
Decline of a Tropical Montane Amphibian Fauna

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Abstract: *On the basis of surveys conducted between 1991 and 1996, I report a decline of the amphibian fauna at Las Tablas, Puntarenas Province, Costa Rica. I propose that the reduction in the abundance of *Atelopus chiriquiensis* and *Hyla calypsa*, the presence of dead and dying individuals of six species of frogs and salamanders, and changes in population sex ratios of *A. chiriquiensis* and *H. calypsa* are evidence for "atypical" population fluctuations. Species with both aquatic eggs and aquatic larvae were most affected (e.g., *Rana vibicaria*, *Hyla rivularis*), whereas species with direct development or those that lack tadpoles, such as rainfrogs (*Eleutherodactylus spp.*) and some salamanders (e.g., *Bolitoglossa minutula*), do not seem to have declined in numbers. In light of this evidence and in comparison with other declines in tropical upland Australia, Brazil, and Costa Rica, I conclude that environmental contamination (biotic pathogens or chemicals) or a combination of factors (environmental contamination plus climate change) may be responsible for declines in the amphibian populations at this protected site.*

Una Reducción en las Poblaciones de Anfibios en una Localidad Tropical Ubicada en las Montañas

Resumen: *Basado en encuestas dirigidas por un período de 5 años, reporto una disminución de la fauna anura en un sitio elevado de la región sur central de Costa Rica. Yo propongo que la reducción en el número de individuos, los individuos muertos o moribundos y los cambios en la proporción radial de los sexos, demuestran que las fluctuaciones no son típicas o normales. Las especies más afectadas son aquellas que tienen posturas de huevos acuáticos y renacuajos acuáticos, mientras que aquellas con desarrollo directo (sin renacuajos) no parecen haber disminuido en la misma cantidad. Tomando en cuenta estos datos y comparándolos a las disminuciones observadas en otros sitios montañosos del trópico, concluyo que la contaminación del medio ambiente (causado por un microbio patógeno o químico) o quizás causado por una combinación de factores (contaminación del medio ambiente más cambios del clima) puede ser la causa de la disminución de la población anfibia de este sitio protegido.*

Introduction

Years after the first realization of global patterns of amphibian declines (First World Congress of Herpetology 1989), we are still uncertain about how to determine whether declines are "normal population fluctuations" (Pechmann et al. 1991; McCoy 1994; Travis 1994) or whether they are due to anthropogenic changes in the habitat (Blaustein 1994; Blaustein et al. 1994b; Pechmann & Wilbur 1994), nor is there agreement as to

whether these concurrent declines around the world are isolated incidents or whether global changes are responsible. The long-term population and climatic data necessary for statistical and biological proof is lacking in many cases, particularly for tropical montane sites where many declines have been reported (Laurance et al. 1996). Rather than long-term data from a particular site, we must resort to comparisons among sites. Even more problematic, the natural history (e.g., breeding site, larval characteristics, reproductive phenology) of many tropical montane amphibians is unknown.

Regardless, certain amphibian species have not been seen for several years (Crump et al. 1992; Carey 1993), and certain sites have shown sudden multiple declines of several amphibian species (Weygoldt 1989; Pounds &

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Crump 1994; Drost & Fellers 1996; Laurance et al. 1996). In general, unexplained declines tend to occur in montane sites over a 2- to 5-year period, to affect aquatic species more than terrestrial species, and to occur among a variety of species, reproductive modes, and life histories. Sudden coincidental declines of several species over a large area are suggestive of atypical population decreases (Drost & Fellers 1996; Laurance et al. 1996). Known causes of declines (reviewed in Pounds & Crump 1994; Laurance et al. 1996) include ultraviolet radiation, acidification, introduction of predators, and environmental contaminants. Some investigators (Carey 1993; Pounds & Crump 1994; Laurance et al. 1996) posit a combination of factors as the cause of declines, with strong suggestion that changes in the environment have compromised the immunology of amphibians. This means that amphibians may succumb to infections that are not usually fatal or may be killed by pathogens that do not normally cause mortality.

Three aspects of their biology make amphibians particularly susceptible to environmental perturbation and may provide insights into understanding population declines: (1) possession of a complex life cycle, wherein the embryo or larva requires a different habitat and ingests different food items than the adult; (2) diversity of reproductive modes (location of embryonic and larval stages; Crump 1974) among the amphibians at a particular site; and (3) permeable skin. Understanding the mechanisms of these declines requires investigation of all stages in the life history of amphibians and examination of all habitats experienced by the amphibians at a site.

In 1991 I began research on the population biology of *Hyla calypsa*, a stream-breeding tree frog at Las Tablas, a remote, high-elevation cloud forest in Costa Rica previously renowned for its abundance of amphibians (F. Bolaños, personal communication). Based on my reports, Pounds and Crump (1994) wrote that *Atelopus chiriquiensis* and *Bufo fastidiosus* appeared to be thriving at Las Tablas, whereas related species, *A. varius* and *B. periglenes*, at Monteverde were declining. Since that time the populations of many amphibian species at Las Tablas have either disappeared or declined to a fraction of pre-1994 levels. I present data on changes in the demography and phenology of the amphibian fauna of this high-elevation site and discuss possible mechanisms of this decline. Las Tablas is now the sixth reported upland site in the tropics to suffer unexplained declines of amphibian populations (Atlantic coast Brazil, Heyer et al. 1988 and Weygoldt 1989; Venezuelan Andes, LaMarca & Reinthaler 1991; Costa Rica, Pounds & Crump 1994; Eastern Australia, Laurance et al. 1996). I compare events at Las Tablas to those at these other sites because similarities in target taxa, habitat characteristics, and/or patterns of decline may provide direction for research into the mechanisms of these declines.

Study Area

All surveys were conducted at Finca Jaguar, approximately 18 km north-northeast of La Lucha, Canton Coto Brus, Puntarenas Province, Costa Rica (8°55'N, 82°44'W). This private farm is an isolated human residence within the Zona Protectora Las Tablas, a component of the Amistad Biosphere Reserve. This protected area is the source of the aqueduct that supplies the entire Canton of Coto Brus with drinking water; Las Tablas was included in the Biosphere Reserve to protect the water supply. This site is approximately 250 km southeast of Monteverde and is similar to that site in terms of forest composition, general climate patterns, and the taxonomic composition of the herpetofauna. Las Tablas supports a high-elevation (1900 m) cloud forest (Lower Montane Rainforest in Holdridge [1982]) and experiences pronounced wet (May–December) and dry (January–April) seasons with daily heavy precipitation during the rainy season. Soils are acidic throughout this area (L. D. Gomez, personal communication).

Surveys were centered along a stretch of the headwaters of the Río Cotón, the surrounding forested hillsides, and a small, nearby pasture. The Río Cotón is a swiftly flowing permanent stream with a rocky bed, deep pools, and numerous mossy rocks and boulders along the banks. Dense vegetation overhangs the stream. Stream width ranges from 1 to 15 m, and maximum depth reaches 97 cm. Water is cool (about 15°C) and acidic (pH = 5.0–5.5), and its clarity probably indicates nutrient-poor conditions; there are no aquatic plants.

Methods

Precipitation was measured daily with a standard rain gauge located in a pasture between two stream transects. These data overestimate the amount of rainfall received by the stream but underestimate the amount of moisture derived from cloud water deposition. A maximum-minimum thermometer was placed next to the rain gauge, and temperatures were measured daily. Because of unequal sampling effort during the study, climatic data were combined into 24 2-week periods (Appendix 1).

In July 1991 I began research at Las Tablas on *Hyla calypsa*. In addition to collecting mark-recapture data on adults of this species, I noted the phenology of the other amphibian species at this site and, where possible, measured and marked adults for population estimates. The extent of research on these other species varied with available time and accessibility during this 5-year period. Except where noted, censuses were conducted along two 400-m transects along the headwaters of the Río Cotón. The two stream transects were separated by 50 m and were located about 1.5 km north (upwind and up-stream) from the apple orchards, aqueduct, and finca

proper. I walked 117 nocturnal and 352 diurnal censuses during this period, using a combination of visual and audio cues to locate amphibians and their life stages (eggs and larvae). Upon capturing a frog or toad, I toe-clipped new individuals, measured snout-vent length and mass, and determined sex and age. I collected extensive mark-recapture data from *Hyla calypsa* and *Atelopus chiriquiensis*, the most abundant diurnal amphibian at the site. The data I collected on other species of the amphibian fauna are less detailed.

Results

The cumulative rainfall during the study varied among 2-week periods (Fig. 1). In 1992 the rainy season began in mid-April, but in 1994 rains were delayed until June. Rainfall distribution also varied by year; I combined the rainfall data from 1991–1996 to derive the average cumulative rainfall per 2-week period (Fig. 2). Distinct wet (April–December) and dry (January–March) seasons were distinguished. Even during the height of the rainy season, however, average cumulative rainfall varied among

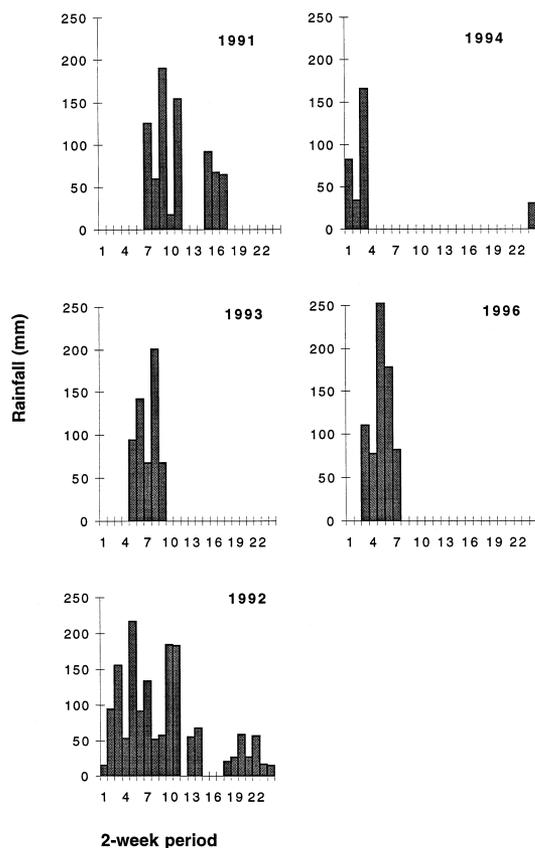


Figure 1. Average cumulative rainfall during each 2-week period for the duration of the study each year. Timing and intensity of rainfall varies by period and year.

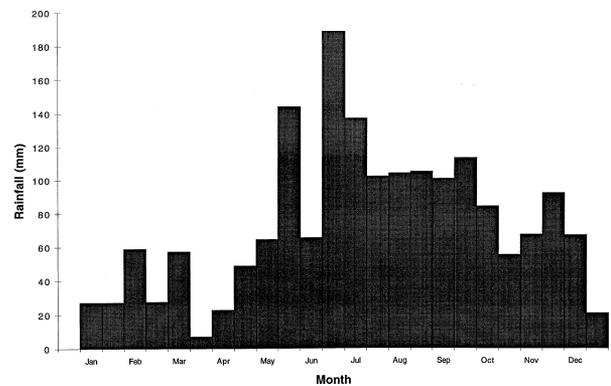


Figure 2. Average cumulative rainfall for each 2-week period for the entire year based on averages from 1991 to 1996.

periods, and some rain fell during the dry season. Average daily temperature was affected by time of day, cloud cover, and rainfall, and it varied considerably, but the 5-year average maximum and minimum temperatures are relatively constant throughout the year (Fig. 3).

Other than obvious reductions in species abundance, I describe three phenomena that may be related to amphibian declines at this site. Before I noticed actual decreases in abundances, I found dead or dying individuals on the transects in September 1992 and between June and August 1993. Six dead animals were found in the stream or on rocks in the stream; they were not obviously damaged or emaciated. One glass frog, a gravid *Hyalinobatrachium fleischmanni*, was dying upon capture and exhibited a trembling of the limbs, a faded dorsal color, and a damaged left foot. The other individuals included two female *Eleutherodactylus melanostictus*, an *Atelopus chiriquiensis* female, an *Oedipina grandis* gravid female, and a *Hyla calypsa* gravid female. The dead animals and some live representatives of these spe-

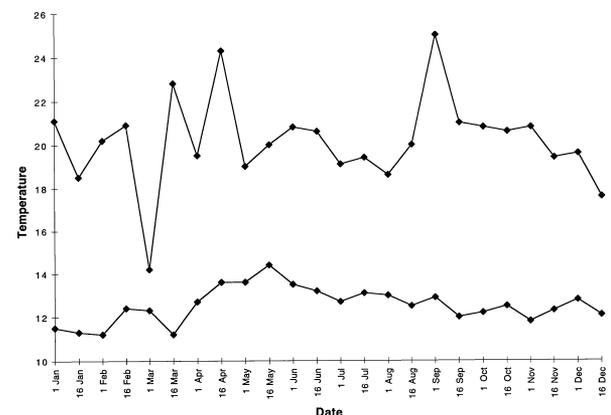


Figure 3. Average minimum and maximum temperatures ($^{\circ}\text{C}$) for each 2-week period based on data collected during 1991–1996. For exact dates of periods, see Appendix 1.

cies were preserved in 90% ethanol or 10% formalin and sent to the University of Florida School of Veterinary Medicine for pathological examination. Some specimens had enlarged fat bodies, suggesting a rapid rather than a gradual demise. No evidence of either a viral or bacterial systemic infection was found, although the superficial degeneration and necrosis of the skin of several individuals of different species (*Atelopus*, *E. melanostictus*, *Oedipina*) suggests the possibility of a common factor such as an external toxin or unfavorable environmental condition. Alternatively, this change may represent a common nonspecific response to various insults, whether infectious or environmental. The possibility of a protozoan parasite in some of the epidermal lesions cannot be further substantiated without electron microscopy or examination of skin scrapings from affected animals prior to formalin fixation (R. Papendick, personal communication).

In 1994 I noticed that tadpoles of *Hyla calypsa* lacked keratinized mouthparts. Many tadpoles have keratinized beaks surrounding the mouth and from 1 to 38 elongate, parallel rows of small, keratinized teeth anterior and posterior to the beaks. It has traditionally been assumed (Altig & Johnston 1989) that these hard structures scrape the microscopic animal and plant material off leaves, rocks, and other submerged structures. In 1994 I measured over 100 tadpoles of *H. calypsa*; none of these individuals had the usual dark keratin covering the five fleshy pads and ridges of the oral disc (Lips 1996). These tadpoles included very early stages (Gosner [1960] stages 25–30) as well as those ready to complete metamorphosis (Gosner stage 42), yet all of the hatchling tadpoles collected from eggs in 1993 (the same cohort of tadpoles) had keratinized mouthparts. All of the tadpoles that hatched from eggs in 1996 also had a complete set of keratinized tooth rows and beaks. In 1996 I netted 50 tadpoles; of those, 3 tadpoles (Gosner stages 25–28) had a few teeth on one tooth row, 4 other tadpoles had keratinized beaks but no tooth rows (Gosner stages 25–27, 36), and the remaining 43 completely lacked keratinized mouthparts. This phenomenon, repeated over a 2-year period strongly suggests that development of the mouthparts is normal but that degradation of the keratinized portions of the mouthparts occurs after the tadpoles have entered the stream. Both bacteria (Friedrich & Antranikian 1996) and fungi (Malvia et al. 1991) can degrade keratin.

The third phenomenon involved leaf-litter plots, a standard technique (Scott 1976; Jaeger & Inger 1994) for quantifying the herpetofauna of the forest floor. In July 1991 a field assistant and I cleared two plots $8 \times 8 \text{ m}^2$ of all the vegetative material and collected the amphibians and reptiles. In July 1996 we cleared two plots $5 \times 5 \text{ m}^2$ in the same manner within 100 m of the original plots. In 1991 we found 15 *Bufo fastidiosus*, 3 *Atelopus chiriquiensis*, 5 *Eleutherodactylus podiciferus*, 1 *E. melanostictus*, and 4 *Oedipina grandis* from the two plots,

for a total of 29 individuals in the 128 m^2 we searched. In 1996 we found no animals in the 50 m^2 searched. Our 1991 density of 22.7 individuals/100 m^2 is surpassed by a value of 58.7 reported for San Vito (actually Las Cruces), a mid-elevation site within 40 km of Las Tablas, and by a value of 45.1 individuals/100 m^2 for a lowland site in Silugandí, Panama (Scott 1976). Scott found that, throughout the wet tropics, mid-elevation sites had the highest densities of leaf-litter herpetofauna, so the reduction from 22.7 to 0 individuals/100 m^2 over a 5-year period is unexpected.

Individual Species Accounts

Atelopus chiriquiensis

Most *Atelopus* species are brightly colored, diurnal bufonids ubiquitous along streams in the foothills and mountain ranges from Costa Rica southward throughout the Andes (Savage 1972). *Atelopus chiriquiensis* is closely related to *A. varius*, the harlequin frog from Monteverde, but *A. chiriquiensis* occurs at higher elevations (Savage 1972). Like other members of this genus, males of *A. chiriquiensis* are abundant along mountain streams and riverine forests; females are less abundant than males and are often found in amplexus when encountered. *Atelopus chiriquiensis* has a long reproductive season and deposits strands of eggs on vegetation and mossy rocks in the fast-moving segments of streams (personal observation). Upon hatching, the small tadpoles use ventral adhesive disks to attach to rocks in the current. When I first visited Las Tablas in June–August 1990, males of this species were abundant enough to carpet the forest floor. I surveyed a trail parallel to a stream transect three times in July 1991. I encountered 7 *A. chiriquiensis* in 30 minutes along 300 m, 20 individuals in 100 m and 30 minutes, and 29 individuals in 250 m and 25 minutes. Considerably fewer individuals were seen along this trail in 1992, very few in 1993, and none in either 1994 or 1996.

Beginning in 1991 I surveyed all individuals of this species during regular stream transect surveys. In 1991 *A. chiriquiensis* was the most abundant species at this site; I observed amplexic pairs laying eggs throughout the wet season, and the abundance of tadpoles was so great that small submerged rocks appeared black. I never encountered juveniles. I measured 348 adult *A. chiriquiensis* and recaptured 21 individuals between 1991 and 1993. The low recapture rate may indicate either a very large population or extensive individual movement. When adult captures decreased substantially in 1994 I ceased toe-clipping and measured only snout-vent length and mass.

To compare changes among years when field work varied in time and duration, I combined survey data into

the same 2-week periods as the climatic data (Appendix 1). I combined surveys from both transects and present the cumulative number of surveys and cumulative number of *A. chiriquiensis* adults found (Fig. 4). This species shows a step-wise pattern of decline (Fig. 4), from very high (1991) to moderate (1992–1993) to very low abundance (1994–1996). I captured this species all year long but captured more individuals during the rainy season. The sex ratio (proportion of males among all captures) was consistently male-biased during this time, with yearly averages of 0.70 (1991) and 0.58 (1992). In 1993 the situation changed to slightly female-biased sex ratios (0.30), although both the average and maximum number of captures were similar to those of 1991–1992. By 1994 I noticed a major decrease in the number of adult captures: the maximum number of individuals dropped to 1 or 2 per survey, for an average of 0.1–0.2 toads per survey, and the average sex ratio was 0.33. By 1996 I saw no animals in any of 64 surveys and only one individual in six surveys, for a total of five individuals (two males, three females, one recapture). No tadpoles or egg masses were noted during surveys in 1994, and I found neither eggs nor tadpoles during specific searches in 1996.

Rana vibicaria

Rana vibicaria, a large ranid, is restricted to montane areas of Costa Rica and Panama (Hillis & de Sa 1988) and breeds in pools of slowly moving streams or temporary pools formed in seepage areas. At Las Tablas I found eggs from November through May. In 1991–1992 I saw tadpoles of all sizes in the temporary and permanent pools in the pasture, suggesting a long larval period. I last saw tadpoles and adults at this site in June–July 1993.

In 1996 I searched and dip-netted intensively in the pasture pools and encountered no tadpoles. I limited manipulations on this species to measuring and toe-clipping 44 adults in 1991.

Hyla calypsa

Hyla calypsa is found along streams above 1800 m elevation in the Cordillera de Talamanca of southern Costa Rica and western Panama (Lips 1996). Males are territorial and call from leafy perches to attract females, which lay clutches of 10–30 eggs on vegetation overhanging the stream (Lips 1996). This is a moderately-lived species: adults may live up to 3 years, eggs require 1 or 2 months to hatch, tadpoles may take 8 or 9 months to reach metamorphosis, and juveniles may require an additional year to reach sexual maturity (Lips 1995). Males and females are site-faithful and have an average home range of 10–20 m², although females return to the stream only to oviposit. For these reasons, it is unlikely that the disappearance of individuals is due to emigration or, even if healthy populations were nearby, that immigration would replenish populations (Blaustein et al. 1994b).

I studied this species from 1991–1994 and in the process handled, measured, and toe-clipped 325 adults and measured both eggs and tadpoles. The total number of captures varied among nightly surveys during the study (Fig. 5). On many survey nights I found unmarked animals, suggesting that recruitment occurred throughout the year. Emigration is a less likely possibility given the high site fidelity of adults. On average, recaptures comprised 67% of nightly captures between 1991 and 1994 (Lips 1995). In 1994 the rainy season was delayed until after I left in June, so I was unable to determine how

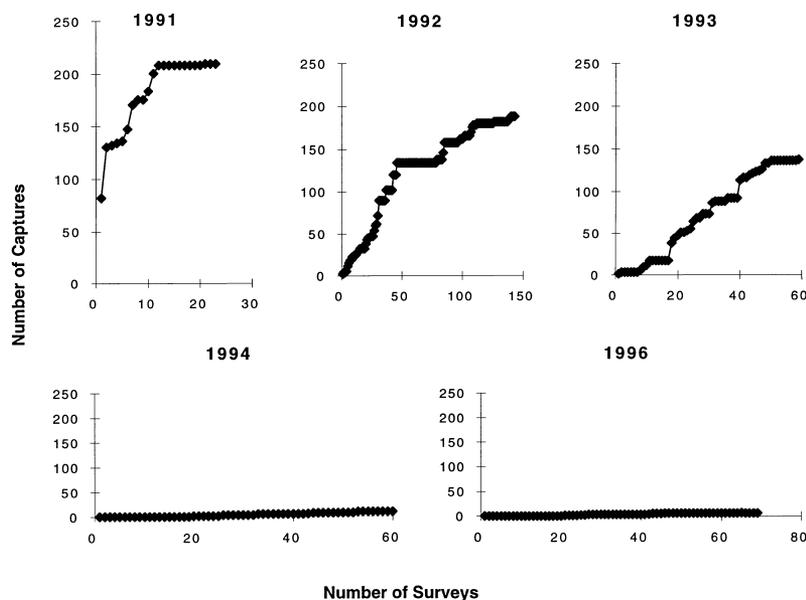


Figure 4. Cumulative adult captures of *A. chiriquiensis* from 1991 to 1996. Transects were surveyed at different times of the year, but, except for 3 months in 1992, all surveys were conducted during the normal breeding season of this frog. For dates of each survey, see Appendix 1.

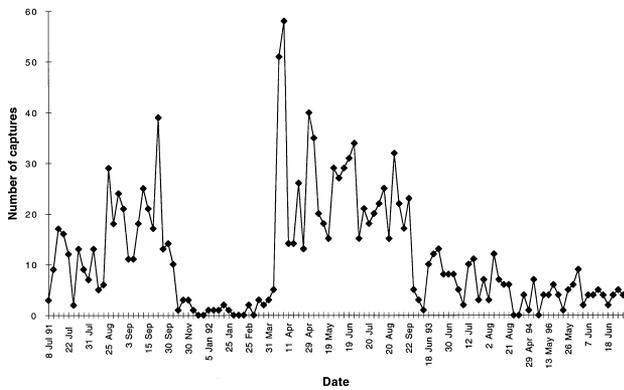


Figure 5. Total number of captures of *Hyla calypsa* for each survey from 1991 to 1996. Except for the dry season from November 1991 to March 1992, all surveys were conducted during the normal breeding season of this frog.

many individuals were present that year. In 1996 the same seven males were present for the 2 months of the study (100% recaptures, no recruitment, and no emigration). One of those males was first captured in 1993, so they were not all recent metamorphs. I rarely found females; however, because they lay one clutch of eggs per visit (Lips 1995) I assumed that the 20 clutches found in 1996 were laid by 20 different females. This female-biased sex ratio (6 males, 20 females = 0.23) differs from the equal male-to-female sex ratio found among marked individuals between 1991 and 1993. Despite receiving the greatest amount and intensity of manipulation, *H. calypsa* currently has the largest population of any stream-breeding anuran at this site.

Hyla rivularis

Hyla rivularis, a small brown tree frog, was an abundant member of the nocturnal stream community; during 1991–1992 I captured and toe-clipped both calling males and gravid females along the stream transects during every month of the year. In 34 nocturnal surveys I found 7.8 adults on average (range = 0–28). The egg deposition site of this species is unknown but is presumed to be in the stream, perhaps under rocks or submerged vegetation. Tadpoles were abundant year-round and easily distinguished by their large oral disc with extensive tooth rows. Recaptures were always low, comprising fewer than five individuals per night (\bar{x} = 1.15). In 1993 this species was present during research conducted between June and August, although by 1994 I saw a few calling males in April and netted some tadpoles (Fig. 6). I found no adults and only one tadpole in 1996, despite extensive searches, and that tadpole (Gosner stage 31) had a complete set of keratinized mouthparts. Like the few tadpoles of *Hyla calypsa* found with

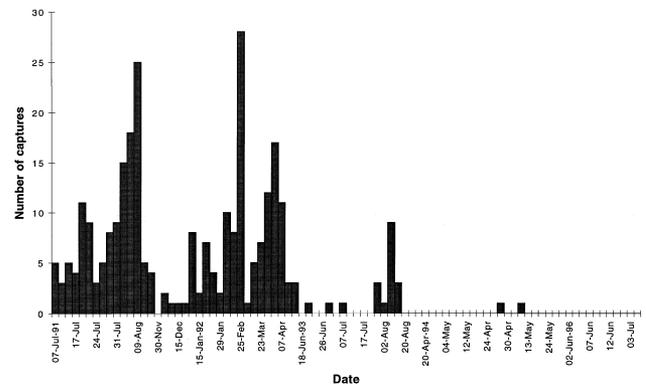


Figure 6. Total number of captures of *Hyla rivularis* for each survey from 1991 to 1996.

some mouthparts in 1996, the tadpole was at an early developmental stage and may not have been exposed long enough for the mouthparts to lose their keratin.

Hyla picadoi

Hyla picadoi is a treefrog that spends its entire life in arboreal bromeliads. I often found two or three adult frogs in the leaf axils of a bromeliad, and I collected tadpoles and metamorphosing juveniles from a water-filled bromeliad in December 1991. Adult males can be heard calling throughout the year but increase calling during the rainy season (personal observation), when breeding probably occurs. I performed no manipulations of this species and did not quantify calling males. I did not notice any obvious change in the amount of vocalizing by males, and I estimated that during the study perhaps half of the bromeliads contained calling males of *H. picadoi*.

Bufo fastidiosus

Bufo fastidiosus is related to *B. periglenes*, the golden toad of Monteverde, and *B. holdridgei* of the Cordillera Central (Savage & Donnelly 1992), and it shows similarities in reproductive behavior with those species (Lips & Krempels 1995). Neither *B. holdridgei* nor *B. periglenes* has been seen in years (Pounds & Crump 1994). Adult *B. fastidiosus* bred in pools formed by pasture seeps between April and May 1992, although I occasionally saw adults and small juveniles along stream transects during the wet season (Lips & Krempels 1995). I measured and toe-clipped 163 adults and juveniles between 1991 and 1993 but saw none in either 1994 or 1996. I was present in March–April 1994 to study these toads; unfortunately, the rainy season was delayed and I left before toads began breeding. We found no toads in litter plots or during haphazard raking of the leaf litter between tree but-

tresses in 1996, although these frogs were abundant in the leaf litter between 1991 and 1993.

Stream-Breeding *Eleutherodactylus*

During nocturnal and diurnal censuses along the stream I occasionally encountered adults of *E. punctariolus* and *E. melanostictus*. Like *E. angelicus* (Hayes 1985), these two large, stream-dwelling species may deposit egg clutches in sandy banks or sand bars along the stream, and both species probably have direct development and lack tadpole stages. During 1991–1992 I captured 9 adults of *E. punctariolus* during stream censuses, but I saw no frogs after November 1992. Adults of *E. melanostictus* were more common. I marked 23 individuals during 24 of the 77 surveys between July 1991 and November 1992, but I saw only 1 individual in each of the following years.

Forest-Breeding *Eleutherodactylus*

Eleutherodactylus podiciferus, *E. bylaeformis*, and *E. cruentus* are the common leaf-litter frogs of the forest understory at this site. All three species probably lay clutches of eggs in the leaf litter of the forest and, like other *Eleutherodactylus* species, have direct development. All three species were present in 1996, although I have never determined population densities.

Salamanders

Six species of salamanders are known from this site: *Oedipina grandis*, *Bolitoglossa minutula*, *B. compacta*, *B. marmorea*, *B. nigrescens*, and *B. "red tail"* (D. Wake, personal communication). *Bolitoglossa compacta*, *B. "red tail"*, and *B. marmorea* occur at such low densities that I cannot quantify their past or current status, and *B. nigrescens* was never found in the immediate study area. Like species of *Eleutherodactylus*, tropical plethodontid salamanders have direct development. *Oedipina grandis* is an elongate, fossorial salamander that "swims" through the soil. Between 1991 and 1993 this species was easily located in the leaf litter between tree buttresses or under rotting logs in the riverine forest. The forested ridge where I sampled leaf litter plots was an especially good location: 5–10 individuals could be collected in an hour. In 1996 I found no *Oedipina* in the two leaf litter plots nor in cursory raking of the leaf litter between tree buttresses along this ridge. One adult female *O. grandis* was found dead and floating in the stream; this is the only salamander that seems to have decreased in abundance. Throughout this study I found adults of *B. minutula* on low vegetation during nightly walks through the forest. During three nocturnal surveys in 1996 along a riverine forest trail, I found 7 adults

in 100 minutes and 500 m, 6 adults in 90 minutes and 400 m, and 3 adults in 45 minutes and 250 m.

Possible Causes of Decline

Because biologists rarely intend to study declining populations, it is unusual to have demographic data for all amphibians at a site; therefore, it is difficult with haphazardly collected data to demonstrate conclusively that the amphibian fauna has declined. Once a decline is suspected, it is often too late to collect enough amphibians for pathological examination or to design experiments to determine the cause of the decline. In such a case one should (1) examine survivorship at each stage in the life history of affected species (e.g., mortality of aquatic eggs and/or tadpoles might indicate a water-borne vector) and (2) look for differential mortality among reproductive modes (e.g., all stream-breeders or all species with direct development) or environmental requirements. Because I lacked reliable, long-term climatic data and survey data for the entire amphibian fauna of Las Tablas, I compared my results to patterns of amphibian decline from four other tropical upland sites using these guidelines.

Habitat Destruction

Habitat destruction and/or degradation has probably caused the extermination of more amphibian populations than any other factor (Blaustein 1994), but it is probably not a major source of mortality at this protected site. The transects do border a pasture, but it is small and surrounded by unlogged forest, and it was cleared over 15 years ago (M. Sandí, personal communication). About 2 km downhill reside the only other human inhabitants of this Zona Protectora: the Sandí family grows apples and raises cattle, but only cattle occupy the pasture near the study site. No logging occurs at this site, and additional forest has not been cleared since this area became part of the Amistad Biosphere Reserve in 1982.

Introduced Fishes

Like many of the montane streams of Central and South America (LaMarca & Reinthaler 1991), the Río Cotón has been stocked with rainbow trout (*Oncorhynchus mykiss*) several times over the past 15–20 years, although trout were last introduced at Las Tablas over 5 years ago (M. Sandí, personal communication). It is likely that introduced trout would feed on the aquatic eggs and larvae of native amphibians, although the few trout stomachs I examined between 1991 and 1994 were filled with aquatic invertebrates. Predation by introduced fish has reduced anuran populations in the western United States (Bradford 1989) and may be a factor in Central America, but amphibians that occupy forest pools, bromeliads, and

other isolated bodies of water are safe from trout predation. Because *Rana vibicaria* (a pool-breeder found in the pasture and forest) has disappeared, it is unlikely that trout are the sole cause of site declines. Two species with aquatic eggs and larvae (*Hyla rivularis* and *Atelopus chiriquiensis*) have disappeared, however; their disappearance might be consistent with trout predation of eggs or tadpoles.

Researcher Disturbance

Scientists always affect their study species in some way. It is possible that my presence from 1991 to 1994 caused the direct mortality of several species. Toe-clipping may (Clarke 1972) or may not (Lemckert 1996 and references therein) reduce survivorship of anurans. I toe-clipped many individuals of *Hyla calypsa*, *H. rivularis*, *Atelopus chiriquiensis*, and *Bufo fastidiosus* but very few or no individuals of the other species. Whereas *A. chiriquiensis* and *B. fastidiosus* may soon be extinct, *H. calypsa* has the largest population of any stream-breeding frog at this site despite the greatest amount and intensity of handling. Blaustein et al. (1994b) reviewed long-term studies of amphibians; although many of these populations were fluctuating, none showed sudden declines, despite a variety of marking techniques, including toe clips. In Las Tablas I marked few individuals of *Oedipina grandis*, *Rana vibicaria*, and the stream-breeding *Eleutherodactylus*, and these populations should not have declined from this level of researcher handling.

Ultraviolet Radiation

Blaustein et al. (1994a) demonstrated that greater exposure to UV-B radiation results in increased embryonic mortality of some amphibians. Only a few species from the Pacific Northwest have been tested for susceptibility to UV-B radiation, but increased UV-B radiation should have similar effects on many amphibians because amphibian eggs lack a hard coating and few species have protective egg pigments. While UV-B radiation may have reduced the abundance of some species at Las Tablas (e.g., *Rana vibicaria*), it cannot be the sole effect because there was no increase in embryonic mortality in 1994–1996 compared to 1991–1992 for the arboreal egg clutches of *Hyla calypsa* (Lips, unpublished data). Egg clutches of this tree frog are laid underneath leaves that overhang the stream, but most clutches experience some exposure to sunlight and incidental radiation during the 3- to 8-week developmental period (Lips 1996).

Habitat Acidification

Throughout parts of Europe and North America acid rain has reduced the biodiversity of many ponds and lakes.

Field and laboratory work has shown that many amphibian species are particularly sensitive to low pH. For example, many temperate amphibians belonging to the families Hylidae, Ranidae, and Bufonidae have reproductive problems below pH 5.0 (reviewed in Sparling 1995). The tropics are renowned for their acidic soils (Mabberley 1986); because stream water must percolate through and across the soil, many tropical montane streams and pools are also acidic. Crump et al. (1992) found that water from rain and fog has a pH higher than that of the temporary forest pools. Resident amphibians should be adapted to these acidic conditions, although a reduction in pH of acidic water could have detrimental effects. In 1991 I used wide range litmus paper and measured the pH of the Río Cotón as 5.0–5.5. This value is comparable to the pH of forest pools at Monteverde (Crump et al. 1992). Other evidence is equivocal for aquatic acidification at Las Tablas. Luis Diego Gomez, director of the Jardín Botánico Wilson of the Organization for Tropical Studies in Las Cruces (about 45 km southwest of Las Tablas), periodically tests rain water for acidity and has not noticed any changes in pH (personal communication). Also, if acid rain were killing animals at Las Tablas, then many species would be exposed to acid rain, including terrestrial *Eleutherodactylus* and salamanders and the bromeliad frogs (*H. picadoi*). Likewise, amphibian embryos are the most sensitive life stage (Sparling 1995), yet many tadpoles were seen subsequent to reductions in adult abundances. The skin necroses of the dead animals is consistent with an acidified environment, however, and these animals included a fossorial salamander. Laboratory experiments could determine the pH tolerance of these species.

Alteration of Rainfall Patterns

Moisture is a crucial resource for amphibian reproduction regardless of reproductive mode. Reduction or changes in rainfall patterns could reduce amphibian reproduction or recruitment, as could changes in the timing, duration, or source of rainfall (reviewed in Donnelly & Crump in press). Deforestation has been correlated with reduced rainfall in the tropics, and Costa Rica has high rates of deforestation (Mabberley 1986). Rainfall data from Monteverde (Pounds & Crump 1994) and north-eastern Australia (Laurance 1996) reveal significant changes in rainfall patterns within the past 8 years. The Costa Rican electric company maintains weather stations throughout the country, but Las Tablas differs from the closest stations in both life zone and elevation, so I cannot compare recent weather patterns at Las Tablas to historical levels. The decline at Las Tablas did not coincide with either a drought or an El Niño–southern oscillation event but spanned a period in which such events influenced the climate and rainfall patterns to varying degrees. If changes in rainfall per se are responsible for

population declines, then amphibians that deposit eggs into this permanent stream should be less affected than those species with either direct development or arboreal eggs. As was also reported for Australia (Laurance 1996), just the opposite is the case: species that reproduce in permanent streams are affected more than those that oviposit terrestrially.

Environmental Contamination

Environmental contamination (agrochemicals, industrial pollution, or other human influences) is one of two likely causes of declines at Las Tablas. Unlike Monteverde, Las Tablas is far from any industrial center: the closest is in Villa Neily, 50 km to the south-southwest, where there is an oil palm refinery. Las Tablas is also far from any active volcano that could promote acid rain formation. Many agrochemicals persist in the environment for a long time, however, and many chemicals that have been banned in the United States and Europe are in widespread use throughout developing countries of the tropics (Colborn et al. 1993). Large numbers and quantities of endocrine-disrupting chemicals have been released into the atmosphere since World War II (Colborn et al. 1993), and many of these chemicals, including DDT and PCBs, vaporize readily and can be transported long distances via the atmosphere (Eisenreich et al. 1981; Rapaport et al. 1985). "Pristine" or otherwise legally preserved or isolated habitats will not be protected from airborne contaminants. In Monteverde, for example, clouds deposit on vegetation nitrogen and phosphorus derived from agrochemicals (Pounds & Crump 1994).

Not only do these chemicals toxify the environment, but many cause reproductive and estrogen-disrupting effects in a variety of organisms (reviewed by Schmidt 1994). Known health effects include morphological changes in secondary sex characteristics, changes in the population sex ratio, developmental abnormalities, and even alteration of immunological function (Erdman 1988 in Colborn et al. 1993; Martineau et al. 1988). I noticed unusual female-biased sex ratios in *A. chiriquiensis* and *H. calypsa* in 1996. This bias could indicate reproductive disruption from chemical contamination, or it may be a result of greater mortality of males because of increased exposure to predation or chemicals during territory defense, vocalization, and other reproductive activities. In any case, of the three common chemicals sprayed on the apple orchards at Las Tablas, two (Mancozeb and Belnate) are known to have reproductive and endocrine-disrupting effects (Colborn et al. 1993), and all six dead or dying individuals were females. Amphibian species exhibit different responses to a variety of pesticides (Berrill et al. 1994); if a site were contaminated by pesticides, different species might exhibit different symptoms and susceptibility. Pounds and Crump (1994) propose that amphibian declines at Monteverde are due to a syn-

ergistic effect between climate change and environmental contamination. I suggest that amphibian declines at Las Tablas are consistent with patterns from Monteverde and this hypothesis.

Pathogen Outbreak

An outbreak of some pathogen is the second likely cause of declines at Las Tablas, and perhaps for the decline of many amphibian faunas. Laurance et al. (1996) reason that an exotic and highly virulent pathogen could cause sudden declines like those seen in eastern Australia. Declines in Australia spread at a mean rate of 100 km/year; Laurance et al. (1996) liken these patterns to those described by Scott (1993) for some sites in the western United States. Scott (1993) described a wave-like spread (south to north), rapid and precipitous mortality, greater effects at higher elevations, and selective declines (usually adults of particular taxa). Laurance et al. (1996) argue that the long-distance spread of pathogens could be facilitated by fish introductions. If pesticides, herbicides, and other agrochemicals can be spread through the atmosphere, so can pathogens. Other vectors of long-distance dispersal might include cattle or humans.

The Atlantic coast of Brazil may be another region experiencing a wave-like spread of sudden mortality of diurnal or stream frogs from montane areas (Heyer et al. 1988; Weygoldt 1989). Heyer et al. (1988) suggest that a serious frost in 1979 caused the decline, but they could not rule out aerial pollution as a factor. The sudden decline of closely related frogs to the north (Weygoldt 1989) between 1981 and 1986 may be evidence for a pathogen moving northward between 150 and 50 km/year depending on whether declines occurred in Santa Teresa in 1981 or 1986. Weygoldt (1989) believes that these two extinctions may have a common cause but argues for acid rain. Weygoldt (1989), however, provides evidence for a possible bacterial infection of stream tadpoles. This case argues for a common sampling program so that similar data are collected at every site.

Costa Rica is the third area to experience two widely separated declines, at Monteverde (Pounds & Crump 1994) and Las Tablas (this study). As in the Brazilian example, different causes are proposed for the two sites, but the similarity in the climatic conditions, the close phylogenetic relationships between the herpetofauna at these two sites, and especially the similarity in patterns and timing of declines argue for a common cause. Declines occurred in Monteverde in 1986–1987 and in Las Tablas in 1993–1994; these declines correspond to a movement of about 250 km in 6 years, or about 42 km/year. The rate of spread of declines in Australia (100 km/year), Brazil (150 and 50 km/year), and Costa Rica (42 km/year) are strikingly similar.

A similarity among these regional collapses is the large number of tadpoles present while adults are dying (Lau-

rance et al. 1996). I saw many tadpoles of several species at my site during the early decline period, but the tadpoles of at least one species at Las Tablas have morphological deformities of the mouthparts, and Weygoldt (1989) saw high mortality in laboratory-reared tadpoles until he treated the water with a bactericide for aquarium fish. Both bacteria and fungi can degrade keratin (Malvia et al. 1991; Friedrich & Antranikian 1996), so the loss of keratinized mouthparts in tadpoles of *H. calypsa* at Las Tablas may be an indication of infection by a pathogen. Alternatively, this loss could indicate chemical contamination. Normal sloughing of mouthparts occurs just prior to metamorphosis and is regulated by the thyroid; thyroid function has been shown to be altered by exposure to hormone-disrupting chemicals (Moccia et al. 1981, 1986). Future research should focus on larval condition in addition to abundance and should test for larval responses to agrochemicals. I suggest that declines at Las Tablas and Monteverde, Costa Rica (Pounds & Crump 1994), are consistent with patterns seen in Australia (Laurance et al. 1996) and Brazil (Heyer et al. 1988; Weygoldt 1989) and with the hypothesis of a pathogen outbreak.

Conclusions

Results from Las Tablas are strikingly similar to those patterns described for Australian rainforests (Laurance et al. 1996), Costa Rica (Crump et al. 1992; Pounds & Crump 1994), the Venezuelan Andes (LaMarca & Reintaler 1991), and the Atlantic coast of Brazil (Heyer et al. 1988; Weygoldt 1989). Similarities among these five sites argue for a common cause of amphibian declines at these tropical montane sites; they include: (1) extinction waves moving directionally (north to south in Costa Rica, south to north in Australia and Brazil); (2) taxonomic (bufonids, ranids) and ecological specificity (diurnal species and stream-breeders); (3) upland tropical sites with high endemism; and (4) rapid concurrent crashes of many species at a site. I found that species most affected were those with both eggs and larvae in aquatic sites (*Rana vibicaria*, *Hyla rivularis*, *Atelopus chiriquiensis*). The abundance of frogs that breed in bromeliads (*H. picadoi*) and of those amphibians that have direct development (salamanders) and breed in the leaf litter (*Eleutherodactylus* spp.) also suggests that the causative agent is water-borne. Some species in decline showed a change in the sex ratio from usually male-biased sex ratios to female-biased sex ratios (*H. calypsa*, *A. chiriquiensis*); this argues for future investigation into environmental contamination. The sudden nature of declines and the presence of dead and dying individuals suggests an epidemic of some bacteria or virus, although novel weather patterns could also deposit unusual types or quantities of chemicals. Because of the isolated na-

ture of Las Tablas, it seems likely that declines may be caused by or aggravated by long-range atmospheric transport. Long-term weather data might indicate whether weather patterns have recently changed over Las Tablas, and atmospheric testing could determine whether cloud or rain water carries chemical contaminants. Finally, monitoring of amphibian populations needs to be continued at Las Tablas, and pathological surveys need to be initiated on the remaining species.

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Appendix

Dates of climatic (periods 1–24) and amphibian data collection.

Period	Dates	Surveys conducted				
		1991	1992	1993	1994	1996
1	16–30 April		X		X	
2	1–15 May		X		X	
3	16–31 May		X		X	X
4	1–15 June		X	X		X
5	16–30 June		X	X		X
6	1–15 July		X	X		X
7	16–31 July	X	X	X		X
8	1–15 August	X	X	X		
9	16–31 August	X	X	X		
10	1–15 September	X	X			
11	16–30 September	X	X			
12	1–15 October	X	X			
13	16–31 October		X			
14	1–15 November					
15	16–30 November	X				
16	1–15 December	X				
17	16–31 December	X				
18	1–15 January		X			
19	16–31 January		X			
20	1–15 February		X			
21	16–28 February		X			
22	1–15 March		X			
23	16–31 March		X			
24	1–15 April		X		X	

