vouchers have been deposited in the Milwaukee Public Museum: MPM P745 (male) and MPM P746 (female). The identity of these lizards was confirmed from photographs by Robert W. Henderson.

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## Knight Anoles (Anolis equestris) on Grand Cayman Island

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Knight Anoles (*Anolis equestris*) are native to Cuba, but have become established in southern Florida (King and Krakauer 1966) and Hawaii (McKeown 1996). Secondary introductions from Florida, primarily with landscaping vegetation, have been documented for several species (e.g., Cuban Treefrogs, *Osteopilus septentrionalis*, and Cuban Brown Anoles, *A. sagrei*) on West Indian islands (Henderson and Powell 2009, and references therein).

On 8 June 2007, we found a Knight Anole on the grounds of the Ritz-Carlton Hotel on Seven Mile Beach, Grand Cayman Island (photographic voucher, Milwaukee Public Museum MPM P748, photograph by K.D. Godbeer, confirmed by A.C. Echternacht). Subsequently, an additional individual was collected in the Savannah area. Both presumably arrived from Florida with decorative plants. To date, we have no evidence that suggests the presence of a breeding population in the wild.

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A Knight Anole (Anolis equestris) from Florida, the presumed origin of the animals found on Grand Cayman.

#### BOOK REVIEW

# Conservation of Venomous Snakes is a Delicate Balance of Science, Sociology, and Politics

Timber Rattlesnakes in Vermont and New York: Biology, History, and the Fate of an Endangered Species. 2007. Jon Furman. University Press of New England, Lebanon, New Hampshire (www.upne.com/1-58465-656-5. html). 207 pp., 12 color illustrations, 8 halftones. Paperback – ISBN: 978-1-58465-656-2. \$24.95

Announced by the Center for North American Herpetology (CNAH) in 2008, this authoritative and well-illustrated book is an important acquisition for all of us who work to advance the conservation of Timber Rattlesnakes (*Crotalus horridus*) throughout the wide range of the species. Readers may well wonder why I feel that a book grounded in the biology of this impressive species in two northeastern states is so relevant elsewhere. Simply put, conservation — especially of venomous snakes — is a delicate balance of science, sociology, and politics. Furman has carefully researched and thoroughly documented the interplay of these three elements as they relate to the sundry (and increasing) anthropogenic threats faced by Timber Rattlesnake populations in two eastern states that only in relatively recent times have recognized the species as Endangered and have moved to try to reverse declines (or even extirpations) resulting from earlier flawed management practices.

A talented writer, Furman explores the troubling decline of the northeastern populations caused by bounty hunting from the 1890s to the early 1970s. His friendships with contemporary researchers such as Randy Stechert, William Brown, and others, whose individual and combined research and conservation work with *Crotalus horridus* have been crucial to reversing historical trends of persecution of the species, adds much to

the book. Vignettes of the legal battles waged on behalf of these snakes, along with Furman's observations on the personalities involved and their varied approaches to preventing further human damage to dens and birthing areas offer effective models of appropriate conservation measures.

An unusual aspect of the book is the time Furman invested in interviewing the most noted Crotalus horridus bounty hunters of the area. Despite the great toll these people took on the snakes, few were motivated by animosity toward them. Rather, they were people eking out a living in a largely agricultural area during difficult economic times, and they saw the poorly conceived state bounties on rattlesnakes as another way to earn income. One or two of the hunters went so far as to study wild and captive Crotalus horridus behavior, ecology (although not using that term), and physiology, the better to locate snakes and ply their trade. Even the interviews involving preparation of



A male dark-phase Crotalus horridus from Warren County, New York.

rattlesnake oil as an anti-inflammatory, a topic that initially brought a smirk to my face, proved valuable in understanding another aspect of why the hunters pursued their quarry. So, delving into the pharmacological literature in December 2009, I found that certain snake oils are higher in eicosapentaenoic acid (Omega-3) than many fish oils (Kunin 1989, Graber 2007)!

Overall, the book is solidly anchored in biology, sociology, and history of science. Although parts of Furman's oral history interviews with old-time bounty hunters often are unpleasant for herpetologists to read, they are important for understanding the sociological realities that historically have hampered conservation of any venomous snake species. If herpetologists are to successfully work to change public attitudes about rattlesnakes, such understanding is crucial (Pisani and Fitch 1993).

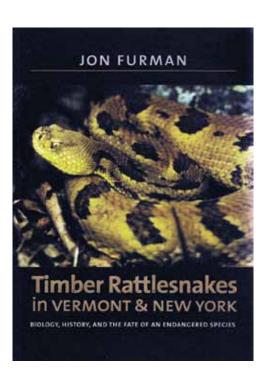
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#### NATURAL HISTORY RESEARCH REPORTS

#### Copperheads in the **Northeastern United States**

SMITH ET AL. (2009. Herpetological Monographs 23:45-73) studied the spatial and reproductive ecology of a population of Copperheads (Agkistrodon contortrix) in a basalt trap-rock ecosystem in the central Connecticut River Valley, a region that constitutes the northeastern extreme of this species' geographic range. Adult males (n = 20) and females (n = 15) were surgically implanted with radio-transmitters and tracked every 48 h during the active season (April-October) for three consecutive years (2001-2003). From late autumn to early spring (November through March), when snakes were hibernating and thus inactive, tracking was reduced to once per week. Activity range size and multiple movement parameters differed significantly by sex. Throughout the active season, males had greater activity range sizes and showed greater movement than females. This trend was pronounced during the mating season, which was restricted to late summer and early fall (late July through September). In contrast to most populations of A. contortrix from more southern and western localities, the authors observed no sexual activity (e.g., courtship, coitus, and malemale fighting) in the spring. Individuals of both sexes showed annual fidelity to: (i) Activity range location, (ii) activity range size, (iii) movement distances, (iv) particular features of their activity ranges (e.g., refuges), and (v) hibernation sites. Males and females showed no difference in preferred seasonal habitats. In both sexes, shifts in habitat associations during the active season included migrations from over-wintering sites within basalt trap rockslides to higher-elevation open deciduous forest during the summer foraging and reproductive season. Parturition in the field was recorded in eight instances and was always close to one of the two hibernacula used by the individuals in the study area. The authors dedicated this paper to Henry S. Fitch.



Unlike populations of Copperheads (Agkistrodon contortrix) from more southern and western localities (like this snake from Kansas), a population from the northeastern extreme of the species' range exhibited no sexual activity in the spring.

#### Secretive Snakes in a **Grassland Community**

Fitch (1999) summarized his fifty years of intensive fieldwork on the snake fauna of the Fitch Natural History Reservation (FNHR) and adjacent study areas, commenting upon the relative scarcity of two small, secretive species, the Smooth Earth Snake (Virginia valeriae) and the Brown Snake (Storeria dekayi). Location of a population of V. valeriae (Pisani 2005) as a component of a diverse snake fauna that includes S. dekayi on land adjacent to Fitch's main study areas provided an opportunity to accumulate considerable new information on these species in a similar snake community. PISANI (2009. Journal of Kansas Herpetology 32:20-36) conducted an intensive mark-recapture study of this community from September 2006 through





Smooth Earth Snakes (Virginia valeriae) and Brown Snakes (Storeria dekayi) exploit available grassland habitats in northeastern Kansas to a much greater extent than had been documented.

November 2008. The ongoing study included observations on feeding, defense, home range, morphology, and population sizes along with relevant microhabitat characteristics. Data accumulated indicate considerably greater use of available grassland habitat by these and syntopic small snake species than had been recognized. An extensive review of literature and unpublished dissertations provided insights to aspects of the community interrelations of small vermivorous snakes in northeastern Kansas. These interrelations are considered in light of landmanagement and other anthropogenic factors affecting the abundance of earthworms.

#### **Eavesdropping Lizards**

Madagascar Spinytail Iguanas (Oplurus cuvieri cuvieri) use their ears to eavesdrop on the Madagascar Flycatcher's (Terpsiphone mutata) alarm calls to protect themselves from predators. RYO ITO AND AKIRA MORI (2009. Proceedings of the Royal Society B, Biological Sciences 277:1275-1280) conducted a study in the Ampijoroa dry deciduous forest and discovered that the lizards use auditory signals for predator detection. The iguanas have well-developed ears, but are not vocal like the flycatchers. Eavesdropping is the first step for the lizard; it then moves its head while keeping its body still to help identify the predator and evaluate the risk. The lizards and the flycatchers do not have direct interactions nor do they compete for resources, but they do share predators such as raptors and snakes. Evidence suggesting that Galápagos Marine Iguanas (Amblyrhynchus cristatus) also eavesdrop on heterospecific alarm calls led the researchers to believe that this might be a widespread phenomenon in iguanid lizards.



Madagascar Spinytail Iguanas (Oplurus cuvieri cuvieri) eavesdrop on the alarm calls of Madagascar Flycatchers to alert themselves to potential predators.

#### Repeated Adaptations of Garter Snakes to Deadly Prey

Where do the genetic variants underlying adaptive change come from? Are currently adaptive alleles recruited by selection from standing



Pacific Newts, such as this California Newt (Taricha torosa), contain deadly tetrodotoxins that are lethal to many potential predators. However, at least three species of Garter Snakes in the genus Thamnophis have independently evolved a resistance to those toxins and readily prey on newts.

genetic variation within populations, moved through introgression from other populations, or do they arise as novel mutations? **FELDMAN ET AL.** (2009. *Proceedings of the National Academy of Sciences* 106:13415–13420) examined the molecular basis of repeated adaptation to the toxin of deadly prey in three species of Garter Snakes (*Thamnophis*) to determine whether

adaptation evolved through novel mutations, sieving of existing variation, or transmission of beneficial alleles across species. Functional amino acid substitutions in the skeletal muscle sodium channel are largely responsible for the physiological resistance of Garter Snakes to tetrodotoxin found in their Newt (*Taricha*) prey. Phylogenetic analyses rejected the hypoth-

eses that the unique resistance alleles observed in multiple species of *Thamnophis* were present before the split of these lineages, or that alleles were shared among species through occasional hybridization events. The authors' results demonstrated that adaptive evolution occurred independently multiple times in Garter Snakes via the *de novo* acquisition of beneficial mutations.

#### NEWSBRIEFS

#### Loggerhead Turtles Nesting in Pakistan

Renowned turtle expert Nicolas J. Pilcher, who was in Karachi for a seminar on threats to the turtles in Pakistan, has confirmed that a third species, the Loggerhead (Caretta caretta), was also nesting on these shores. Until now, the only two species recorded nesting in the country were Green Turtles (Chelonia mydas) and a smaller number of Olive Ridleys (Lepidochelys olivacea). By far the most widespread nesting is by the Green Turtle, from the eastern shores of Sindh Province all the way to the western shores of Balochistan. Recent findings by the IUCN Pakistan team, under the auspices of the Balochistan Partnerships for Sustainable Development project, have documented a third species, the Loggerhead, nesting at Daran beach, some 11 km southeast of Jiwani.

Positive identification of adults and hatchlings was made by Dr. Nicolas Pilcher, Co-Chair of the IUCN Marine Turtle Specialist Group, and a long-time turtle researcher and conservationist. Some sixty nests were recorded during 2009, and the work will expand in the coming months to determine the extent of this nesting. Loggerheads are known to nest in large numbers in Oman, on Masirah Island, and a small number nest in Yemen, but this is the first record of Loggerhead nesting in Pakistan. This latest discovery expands the nesting range for Loggerheads and raises their survival outlook in a climate where critical nesting habitats are being rapidly lost to development. The discovery also boosts known diversity of wildlife in Pakistan.

Pakistan used to host substantial numbers of Olive Ridleys along the shores of Sindh Province, but most have ceased to nest. Commercial fisheries are the main reason for this decline; with over 1,900 active trawlers operating just offshore, turtles have been accidentally lost to fishing nets. Trawling for shrimp and fish is known as one of the major causes of sea turtle mortality.

Luckily for the Loggerheads, Sindh-based commercial fisheries do not generally operate as far away as the western end of Balochistan, so the turtles have avoided the threats. Turtles can be saved from drowning in fishing nets through the use of Turtle Excluder Devices (TEDs), which are clever adaptations to nets that allow fish and shrimp to enter the net but turtles to

escape through a special opening. The IUCN intends to work with partners in the country to help introduce and promote TEDs so that fishing will have less impact on turtles. This may also result in the reappearance of Olive Ridleys.

For the past several decades marine turtle conservation programs have been underway in Pakistan. Most noticeable is the work undertaken in Sindh Province, on Sandspit and Hawkes Bay, where thousands of turtles have been protected through hatchery enclosures.

IUCN 14 February 2010



Nesting Loggerhead (*Caretta caretta*) have been documented at Daran beach, near Jiwani, Pakistan.

## New Specialist Group for Chameleons

Chameleons are primarily found in Madagascar and Africa, with a few species distributed in the near east and along the coast of southern Europe. Although some species have broad distributions, many have extremely small ranges. Important habitats for chameleons are heavily impacted by human activities, and some restricted-range species are particularly vulnerable. Because of their unique appearance, and, in some cases, their exceptional ornamentation, chameleons are one of the most sought-after reptiles in the pet trade. Tens of thousands of wild chameleons are legally exported every year, which, with an illegal trade at unknown levels, is cause for concern. A Chameleon Specialist Group was established in February 2010 to address issues of sustainability and conservation of these unique reptiles. Its first major objective is to conduct a conservation assessment of all chameleon species for the IUCN Red List.

> IUCN SSC e-bulletin March 2010



Veiled Chameleons (*Chamaeleo calyptratus*) are but one of many species exploited in the pet trade. An IUCN Chameleon Specialist Group has been established to address issues of sustainability and conservation of these spectacular reptiles.



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## Editors' Remarks

The second installment of our year-long tribute to Henry S. Fitch appears in this issue. A third installment will be in the September issue and the fourth and final portion will appear in December. We would like to think that Dr. Fitch would have enjoyed these notes and articles about the natural history of the animals to which he devoted much of his professional life.

Also in this issue is the second inclusion of our Invasive Species section, documenting species of amphibians and reptiles in places where they do not occur naturally and do not belong. Alien species are a major and growing concern for the conservation of native and endemic taxa throughout the world. Although interesting, the accounts that appear in this section document a tragedy imposed on natural biotas. We ask that readers of *Reptiles & Amphibians* not contribute to this problem by releasing captive animals into nature or by patronizing irresponsible breeders and merchants.

The Editors of Reptiles & Amphibians

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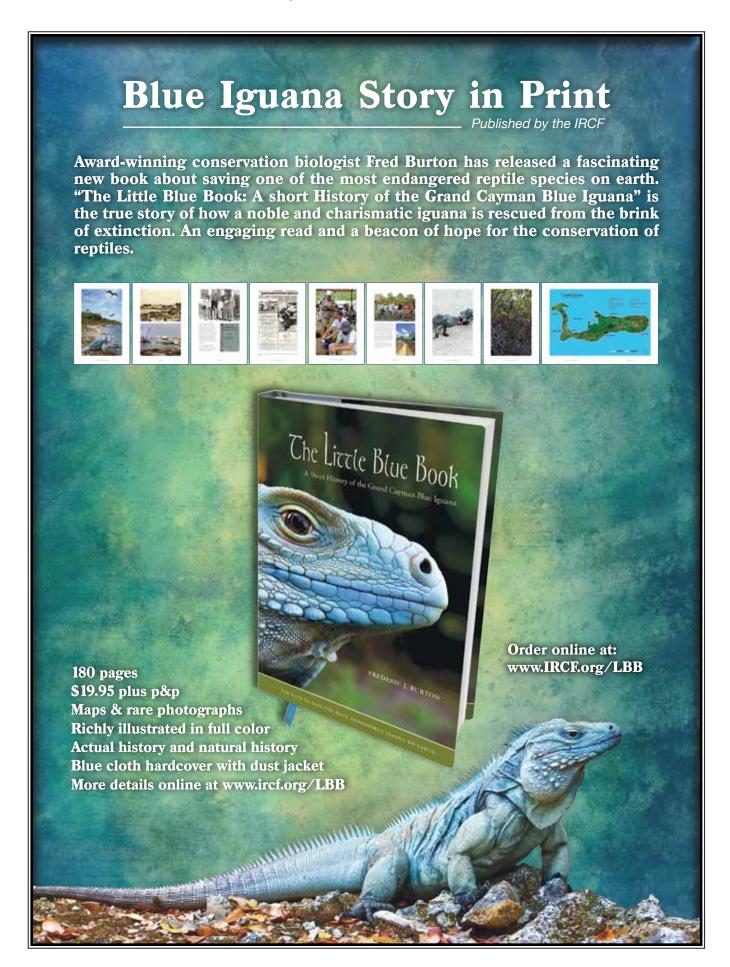
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One of the most problematic invasive species in the West Indies is the Cuban Treefrog (Osteopilus septentrionalis), with many introductions of a secondary nature originating from introduced populations in Florida and dispersed primarily with nursery plants. These frogs readily act as human commensals and have a catholic diet that includes other vertebrates. Severe ecological effects are likely, especially when these frogs invade relatively natural areas.

