

Food Habits of the Snake *Psammophis phillipsi* from the Continuous Rain-Forest Region of Southern Nigeria (West Africa)

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ABSTRACT.—The food habits of the snake *Psammophis phillipsi* were studied in the rain-forest region of southeastern Nigeria, where this is the most common snake species of the area. A total of 120 prey items were recorded from 327 specimens (73 juveniles; 55 gravid females); many gravid females contained prey. Lizards (mainly *Agama agama* and *Mabuaya* skinks) were the most common prey type for adult snakes, both gravid and nongravid, and for subadults as well; small mammals were the second most common prey type for all snake categories. Insects and small snakes (including conspecifics) were occasionally consumed. Diet composition did not differ significantly between gravid and nongravid specimens, but gravid specimens more frequently contained small mammals and fewer lizards. Ontogenetic dietary change was relatively minor. Prey and predator mass were significantly related in both adults and subadults.

Snakes of the genus *Psammophis* are conspicuous elements of the African fauna and are abundant in such disparate habitats as savannas (Trape and Mane, 2000), rain forests and forest-derived habitats (Akani et al., 1999), and mangroves (Luiselli and Akani, 2002). They are expected to be important predators in these varied habitats (Luiselli et al., 1998) and deserve careful attention by ecologists involved in the study of ecosystem dynamics.

General comments on the feeding habits of these snakes are available in the literature (e.g., Schmidt, 1923; Cansdale, 1961; Gauthier, 1967; Pitman, 1974; Chippaux, 1999). This information and observations on captive specimens (e.g., Trutnau 1981) suggest that *Psammophis* feed mainly on lizards and small mammals and less frequently on small snakes and anurans. Clearly, the feeding ecology of a given species should be based on more accurate information, including detailed lists of prey items taken from free-ranging specimens and analysis of prey-size versus predator-size relationships; such information is lacking for any species of Afrotropical *Psammophis*.

Here we present a detailed account of the feeding ecology of free-ranging *Psammophis phillipsi* from an African region situated inside the continuous Guinea-Congo rain-forest belt (i.e., southern Nigeria, West Africa), with emphasis on both original data from our long-term field research, and literature data relative only to specimens of this geographic area.

Psammophis phillipsi (Colubridae: Psammophiini) is an oviparous, medium-sized (to 1.8 m long), diurnally active snake, widely distributed in the forest and forest-derived savanna regions of west and central Africa. Its taxonomy is still unresolved, and it is suspected to be a species complex rather than a single species (Hughes, 1999). Our specimens were typical *P. phillipsi* in terms of meristic and morphological characteristics (e.g., uniform coloration and shape of the snout) but possessed a divided cloacal scale (CSD) in most cases

(Hughes, 1999). Therefore, they should be referred to the form considered by Hughes (1999) as typical of the central African countries (westward to Nigeria).

MATERIALS AND METHODS

Our field study was carried out from September 1996 to July 2001 (with additional data recorded in 1994 and 1995), in some localities of southeastern Nigeria (for the territories surveyed, see Luiselli and Angelici, 2000; and for a detailed description of the environment, see Luiselli et al., 2000), situated in the eastern axis of the Niger Delta (Bayelsa and Rivers States), in Anambra, Akwa-Ibom, and Cross River states. The study region is tropical, with a wet season from May to September and a dry season from October to April. The wettest period of the year is June through July, and the driest period between late December and February.

Methods used to survey the study area, capture snakes, and analyse their food items, are detailed elsewhere (e.g., Luiselli et al., 1998, 2002). Fieldwork was conducted under all climatic conditions but with a bias toward diurnal hours (0800–1800) because of security constraints related to the prevailing unstable sociopolitical situation. Field effort was almost identical in the wet (408 field days) and dry (395 field days) seasons.

We searched for snakes along standardized routes in the various microhabitats frequented by snakes at the study areas. We captured snakes by hand, but additional free-ranging specimens were captured by pitfall traps with drift fences and by traps used by locals to capture terrestrial animals. We always recorded the site of capture and the habitat at each capture site. Each snake was measured for snout–vent length (SVL, to the nearest 0.5 cm), weighed with an electronic balance, and individually marked by ventral scale clipping for future identification. Then, the snakes were palpated in the abdomen until regurgitation of ingested food or defecation occurred. In addition, specimens found already dead during our surveys (e.g., snakes killed by farmers, or by cars, etc.) were dis-

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sected to determine whether prey were present. We identified prey items to the lowest taxonomic level possible. We estimated mass of prey items at the time of its ingestion, when possible, by comparing the item to intact conspecifics of various sizes from our own personal collection, or measuring the fresh biomass in perfectly preserved items. This was not possible in faeces items, which generally consisted of scales for reptiles and fur for mammals.

Because determination of sex in *P. phillipsi* is often problematic even in adults (if not using invasive techniques) and may lead to misidentifications (Akani, Angelici, Eniang and Luiselli, unpubl. obs.), we subdivided our specimens in two categories: gravid (GR) and nongravid (NGR). GR were all females obviously carrying eggs, and NGR were all adults that were obviously not pregnant (males plus nongravid females). To discriminate between juveniles and adults, we followed Butler (1993): the smallest mature *P. phillipsi* female he identified was 650 mm SVL, and given that he found females were significantly smaller than males, we assumed that all specimens shorter than 650 mm were immature.

Vouchers were deposited in the herpetological collections of the Rivers State University of Science and Technology (Port Harcourt, Nigeria), of the Department of Agricultural Sciences of Uyo University (Uyo, Nigeria), of the Faculty of Sciences of the University of Calabar (Calabar, Nigeria), and of the Cross River National Park (collections in both Akamkpa and Butatong, Nigeria).

We also reviewed available literature for data on the diet of *P. phillipsi* from southeastern Nigeria. We did not accept general comments (e.g., "this snake feeds on lizards, mice, etc.") but only precise dietary records (Butler and Reid, 1990; Luiselli et al., 1998). We also examined over 40 dissertations from local universities and over 30 environmental reports (EIA) by companies working in southeastern Nigeria, to check whether additional dietary data were available. In most, cases our efforts were unfruitful, because either no mention of these snakes is made (e.g., Powell, 1993, 1996; Singh et al., 1995; Isoun et al., 1996) or they are mentioned but no precise dietary data are provided (e.g., Reid, 1989; Schmitt, 1996; Politano, 1998). Nevertheless, in a EIA report for AGIP oil company (Politano, 1985), raw data are given on morphometrics (SVL, tail length, number of ventrals [without indication of the counting method], locality, habitat of capture, and food items), of many snakes found during the assessment surveys, including several *Psammophis* (identified, following Villiers, 1975, as *Psammophis sibilans phillipsi*).

All statistical tests were two-tailed, with alpha set at 5%. Means are followed by ± 1 SD.

RESULTS

We analyzed dietary contents of 327 specimens captured in the wild; of these, 73 were juveniles, and 55 were gravid. A total of 120 prey items were recorded (Table 1). Prey were collected frequently from heavily gravid females, which is a demonstration that in this oviparous species, contrary to other snake species, females feed regularly during gestation.

Lizards were the main prey type for both GR and NGR adults (respectively 45% and 50% of the total

TABLE 1. Compilation of the original data available on food items of *Psammophis phillipsi* from southeastern Nigeria. These data came from a total of 327 specimens, of which 73 were juveniles and 55 were gravid. Data from feces and stomachs are cumulated.

Prey	Num- bers of prey items in non- gravid adults	Num- bers of prey items in gravid adults	Num- bers of prey items in juve- niles
Invertebrates			
Mantodea	0	1	1
Vertebrates			
Mammals			
<i>Crocidura</i> sp.	2	2	0
<i>Rattus rattus</i>	0	1	0
<i>Mus musculoides</i>	8	2	2
<i>Lemniscomys striatus</i>	5	2	0
Unidentified adult mice	7	5	1
Unidentified newborn mice	0	2	3
Reptiles			
<i>Psammophis phillipsi</i> (newborn)	1	0	0
<i>Natriciteres</i> sp.	1	0	0
<i>Mabuaya</i> sp.	11	4	5
<i>Mochlus fernandi</i>	1	0	0
<i>Agama agama</i>	33	11	9
TOTAL	69	30	21

number of items, see Table 1), and for subadults as well (66.7%). Small mammals were the second most common prey type for all snake categories. Insects and small snakes (including conspecifics) were occasionally consumed. NGR adults and GR adults did not differ significantly in terms of taxonomic dietary composition ($\chi^2 = 12.7$, $df = 7$, $P = 0.08$), but if we restrict the contingency-table analysis to the two most important types of prey (lizards and small mammals), GR specimens fed significantly more frequently than NGR specimens on small mammals and the reverse was true for lizards ($\chi^2 = 9.6$, $df = 3$, $P = 0.022$). Although adults consumed a higher number of small mammals than juveniles (36.4% vs. 28.6% of the total diet), the overall taxonomic composition of the diet of adults and juveniles was similar ($\chi^2 = 9.5$, $df = 7$, $P = 0.22$).

Prey mass and predator mass (log-transformed) were significantly related in both adults (for NGR specimens: $r = 0.44$, $N = 41$, $P < 0.001$; for GR specimens: $r = 0.38$, $N = 22$, $P < 0.05$) and subadults ($r = 0.51$, $N = 12$, $P < 0.05$). Prey mass averaged $10.7 \pm 3.2\%$ ($N = 41$) of predator mass in NGR specimens, $11.2 \pm 1.2\%$ ($N = 22$) of predator mass in GR specimens, and $11.7 \pm 2.7\%$ ($N = 12$) of predator mass in subadult specimens. These ratios did not differ significantly among the three snake categories (one-way ANOVA, $F_{2,74} = 1.157$, $P = 0.403$).

DISCUSSION

In general, our study confirms previous studies (e.g., Cansdale, 1961; Pitman, 1974) stating that the

bulk of the diet of *P. phillipsi* (or *sibilans*, as *phillipsi* was simply considered a subspecies of *sibilans* in much old literature) consists of lizards and small mammals. Literature data on food of *P. phillipsi* from the continuous forest region of Nigeria (provided in Politano, 1985; Butler and Reid, 1990; Luiselli et al., 1998) reported a total of 30 items, of which the majority were lizards (*Mabuaya* sp. and 13 *Agama agama*). These data suggested that the diet should consist almost exclusively of vertebrates (96.7% of the total preys), and more of reptiles (66.7%) than mammals (30%). In general, these data were fully consistent with our, much more detailed, observations.

We demonstrated that there is no significant ontogenetic change in the diet composition of this species in terms of prey types, although juveniles took a higher proportion of lizards and fewer rodents than adults. However, lizards were still a crucial prey type for adult snakes. The presence of a high abundance of lizard prey in juvenile *P. phillipsi* is very important if we take into account the reproductive cycle of this species in the tropical forests of southern Nigeria. Here, the annual reproductive cycle of *P. phillipsi* is a mono-estrous dry season cycle (sensu Saint Girons, 1982; Saint Girons and Pfeffer, 1971), with testicular recrudescence beginning at the end of the rainy season, vitellogenesis by the end of the rainy season, oviposition by mid-dry season and egg hatching at the onset of the rainy season (Butler, 1993). Thus, the offspring should find an abundant prey source, and they may rely on small *Agama agama* that are born in the same period (Harris, 1964; Butler, 1986) and typically abundant in the environment (Butler, 1993).

Our study also documents significant differences in some diet components among adults of different physiological conditions. Indeed, GR specimens fed on a higher number of small mammals than NGR specimens and juveniles. Similar shifts in prey preferences between gravid and nongravid snakes have been rarely reported in snakes (Luiselli et al., 1996) and to our knowledge, in no previously studied Afrotropical species. Our study demonstrated that reproductive females continue feeding even when heavily gravid, which may have important consequences for reproductive strategies (e.g., Bonnet et al., 2001), because it has been experimentally demonstrated that, in oviparous colubrids, food intake during vitellogenesis may affect clutch size but not offspring size (Seigel and Ford, 1991).

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Spatial Organization and the Dear Enemy Phenomenon in Adult Female Collared Lizards, *Crotaphytus collaris*

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ABSTRACT.—Reduced aggression toward territorial neighbors relative to strangers, the dear enemy phenomenon, is a widespread occurrence in many taxa, presumably because a stranger represents more of a threat to a resident than a neighbor. We recorded the response of 12 adult, nonreproductive, female *Crotaphytus collaris* residents to tethered neighbors or size-matched strangers and found no significant difference between responses to neighbors and strangers. Given that the dear enemy phenomenon is advantageous only to highly territorial individuals that stand to lose a great deal to a stranger, but not a neighbor, and that costs of territoriality may change with the reproductive cycle, we argue that there are no favorable conditions for the dear enemy phenomenon to evolve in this population of female collared lizards.

In many taxa, territory residents respond less aggressively to neighbors than to strangers (i.e., the dear enemy phenomenon; Fisher, 1954), presumably because neighbors represent less of a threat than strangers in terms of time and energy expended on an escalated interaction that could be used for other aspects of an individual's time budget (Jaeger, 1981; Getty, 1987; Temeles, 1994). Neighbors respect one another's boundaries with the "agreement" that they will not escalate encounters, especially if the costs of such encounters are high. Among lizards, the dear enemy

phenomenon has been documented in male *Anolis carolinensis* (Qualls and Jaeger, 1991), *Crotaphytus collaris* (Fox and Baird, 1992), and *Platysaurus broadleyi* (Whiting, 1999). Only females of one species of lizard have been tested for the dear enemy effect (*Urosaurus ornatus*; Mahrt, 1998), and the phenomenon was not found.

The behavior of female collared lizards is well documented (Fitch, 1956; Yedlin and Ferguson, 1973; Baird et al., 1996), but only one paper deals strictly with their social behavior (Sloan and Baird, 1999). The spatial organization of female collared lizards varies among studied populations from high spatial overlap

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(Baird et al., 1996) to very low overlap (Fitch, 1956; Yedlin and Ferguson, 1973; Rostker, 1983). The population studied during this investigation (Husak, 2001), as well as others (Fitch, 1956; Yedlin and Ferguson, 1973; Rostker, 1983), exhibits female spacing patterns that may be indicative of territoriality and may offer appropriate conditions for the evolution of the dear enemy phenomenon. The purpose of our study was to determine whether female *C. collaris* exhibit the dear enemy phenomenon. It represents only the second test for dear enemy recognition with female lizards and the first with female *C. collaris*.

MATERIALS AND METHODS

The study was conducted during May to June 1999 and 2000 on Sooner Lake dam, Pawnee County, in north-central Oklahoma. We surveyed the study area to generate scale maps for the purposes of determining home ranges. The maps were scale representations of the study area with points on the maps designating numbered flags on the actual site. The flags were in close enough proximity so that several could be seen from any given location, and accurate locations could be determined for each lizard sighting by triangulation. Lizards were captured by noosing and permanently marked with toe-clips and a unique pattern of colored beads attached with a short length of monofilament fishing line sewn through the base of the tail (after Fisher and Muth, 1989). When first captured, snout-vent length (SVL) was measured to the nearest 0.5 mm for each lizard. Home ranges were determined by daily scans of the study area and the minimum convex polygon procedure (Rose, 1982) from at least 20 sightings per lizard. Home-range size and overlap were calculated using ArcView GIS version 3.1 (Environmental Systems Research Institute, Redlands, CA). Home-range overlap was calculated as the percent overlap in home range for each resident female and the neighbor used as the intruder.

Once home-range boundaries were defined, staged intrusions were conducted in June 2000 on 12 randomly chosen adult females by tethering neighbor or stranger adult females at the boundary of a target resident's home range when the resident was 5–10 m away from the boundary. We began intrusions once we had withdrawn to 20 m away and the resident had full view of the intruder (following Fox and Baird, 1992). The following trials were conducted with 12 resident female subjects, each against: (1) neighbor female at familiar boundary and (2) stranger female at the same boundary (size-matched within 1 mm SVL to the neighbor). Strangers were captured from areas at least 2 km away from the study site to ensure their unfamiliarity to residents. The order of intrusions was random and no lizard was used in more than one trial on a given day so as to avoid potential confounds of elevated hormone levels or other factors that may keep a lizard temporarily in an artificially aggressive state as a result of multiple intrusions in sequential order with little time for rest. All lizards used as intruders were released within an hour after the intrusion was conducted. This investigation was part of a larger study concerning collared lizard social behavior (Husak, 2001), so ages of all lizards were known with certainty. All intrusions were conducted between the first and second clutch of eggs, using only adult (1.5+

TABLE 1. Scores given to agonistic behavior patterns recorded and used in the graded agonism analysis to weight relative cost to lizard.

Behavior	Score
Flee	-1
Retreat	-1
Approach	1
Throat display	2
Lateral throat display	2
Head bob	2
Push up	2
Circle	2
Chase	2
Attack	3
Bite	3

year-old) individuals. The "nonreproductive" time of the reproductive cycle was chosen because behavior should not be biased by postovipositional aggression (Sloan and Baird, 1999) or by a late-term gravid condition (Woodley and Moore, 1999), which may alter the costs and benefits of being aggressive (Mahrt, 1998). Residents and intruders were matched as best as possible so that they were in the same reproductive state, bearing only slight orange, gravid coloration. Ten-minute focal observations were conducted to quantify the latency to the first aggressive act and the frequency of aggressive and submissive displays of each target resident (Carpenter and Ferguson, 1977) during encounters.

Comparisons were made for the following measures of aggression as defined in Fox and Baird (1992): (1) latency to first aggressive act; (2) maximum aggression (scaled responses: 5 = fight then display; 4 = display then fight; 3 = display but not fight; 2 = display then flee; 1 = no response; 0 = flee); (3) total aggressive acts; and (4) graded agonism score (sum of frequencies of behavior patterns weighted by level of escalation: Table 1; modified from Fox and Baird, 1992). To avoid potential problems of intercorrelation among our variables, we analyzed the relationship between variables using a correlation matrix, discarding any redundant variables (those highly correlated to retained variables). One-tailed Wilcoxon signed-ranks tests were used to compare the response of residents to neighbors and strangers. The Wilcoxon signed-ranks test statistic is calculated based on ranks of differences between two paired groups, so the four females that did not respond to either neighbors or strangers were not included in the analysis. Correlation analysis was used to test for a significant relationship between home-range size and SVL, home-range overlap and SVL, and home-range overlap and the difference in SVL between the neighbors. Home-range sizes and overlaps used in the analyses were for those females used as target residents during the intrusions.

RESULTS

There was significant correlation among all variables (pairwise $r > 0.63$ among maximum aggression, total aggressive acts, and graded agonism score; pairwise $r < -0.64$ between latency and the other three

variables). We chose the graded agonism score as most representative of the data since it is a weighted count of escalation, and results are presented only for this variable. For the graded agonism score, we found no significant difference between responses to neighbors and strangers ($Z = 0.985$, $P > 0.25$). There was a great deal of individual variation in the responses to neighbors versus strangers, and no consistent pattern was apparent. Four females (33.3%) did not respond to either intruder, one female (8.3%) displayed equal aggression to both intruders, five females (41.7%) displayed more aggressive behavior toward strangers, and two females (16.7%) displayed more aggressive behavior toward neighbors.

Whenever statistical tests fail to reject the null hypothesis, the question of statistical power of the test is raised. However, a consequence of using distribution-free nonparametric statistical tests is that conventional power analyses are not applicable (Cohen, 1988). Methodologies developed to estimate power of nonparametric tests (Thomas and Juanes, 1996; Peres-Neto and Olden, 2001) using randomization techniques are conceptually inadequate when applied to the paired nature of our data as used in a Wilcoxon signed-ranks test. Because of these problems, the fact that our test was not close to significance and because of the controversy over retrospective (a posteriori) power analysis (Steidl and Thomas, 2001), we made a conservative conclusion that we could not reject the null hypothesis.

Average home-range size (± 1 SE) was 166.7 ± 13.2 m². No relationship was found between home-range size and SVL ($r = -0.48$, $P > 0.10$). There was extremely low home-range overlap, with a mean (± 1 SE) of 2.6 ± 0.9 %, and no significant relationship was found between home-range overlap and SVL ($r = -0.30$, $P > 0.25$), nor between overlap and difference in SVL ($r = 0.23$, $P > 0.25$).

DISCUSSION

The dear enemy phenomenon was not detected in this population of female collared lizards, in agreement with the one other dear enemy study conducted on female lizards (Mahrt, 1998). The absence of the dear enemy phenomenon in this population suggests several things about the social organization of female collared lizards. There is likely little threat to a resident female from a neighbor, and there is also likely no more threat from a stranger (see below). Because there is little threat from either type of intruder, there is no benefit to warrant escalation in either case (Jaeger, 1981; Getty, 1987). The dear enemy phenomenon is by definition a reduction in aggression toward a neighbor in relation to high levels of aggression directed toward a stranger, so low levels of aggression directed at both types of intruders (graded agonism score mean = 7.3 toward intruders) and a lack of significant difference between the responses suggest that the phenomenon was not in evidence. In contrast, male collared lizards have been shown to display the dear enemy phenomenon (Fox and Baird, 1992; Husak and Fox, in press), and graded agonism scores of males in the same population were much higher (graded agonism score mean = 118.9 toward strangers; Husak and Fox, in press).

The definition of territoriality has remained contro-

versial for many years (Noble, 1939; Brown and Orians, 1970; Maher and Lott, 1995), but inherent in most definitions of territoriality are three components: (1) site fidelity; (2) defense of the site; and (3) exclusive use (Sheldahl and Martins, 2000). With respect to the first criterion, our data suggest some degree of both intra- and interyear site fidelity among female collared lizards. Females of this population have well-defined home ranges, and daily observations confirm that they do not leave those areas. This study was part of a larger investigation of collared lizard social behavior, so we had spatial data for a subset ($N = 16$) of adult females that survived from 1999 to 2000. Fourteen of the 16 females (87.5%) had home ranges in 2000 that overlapped $> 90\%$ of their 1999 home range. The two exceptions to this pattern were lizards that shifted their home ranges from 1999 to 2000 to fill a vacancy created by the disappearance of a large female (at least five years old; lizard marked in study by Yoshioka, 1996). Males of the species are also known to show such year-to-year site fidelity (Baird et al., 2001; JFH and SFF, unpubl. data). The second criterion was only weakly met by this population of female lizards. We observed aggression toward neighbors and strangers, but it was of very low intensity. The third criterion was strongly met, with a very low degree of overlap among neighbors.

Previous studies have yielded mixed results in terms of whether female *C. collaris* are territorial (see above). The results of our study cannot definitively conclude whether these females were territorial, but they do suggest some degree of home-range defense, albeit weakly so. The fact that there was little home-range overlap (much less than in previous studies, e.g., Baird et al., 1996) suggests that there is some advantage to having an exclusive home range in females, but the advantages are most likely different than those conferred to males having an exclusive territory. Females are probably not defending access to mates as males of the species do, since a given adult male's territory may overlap numerous females (Baird et al., 1996; JFH and SFF, unpubl. data). The homogeneous structure of the habitat suggests that they are not likely contesting resources such as basking sites, nest sites, or food resources. In this situation, there are not enough benefits to outweigh the costs of aggressively defending the boundaries of a home range (e.g., costs of patrolling, increased risk of injury or predation). However, we cannot rule out the possibility that they may show the observed site fidelity caused by defense of other resources such as elevated look-out perches or refugia. The lack of a significant relationship between either home-range size or overlap and body size, or overlap and difference in body size, suggests that there may be no advantage to larger females having a larger home range with less overlap than smaller females (e.g., see Turner et al., 1969; Simon, 1975). Our findings agree with what is known about female spatial organization and the relationship between home-range size and body size in *C. collaris* (Baird et al., 1996), *Anolis carolinensis* (Nunez et al., 1997; Jensen and Nunez, 1998), and *Sceloporus virgatus* (Smith, 1995; Abell, 1999).

The dear enemy phenomenon is advantageous only to highly territorial individuals that stand to lose a great deal to a stranger but not a neighbor (Temeles,

1994). Female *C. collaris* apparently have little to lose from either neighbors or strangers, suggesting that if they are territorial, they are not defending resources that are limiting to other females. Defending a territory while carrying eggs is potentially costly because of the extra burden of the eggs (Sloan and Baird, 1999) and the heightened risk of injury or loss of eggs, so escalation should not occur toward any intruder during this time in their reproductive cycle. Sloan and Baird (1999) attributed heightened postovipositional aggression by female collared lizards to reestablishing social dominance after being absent from oviposition. If the resident expects to regain dominance upon return from oviposition, then equal, but high, postovipositional aggression should be directed toward both neighbors and strangers since they both represent a substantial threat. Perhaps since a neighbor may be more likely than a stranger to usurp portions of an absent female's home range, aggression may be directed even more toward neighbors than strangers (e.g., see Temeles, 1990). Given these circumstances, it is unlikely that the dear enemy phenomenon could evolve among female collared lizards.

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Chytridiomycosis in Wild Frogs from Southern Costa Rica

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ABSTRACT.—In 1993, the amphibian fauna of Las Tablas, Costa Rica, began to decline, and by 1998 approximately 50% of the species formerly present could no longer be found. Three years later, at the Reserva Forestal Fortuna, in western Panama, a site approximately 75 km east southeast of Las Tablas, KRL encountered a mass die-off of amphibians and a subsequent decline in abundance and species richness. The epidemiological features of the anuran population declines and die-offs at both sites were similar, suggesting a similar cause. Herein we document the presence of the fungus, *Batrachochytrium dendrobatidis*, in dead and dying wild frogs collected at Las Tablas just prior to population declines of several anuran species.

Since 1991, KRL has monitored amphibians on a private farm (8°55'N, 82°44'W) located at 1900 m elevation within the Zona Protectora Las Tablas of the Amistad Biosphere Reserve, Puntarenas Province, Costa Rica (Fig. 1). In 1993, she encountered 10 dead and dying amphibians along two adjacent 400-m transects along the headwaters of the Río Cotón, including two each of *Eleutherodactylus melanostictus*, *Atelopus chiriquiensis*, and *Hyla rivularis*, and one each of *Hyla calypsa*, *Rana vibicaria*, *Hyalinobatrachium fleischmanni*, and the salamander *Oedipina grandis* (Lips, 1998). She collected nine of these carcasses and nine additional, live, normal-appearing frogs (“controls”) from the same streams during the same month. She euthanized and preserved all specimens for future diagnostic examinations.

In 1995, RP performed microscopic diagnostic exams on three dead frogs and three control frogs, and reported a “possible epidermal protozoal parasite” as-

sociated with hyperkeratosis in all three dead frogs, but was unable to identify this to any known pathological agent. Approximately four years later, *Batrachochytrium dendrobatidis*, a frog-killing fungus, was described from the skin of dying captive frogs (Longcore et al., 1999). Concurrently, this same fungus was identified as the probable cause of death of 54 frogs found in Fortuna, Panama (Berger et al., 1998), an upland (1000–1400 m elevation) site located about 75 km east southeast of Las Tablas (8°42'N, 82°14'W). In both cases, infection was associated with hyperkeratosis of the epidermis, as had been seen in the dead frogs from Las Tablas. This prompted a retrospective diagnostic survey of the amphibians collected from Las Tablas in 1992–1993 to look for chytrid infection. We also surveyed additional skin samples from Fortuna specimens and from several species of amphibians collected from Las Alturas and the Jardín Botánico Wilson, in southern Costa Rica (Fig. 1). All of these sites have suffered recent losses of amphibian populations (Lips, 1999; unpubl. data), and we examined material to determine whether chytrids were present in frogs prior to population losses (Appendix 1),

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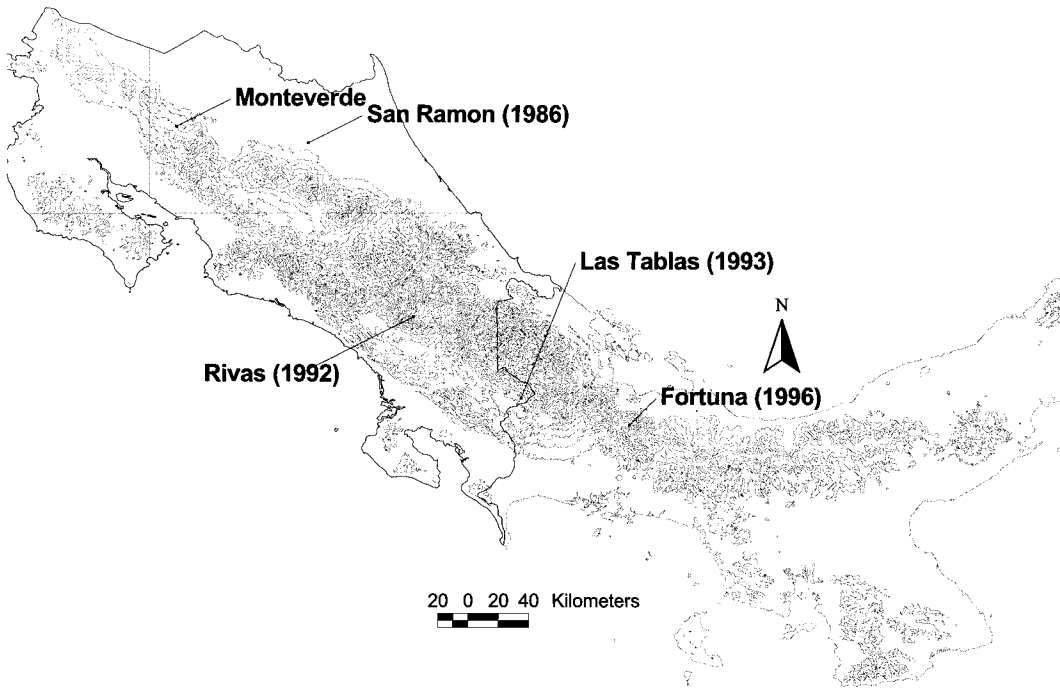


FIG. 1. Map of Costa Rica and Panama indicating sites mentioned in text. Sites with dates indicate documented cases of chytrid infection of amphibians (Berger et al., 1998; Puschendorf, 2003; this study).

which might provide information on the epidemiology of this disease.

MATERIALS AND METHODS

DEG destructively sampled 10 formalin-fixed carcasses (four dead, seven controls) collected from Las Tablas in 1993 and examined 29 2×2 mm skin swatches sampled by KRL from museum specimens (Appendix 1). Because of limited sample sizes, we could only determine presence or absence of chytrid; therefore, we did not examine all specimens, but deposited some dead frogs as vouchers in the CRE collection of J. M. Savage, now housed in the LACM. Tissues were decalcified, processed routinely into paraffin blocks, sectioned and stained with hematoxylin and eosin. RP's original paraffin blocks made from tissues of dead frogs collected in 1993 were reaccessed and embedded tissues were reexamined where possible.

RESULTS

The dead amphibians collected from Las Tablas in 1993 appeared well nourished and showed no external gross abnormalities, although four frogs had epidermal chytrid infections. The fungal infection was most extensive in the skin from chin to vent and in the digital and tarso-metatarsal skin of the hind limbs. Additionally, one apparently healthy *Atelopus chiriquiensis* collected as a control had a minimal infection characterized by widely scattered minute clusters of chytridial sporangia on the skin of the thorax, abdomen, and digits. In histologic sections of eight hind-

limb digits of this frog, only two minute clusters of chytrids were found. In all cases, only a few scattered chytrids were found in the epidermis of the head and dorsal body. Cultures for viruses, bacteria, and fungi could not be done on amphibians captured in 1993 because all animals were fixed in formalin and preserved in ethanol.

Histological examinations of skin snips from 29 additional frogs and toads of 14 species collected from Las Tablas (1990–1991), and the Jardín Botánico Wilson (1974–1987) in Costa Rica, and Fortuna, Panama (1995) were consistently negative for epidermal chytrid fungi (Appendix 1).

DISCUSSION

We document the association of epidermal chytridiomycosis with a previously unexplained die-off and subsequent population decline in several taxa of wild amphibians from Las Tablas, Costa Rica (Lips, 1998). Although we were unable to identify chytrids in 18 animals collected from Las Tablas three years prior to die-offs and from seven animals collected from Fortuna one year prior to that die-off, we acknowledge that this level of effort would only be able to detect chytrid if it had a very high prevalence in the population at that time (R. Alford, pers. comm.). These retrospective examinations were restricted to the pelvic patch where chytrid infection is heaviest and thus most likely to be found, but it is possible that some of these animals had infections elsewhere. One of the seven clinically normal Las Tablas frogs had a minimal infection of epidermal chytridiomycosis com-

pared to the three dead frogs, and we believe that this individual was incubating the fungus and would have eventually died.

Puschendorf (2003) documented the oldest record of infection by *B. dendrobatidis* in Costa Rican museum specimens of *Atelopus varius* collected in San Ramón, Sarapiquí in 1986 and an infected *A. varius* from Rivas, San Isidro de General in 1992 (Fig. 1). We report the first record of chytrid infection from dead Costa Rican frogs from a protected area known to have experienced subsequent population crashes in multiple species of wild amphibians. We hypothesize that chytrid infection is the proximate cause of amphibian population declines at Las Tablas and encourage further examinations of preserved museum material from sites with documented amphibian declines (e.g., Young et al., 2001). We emphasize the usefulness of museum collections for retrospective investigations of parasite load and prevalence of infection in wild populations.

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APPENDIX 1. Material examined and diagnostic findings by D. E. Green (DEG) and R. Papendick (RP). Site abbreviations are as follows: Las Tablas (LT) and Jardín Botánico Wilson (JBW) Costa Rica, and Fortuna, Panama (Fort). All specimens collected in 1993 were destroyed during examination.

Species	Site and year	Diagnostic findings
I. LAS TABLAS DIE-OFF		
(A) Dead amphibians:		
<i>Atelopus chiriquiensis</i> USC 12517	LT 1993	RP: Possible epidermal parasite DEG: Moderate chytrid infection
<i>Eleutherodactylus melanostictus</i> USC 12528	LT 1993	DEG: Moderate chytrid infection
<i>E. melanostictus</i> USC 12516	LT 1993	RP: Possible epidermal parasite DEG: Heavy chytrid infection
<i>Oedipina grandis</i> USC 12518	LT 1993	RP: degeneration of skin, no epidermal parasites DEG: Not examined
(B) "Controls"		
<i>Atelopus chiriquiensis</i> USC 12519	LT 1993	RP: No epidermal parasites DEG: Slight chytrid infection
<i>A. chiriquiensis</i> USC 12520	LT 1993	RP: No epidermal parasites DEG: No chytrids
<i>A. chiriquiensis</i> USC 12525	LT 1993	RP: No epidermal parasites DEG: No chytrids
<i>Hyla rivularis</i> USC 12522	LT 1993	No chytrids
<i>H. rivularis</i> USC 12523	LT 1993	No chytrids
<i>H. rivularis</i> USC 12526	LT 1993	No chytrids
<i>H. rivularis</i> USC 12527	LT 1993	No chytrids
II. Historic resurvey		
<i>Atelopus varius</i> LACM 149590	JBW 1974	No chytrids
<i>A. varius</i> LACM 149593	JBW 1987	No chytrids
<i>A. varius</i> LACM 149595	JBW 1987	No chytrids
<i>A. varius</i> LACM 149592	JBW 1987	No chytrids
<i>A. chiriquiensis</i> LACM 148838	LT 1990	No chytrids
<i>A. chiriquiensis</i> LACM 148841	LT 1990	No chytrids
<i>A. chiriquiensis</i> LACM 148834	LT 1990	No chytrids
<i>A. chiriquiensis</i> LACM 148835	LT 1990	No chytrids
<i>Bufo fastidiosus</i> LACM 149573	LT 1990	No chytrids
<i>B. fastidiosus</i> LACM 149575	LT 1990	No chytrids
<i>Caecilia volcani</i>	Fort 1995	No chytrids
<i>Hyalinobatrachium fleischmanni</i> LACM 149605	Fort 1995	No chytrids
<i>Centrolene prosoblepon</i> USC 12575	Fort 1995	No chytrids
<i>Eleutherodactylus melanostictus</i> LACM 148792	LT 1990	No chytrids
<i>E. melanostictus</i> LACM 148794	LT 1990	No chytrids
<i>Hyla calypsa</i> LACM 146204	LT 1990	No chytrids
<i>H. calypsa</i> LACM 146203	LT 1990	No chytrids
<i>H. calypsa</i> LACM 146200	LT 1990	No chytrids
<i>H. calypsa</i> LACM 146078	LT 1991	No chytrids
<i>H. colymba</i> LACM 149572	Fort 1995	No chytrids
<i>H. lancasteri</i> LACM 149606	Fort 1995	No chytrids
<i>H. rivularis</i> LACM 149599	LT 1990	No chytrids
<i>H. rivularis</i> LACM 149598	LT 1990	No chytrids
<i>H. rivularis</i> LACM 149597	LT 1990	No chytrids
<i>H. rivularis</i> LACM 149596	LT 1990	No chytrids
<i>H. uranochroa</i> LACM 149603	Fort 1995	No chytrids
<i>Rana vibicaria</i> LACM 148829	LT 1990	No chytrids
<i>R. warzewitschii</i> CRE 5231	LT 1990	No chytrids
<i>Smilisca phaeota</i> LACM 149604	Fort 1995	No chytrids