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## Apparent Decline of the Golden Toad: Underground or Extinct?

MARTHA L. CRUMP, FRANK R. HENSLEY,  
AND KENNETH L. CLARK

*Bufo periglenes*, the golden toad, is an endangered species endemic to Costa Rica. Every year from the early 1970s through 1987 golden toads have emerged from retreats to breed during April-June. The most recent known breeding episode occurred during April-May 1987; more than 1500 adults were observed at five breeding pools, but a maximum of 29 tadpoles metamorphosed from these sites. During April-June 1988-90, we found only 11 toads during surveys of the breeding habitat. To examine the species' apparent decline, we analyzed data on rainfall, water temperature, and pH of the breeding pools.

Our baseline data on weather patterns and characteristics of the breeding habitat suggest that warmer water temperatures and less advective precipitation during dry season post-1987 may have produced adverse breeding conditions. The toads may be alive and hiding in retreats awaiting appropriate weather conditions. The apparent scarcity of toads may reflect a normal population response to an unpredictable environment. On the other hand, because other anurans with different breeding specializations seem to be declining from the area as well, one wonders whether warmer temperatures and dry conditions could be responsible for real population declines.

Because the habitat is protected and pristine, potential causes of anuran declines such as habitat destruction, introduced predators, and collecting seem unlikely. Measurements of pH of the breeding pools, cloud water, and precipitation do not suggest acid precipitation effects, although we cannot rule out the possibility of environmental degradation some time prior to our measurements. Long-term monitoring programs combined with carefully controlled field experiments are needed to address factors responsible for declining amphibians.

**G**OLDEN toads (*Bufo periglenes*; Bufonidae) are endemic to undisturbed, elfin cloud forest near the continental divide in the Cordillera de Tilarán, northern Costa Rica. They are almost entirely restricted to an area approx. 0.5 km by 8 km within the Monteverde Cloud Forest Reserve at elevations between 1500-1620 m. Since its description (Savage, 1966), this species has been the focus of only one published study (Crump, 1989). The lack of knowledge about this toad probably reflects its restricted distribution and its secretive behavior; toads are known to be active above ground only for a few days during one to three periods at the end of dry season when they emerge to breed. The toads are listed as endangered in the International Union for the Conservation of Nature (IUCN) Red Data Book (Honegger, 1979), largely based on their restricted geographical distribution. The status of the population is currently of major concern (Barinaga, 1990; Blau-

stein and Wake, 1990) because few individuals have been observed since May 1987.

More than 1500 adult toads were observed at five breeding pools during April-July 1987 (Crump, unpubl. data). Nearly all eggs deposited died before hatching because most pools dried; a maximum of 29 tadpoles metamorphosed from these pools. Since 1987, few individuals have been observed, suggesting that the population has declined. To investigate possible causes for this dramatic decline, we analyzed rainfall and habitat data beginning with the first year the toads did not breed.

Is the apparent decline due to adverse breeding conditions that cause the toads to remain in their retreats, or is the decline due to catastrophic mortality? In this paper we (1) document post-1987 observations of golden toads; (2) describe annual variation in rainfall and the breeding habitat (fluctuation in water depth, duration of the pools, and water temperature);

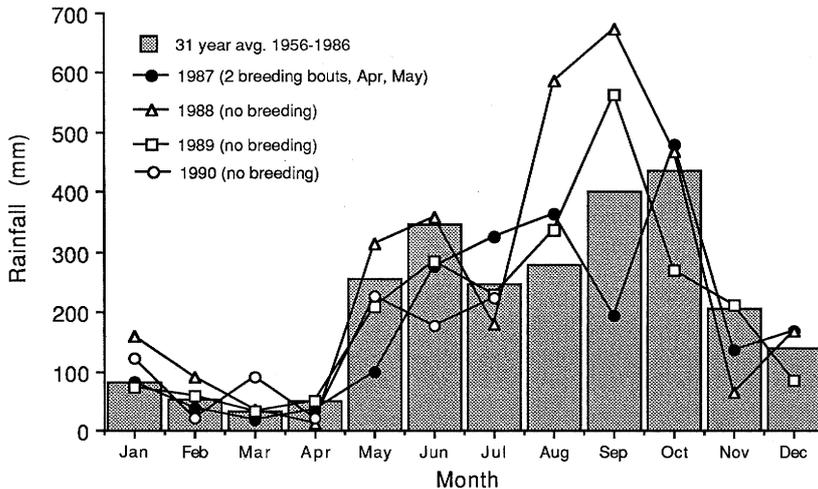


Fig. 1. Monthly rainfall patterns for 35 years (1956–90) in Monteverde, Costa Rica. Note especially variability in rainfall during the toads' breeding season, April–May. Data for 1990 end with July.

(3) report data on pH of local precipitation and water from the breeding pools; and (4) discuss possible factors responsible for the current status of golden toads.

#### MATERIALS AND METHODS

*Natural history of Bufo periglenes.*—The habitat of the golden toad lies within the Lower Montane Rainforest Life Zone (Holdridge, 1967) and has been described as elfin and windward cloud forest (Lawton and Dryer, 1980). These forests are often shrouded in clouds and fog, and the trees are covered with bryophytes, ferns, and other epiphytes. The toads' habitat, which straddles the continental divide, experiences distinct wet and dry seasons (Fig. 1). Tradewind-dominated precipitation (advective precipitation) originating in the Caribbean basin characterizes the dry season, typically from Dec. through April. Convective storms originating from the Pacific lowlands characterize the wet season, although convective precipitation is occasionally interspersed with advective precipitation from the Caribbean basin.

During the transition from late dry season to early wet season (usually April–May), the toads emerge from retreats, presumably underground, to breed. They appear during rainy periods after the soil has become saturated, allowing the breeding pools to retain water. Most of the breeding sites are ephemeral pools that form within the root systems at the bases of trees. Some of these depressions are formed by

intense, local winds rocking the trees and loosening the root mass. Most breeding sites are small (no larger than  $0.5 \times 0.5$  m) and shallow (less than 22 cm deep), yet as many as 20 females may oviposit in a single pool (Crump, unpubl. data). The toads breed explosively (*sensu* Wells, 1977). Oviposition episodes last less than 10 days, but up to three bouts may occur in each breeding season. The operational sex ratio is strongly male biased, with considerable male–male aggression and intense competition for females (Crump, unpubl. data). Females lay 200–400 large eggs ( $\bar{x}$  diameter = 2.98 mm). Eggs hatch within several days, and the tadpoles require about five weeks to metamorphose. The tadpoles are facultatively nonfeeding, being able to subsist on their yolk from hatching to metamorphosis if no alternative source of energy is available (Crump, 1989).

*Toad surveys.*—The habitat where golden toads were known to occur based on past experience was surveyed for adults, tadpoles, and eggs for three years following Crump's study of breeding behavior in 1987. During April 1988, W. Guindon, Field Coordinator of the Monteverde Cloud Forest Reserve, made visual searches of the toads' primary breeding habitat (in the Brillante region of the reserve) following periods of rainfall. From 3 May to 5 July 1988, one of us (MLC), Guindon, and an assistant visually searched along a transect through the main breeding habitat (Brillante) of the golden toads every one to four days. In addition, Guindon

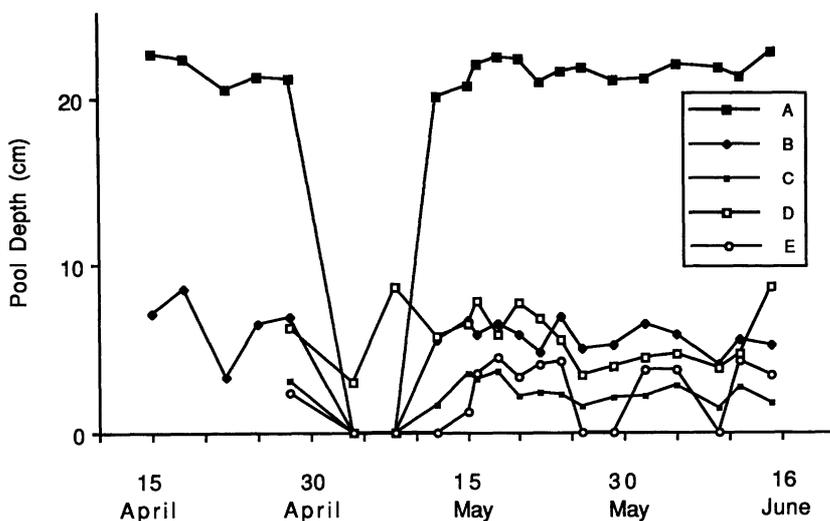


Fig. 2. Fluctuation in depth in 1989 of five pools used as oviposition sites in 1987 by golden toads.

and personnel of the Monteverde Cloud Forest Reserve searched in other areas of the reserve known to be sites of the toads' activity in previous years. The following year, two of us (MLC and FRH) monitored the Brillante transect every two to four days from 6 April to 13 June 1989. Guindon made additional surveys during 1989 in outer areas of the reserve where toads had been sighted in previous years. The third year, Guindon and others continued the survey for golden toads in Brillante and other areas during rainy periods from April–June 1990.

*Environmental monitoring.*—Precipitation was measured daily with a standard rain gauge located at 1540 m, approx. 4 km W of the Brillante breeding site. Although adequate for among-year comparisons, these data undoubtedly underestimate the amount of moisture due to greater advective precipitation and cloud water deposition at the breeding sites.

During April–May 1988–89, one of us (KLC) used standard techniques (Mohnen and Kadlec, 1989) to collect cloud water (nonprecipitating droplets ranging from 10–50  $\mu\text{m}$  in diameter) at a site approx. 1 km from the Brillante breeding site. During April–June 1988, April–July 1989, and May 1990, advective and convective incident precipitation were collected at a site approx. 2 km from the toads' breeding pools. All collecting containers were washed in 10% HCl and rinsed in deionized water prior to use. Acidity was measured at room temperature using a Corning Model 120 pH/millivoltmeter and an Orion Model 910–500 combi-

nation pH probe calibrated with Fisher Scientific pH 4.00 and pH 7.00 standards. On 28 April 1989, water samples were collected from each of five breeding pools used by the toads in 1987. Polyethylene sampling bottles were acid washed and rinsed in a manner identical to that for the rainwater samples. Latex gloves were worn to prevent contamination when bottles were partially submerged in the pools to obtain the samples. The samples were analyzed for pH as described above.

At two to six day intervals between April–June 1989, two of us (MLC and FRH) measured maximum water depth ( $\pm 0.5$  cm) of each of the five breeding pools used in 1987. Water temperature was recorded at the two pools that had received the greatest breeding activity in 1987. At the deeper pool (Pool A in Fig. 2), water temperature was measured with a Schultheis rapid-reading thermometer ( $\pm 0.1$  C) once per survey day between 0900 and 1500. At the shallower pool (Pool B in Fig. 2), water temperature was monitored continuously with a seven-day recording Bacharach Tempscribe thermometer ( $\pm 0.5$  C). Dissolved oxygen content of the water in each of these five pools on 16 May was measured with a LaMotte Chemical kit, Model EDO.

## RESULTS

*Toad surveys.*—During the monitoring period in 1988, only one adult male golden toad was found in the primary breeding area (Brillante) of the reserve. Seven adult males and two adult females were discovered at a site 4–5 kilometers

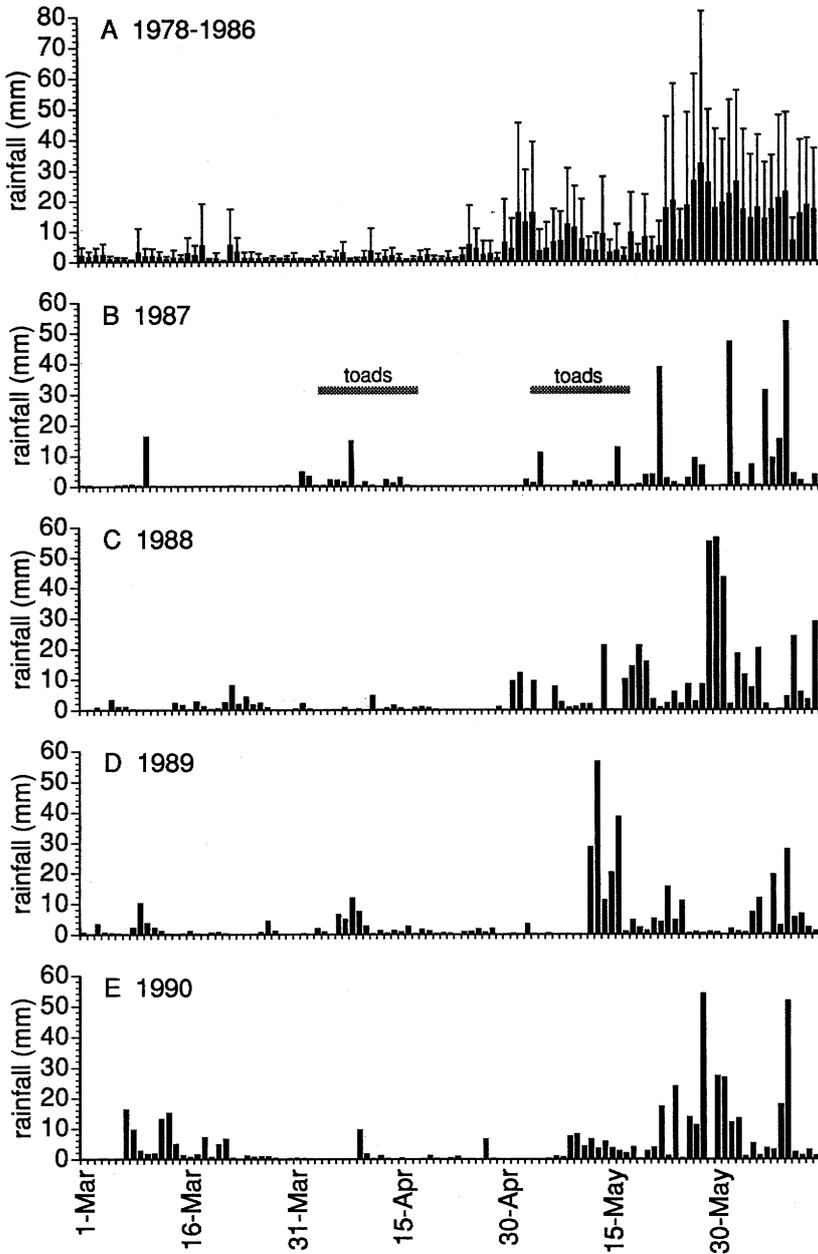


Fig. 3. Daily rainfall patterns at a site 4 km W of the toads' breeding area, between 1 March and 13 June. (A) Daily rainfall (mean + 1 SD) for nine years (1978–86); golden toads were sighted each year. (B) Daily rainfall in 1987; horizontal bars mark periods of golden toad activity. (C–E) Daily rainfall for 1988–90; golden toads did not breed during these years.

SE of Brillante. Subsequent searches for eggs and tadpoles at this latter site were unsuccessful, suggesting that no breeding had occurred (Guindon, pers. comm.). In 1989, only one adult male was found; this individual was encountered within 3 m of the site where the male had

been found in 1988. Extensive searches during April–June 1990 failed to reveal any golden toads.

*Environmental monitoring.*—The distribution pattern of rainfall varies among years (Figs. 1,

3) and directly affects breeding activities because the toads cannot oviposit until after the ground becomes saturated and the pools retain water. In 1987, the breeding pools retained water by 3 April; the first pairs were found ovipositing on 8 April. In contrast, in the subsequent three years, the breeding pools did not retain water until late April to mid-May. Differences in rainfall that affect ground saturation are not reflected in the rainfall data taken 4 km from the study area because advective precipitation and cloud water are not collected efficiently by standard rain gauges. Although the rainfall data presumably reflect the pattern of rainfall in the toads' breeding habitat, the breeding site generally receives more total rainfall.

Neither cloud water nor either type of precipitation was strongly acidic (Table 1). Because cloud water presumably represents only a small fraction of the hydrological input to breeding pools, it probably has little influence on pool pH. Water falling through the canopy (in contrast to incident precipitation) is probably the most significant source of water in the pools; pH of throughfall water measured at a nearby site was usually 1–1.5 pH units higher than values reported in Table 1 for incident precipitation (Clark, unpubl. data). Values of pH for the five breeding pools ranged from 5.40–5.97 ( $\bar{x}$  = 5.61; the mean of the hydrogen ion concentration for the pools was used to calculate the mean pH value).

The breeding pools fluctuated widely in maximum water depth in 1989 (Fig. 2). A deep pool (Pool A, Fig. 2) used repeatedly in past years contained 20–22 cm of water except in early May when it dried completely and then refilled. The other four pools contained a maximum of 8.5 cm, and three of these dried at least once during the two months of the study. Likewise, during the 1987 breeding season, many pools containing eggs and tadpoles dried completely (Crump, unpubl. data). These observations indicate that the breeding habitat of the golden toads experiences extreme fluctuations in duration and water volume.

On the other hand, water temperatures of the pools varied little during 1989. The shallow pool (Pool B, Fig. 2) for which water temperature was continuously monitored was nearly constant. Water temperature varied between 15.0–16.5 C day and night from 15 April to 13 June during which time the water depth varied from 3.3–8.5 cm. During the few days in early May when the pool dried, the substrate tem-

TABLE 1. VOLUME WEIGHTED MEAN pH<sup>a</sup> FOR CLOUD WATER, ADVECTIVE PRECIPITATION, AND CONVECTIVE PRECIPITATION AT MONTEVERDE FOR SAMPLING PERIODS IN 1988, 1989, AND 1990.

Year	Precipitation type	n <sup>b</sup>	pH	Precipitation amount (cm)
1988	Advective	7	5.28	34.0
	Convective	5	4.71	34.7
	Cloud water	4	4.35	—
1989	Advective	11	5.19	50.6
	Convective	7	4.85	48.3
	Cloud water	1	5.40	—
1990	Advective	3	5.58	10.4
	Convective	3	5.39	4.5

<sup>a</sup> Volume weighted mean pH was calculated by multiplying the hydrogen ion content per event by the volume calculated for that event and then dividing by the total amount of precipitation for the type of event.

<sup>b</sup> Number of events sampled.

perature climbed to 18.0 C. In the deep pool (Pool A, Fig. 2; 20–22 cm depth), water temperature likewise varied between 15 C and 16.5 C during the day during this same time period. The same pools showed greater temperature variation during the breeding season in 1987. The toads began breeding during an extremely cold, windy period in early April, when water temperatures at these pools were 11.5–12.0 C; temperatures warmed to 17.0–17.5 C by the middle of this oviposition period. During the second breeding bout (early to mid-May), the water temperatures of these two pools ranged from 17.8–19.0 C.

Dissolved oxygen content for the five pools used for breeding in 1987 varied from 2.8 ppm for Pool B (5.8 cm depth) to 6.6 ppm for both Pool A (22.0 cm depth) and Pool C (3.2 cm depth) on 16 May 1989; values at the two other shallow pools were 3.4 ppm (7.8 cm depth) and 5.6 ppm (3.5 cm depth) on the same date. Given that pools may be crowded (each of 20 females may deposit an average of 300 eggs in less than 10 liters of water), sites with higher dissolved oxygen concentrations might be more conducive than others to growth and development. We present these values to serve as baseline data of golden toad habitat that can be used for comparison to data gathered in future monitoring programs.

## DISCUSSION

Declines in populations of amphibians from diverse areas in the world were the focus of a

conference sponsored by the National Research Council Board on Biology in 1990 (Barinaga, 1990; Blaustein and Wake, 1990; Phillips, 1990). Particularly disturbing is that some of the most drastic declines have occurred in relatively pristine habitats that are protected, such as national park areas and reserves. Apparent population crashes of amphibians in protected areas may signal global environmental degradation; amphibians, with their complex life cycles, highly permeable skin, and extremely sensitive embryonic stages, are good biological indicators of environmental conditions because they are more sensitive to environmental insults than are many other organisms (Blaustein and Wake, 1990; Vitt et al., 1990). On the other hand, short-term climatic fluctuations can also significantly affect amphibian populations, severely alter community interactions, and thus have long-term evolutionary implications. For example, an unusually heavy frost in southeastern Brazil in 1979 is thought to be responsible for regional extinctions of a number of amphibian species (Heyer et al., 1988).

Since the early 1970s, golden toads have emerged from retreats every year through 1987 (Guindon, pers. comm.), although systematic monitoring of their populations was never undertaken. The fact that very few toads have emerged and no reproduction has occurred for the past three years has generated concern. Why have golden toads not appeared? Two possibilities exist: (1) the toads are simply not emerging in usual numbers because breeding conditions are inappropriate, and (2) the near absence of toads reflects catastrophic mortality, caused by environmental degradation, climatic changes, or other factors.

Is there evidence that weather conditions have not been appropriate for breeding by golden toads in the last three years? Anecdotal reports by numerous persons watching the breeding activity of golden toads over the years suggest that the toads emerge and breed during the dry season-wet season transition period, not during the wet season of heavy rains. In 1987, the ground became saturated by early April, and the pools retained water several weeks earlier than they did in 1988-90. In 1988-90, there was less advective precipitation; the wet season began with heavy rains rather than with a transitional period of more moderate rains, causing the breeding pools to fill quickly. We suggest that, if the toads oviposit under these conditions, additional heavy rains could cause the

pools to overflow, and presumably the eggs or tadpoles would be swept out of the pools onto the forest floor. A subsequent day without rain would dry the substrate, and the tadpoles would be left stranded. Thus the toads may have a narrow window of time between dry season and wet season when their offspring can avoid both desiccation and being washed from the pools. The late filling of the pools may have limited toad activity since 1987. Emergence of *B. periglenes* seems to be associated with cold, wet periods (Guindon, pers. comm.; Crump, pers. obs.). In April 1987, water temperatures of the breeding pools were 11.5-12.0 C during the first period of oviposition. In contrast, water temperatures recorded during April-June 1989 were never colder than 15 C. Another possibility is that warmer temperatures associated with reduced advective precipitation may have altered toad activity.

Because of its unpredictable and fluctuating breeding habitat (small pools prone to overflowing or desiccation), *B. periglenes* is a species vulnerable to vagaries of the weather. For this reason, the population might fluctuate widely in size due to variable recruitment success. If the population experiences a year when recruitment is low (as apparently was the case in 1987, Crump, unpubl. data) or a period during which conditions are not conducive to breeding and thus the toads remain in retreats (as may have been the case from 1988-90), the population might become heavily biased toward aging adults and eventually decline beyond any ability to recover. The unpredictable environment might select for long life span, but only future monitoring will allow determination of whether the population has been reduced to such a low level that it cannot recover.

The other alternative is that the near absence of toads reflects a catastrophic decline. If so, what are likely factors responsible for the decline? The fact that the habitat of the golden toads is pristine and was set aside as a reserve in 1973 means that there has been minimal habitat destruction or modification. We know of no introduced predators in the area. Guards patrol the reserve heavily during the time of year when the toads breed, thus limiting illicit collecting for the pet trade.

If there has been mass mortality of golden toads, the cause may also have affected other anurans in the area. In the late 1970s and early 1980s, *Atelopus varius* (Bufonidae), many species of *Eleutherodactylus* (Leptodactylidae), as well as

a variety of hylids, ranids, and centrolenids were commonly found in the Monteverde Cloud Forest Reserve (Crump, pers. obs.). By the late 1980s, most species of anurans were infrequently encountered (Crump and Hensley, pers. obs.). Simultaneous declines of *B. periglenes* and other anurans in the Monteverde region could be explained by a non-species-specific pathogen that attacks anurans; data to address this possibility are lacking.

Environmental factors such as ultraviolet (UV) radiation, pH of breeding ponds, droughts, and warmer temperatures have been implicated as possible factors in the decline of amphibians (Barinaga, 1990; Blaustein and Wake, 1990). However, little agreement exists concerning what global changes are taking place and their possible effects (Abelson, 1990). Any increased UV radiation should have minimal effects on anurans in the Monteverde Cloud Forest Reserve because the heavy cloud cover conditions typical of the habitat would be expected to attenuate the UV wavelengths. In addition, golden toads spend most of the year in retreats.

Although the detrimental effects of acid rain on amphibian embryos are well documented (see Pierce, 1985, for review), we doubt that acid deposition has severely affected golden toads. Published reports of anuran embryo tolerance to acidity reveal that 13 of 14 species discussed exhibit 50% mortality between pH 3.6–4.6 (Pierce, 1985). The only toad included was *Bufo americanus*, with 50% mortality between pH 4.0–4.5. Our data on pool water pH (5.40–5.97) and precipitation pH (4.71–5.58), collected since the decline of the toad populations began, do not include any pH values that are alarmingly low relative to known tolerances for anurans. Because we have no pH values for years when the toads successfully reproduced, however, we do not know whether acidity has changed. Furthermore, because tolerance levels for *B. periglenes* eggs and larvae are unknown, it is possible that pool pH changed some time in the past and that no successful recruitment has occurred for years. Although the possibilities of anthropogenic pollution and volcanic input from Volcán Arenal (an active volcano approx. 18 km from the site) cannot be dismissed, we have no reason to suspect pollution based on our observations and pH values of cloud water, precipitation, and pools. Our pH values for incident precipitation are considerably higher than those reported from sites closer to anthropogenic sources of pollution (Lovett et al., 1982; Fowler et al., 1988;

Weathers et al., 1988) and are consistent with pH values reported from other remote sites, generally ranging from 4.7–5.4 (Galloway et al., 1982; Sanhueza et al., 1987).

Changes in precipitation patterns and temperature may have resulted in population declines of various species of anurans in the Monteverde Cloud Forest Reserve. The monthly rainfall data for 1987–90 are often below the 31-year averages (Fig. 1), and we did measure warmer water temperatures in 1989 than during the last year the toads reproduced. Whether these climatic factors are responsible for the decline of the golden toad (and possibly other anurans in the region) is, however, still a matter of speculation.

Are golden toads hiding out in their retreats awaiting more favorable breeding conditions, or have they undergone catastrophic mortality? We suggest that it is still too early to know. Possibly golden toads have reproduced in areas where we have not surveyed, reflecting behavioral responses to differing local conditions. An unconfirmed sighting of 40 males and four females during late May 1989 and another sighting of small toads the following Aug. were reported in the Aug.–Oct. 1990 newsletter of the Monteverde Conservation League. These individuals reportedly were seen at a site at least 5 km from the main breeding site.

Future research concerning the proximate and ultimate causes of declines of amphibians from pristine habitats should address synergism among possible factors. Only through long-term monitoring programs and carefully controlled field experiments can we determine whether amphibians are signalling environmental degradation or whether other factors are affecting population dynamics of amphibians.

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## LITERATURE CITED

- ABELSON, P. H. 1990. Uncertainties about global warming. *Science* 247:1529.
- BARINAGA, M. 1990. Where have all the froggies gone? *Ibid.* 247:1033-1034.
- BLAUSTEIN, A. R., AND D. B. WAKE. 1990. Declining amphibian populations: a global phenomenon? *Trends in Ecology and Evolution* 5:203-204.
- CRUMP, M. L. 1989. Life history consequences of feeding versus non-feeding in a facultatively non-feeding toad larva. *Oecologia* 78:486-489.
- FOWLER, D., J. N. CAPE, I. D. LEITH, T. W. CHOULARTON, M. J. GAY, AND A. JONES. 1988. The influence of altitude on rainfall composition at Great Dun Fell. *Atmos. Environ.* 22:1355-1362.
- GALLOWAY, J. N., G. E. LIKENS, W. C. KEEN, AND J. M. MILLER. 1982. The composition of precipitation in remote areas of the world. *J. Geophys. Res.* 87:8771-8786.
- HEYER, W. R., A. S. RAND, C. A. GONCALVES DA CRUZ, AND O. L. PEIXOTO. 1988. Decimations, extinctions, and colonizations of frog populations in southeast Brazil and their evolutionary implications. *Biotropica* 20:230-235.
- HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.
- HONEGGER, R. E. 1979. Red data book, vol. 3. Amphibia-Reptilia. International Union for the Conservation of Nature, Gland, Switzerland.
- LAWTON, R., AND V. DRYER. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18:101-116.
- LOVETT, G. M., W. A. REINERS, AND R. K. OLSON. 1982. Cloud droplet deposition in a subalpine balsam fir forest: hydrological and chemical inputs. *Science* 218:1303-1304.
- MOHNEN, V. A., AND J. A. KADLECEK. 1989. Cloud chemistry research at Whiteface Mountain. *Tellus* 41B:79-91.
- PHILLIPS, K. 1990. Where have all the frogs and toads gone? *BioScience* 40:422-424.
- PIERCE, B. A. 1985. Acid tolerance in amphibians. *Ibid.* 35:239-243.
- SANHUEZA, E., N. GRATEROL, AND A. RONDON. 1987. Rainfall pH in the Venezuelan savannah. *Tellus* 39B:329-332.
- SAVAGE, J. M. 1966. An extraordinary new toad (*Bufo*) from Costa Rica. *Rev. Biol. Trop.* 14:153-167.
- VITT, L. J., J. P. CALDWELL, H. M. WILBUR, AND D. C. SMITH. 1990. Amphibians as harbingers of decay. *BioScience* 40:418.
- WEATHERS, K. C., G. E. LIKENS, F. H. BORMAN, J. S. EATON, K. D. KIMBALL, J. N. GALLOWAY, T. G. SICCAMA, AND D. SMILET. 1988. Chemical concentrations in cloud water from four sites in the Eastern United States, p. 345-358. *In: Acid deposition processes at high elevation*, vol. C2562. M. H. Unsworth and D. Fowler (eds.). Springer-Verlag, New York, New York.
- WELLS, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.* 25:666-693.
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