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Amphibian Declines and Climate Disturbance: The Case of the Golden Toad and the Harlequin Frog

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Abstract: *The endemic golden toad (Bufo periglenes) was abundant in Costa Rica's Monteverde Cloud Forest Preserve in April–May 1987 but afterwards disappeared, along with local populations of the harlequin frog (Atelopus varius). We examine the possible relationship between these sudden declines and unusually warm, dry conditions in 1987. For our analyses of local weather patterns, we define a 12-month (July–June) amphibian moisture-temperature cycle consisting of four periods: (1) late wet season; (2) transition into dry season; (3) dry season; and (4) post-dry-season (early-wet-season) recovery. The 1986–1987 cycle was the only one on record (of 20 analyzed) with abnormally low rainfall in all four periods, and temperature anomalies in 1987 reached record highs. Flow in local aquifer-fed streams during the dry season and post-dry-season recovery period reached a record low. This climate disturbance, associated with the 1986–1987 El Niño/Southern Oscillation, was more severe than a similar event associated with the 1982–1983 El Niño, though this earlier oscillation was the strongest of the past century. Demographic data for one harlequin frog population, gathered during these two climatic events, support the hypothesis that in 1987, shortly before the population collapsed, the frogs underwent an unprecedented shift in distri-*

Declinación de anfibios y perturbaciones climáticas: El caso del sapo dorado y la rana harlequín

Resumen: *El endémico sapo dorado (Bufo periglenes) era abundante en la Reserva del bosque nuboso de Monteverde en Costa Rica durante abril–mayo 1987 pero después desapareció al mismo tiempo que poblaciones locales de la rana harlequín (Atelopus varius). Se examinó la posible relación entre esta súbita disminución y las condiciones cálidas y secas de 1987. Para analizar los patrones locales de tiempo, se definió un ciclo de temperatura-humedad de 12 meses (julio–junio) que consiste de cuatro períodos: (1) últimos meses de la estación lluviosa; (2) transición a la estación seca; (3) estación seca; y (4) recuperación después de la estación seca (principio de la estación lluviosa). El ciclo de 1986–1987 fue el único registrado (de 20 analizados) que recibió precipitación anormalmente baja en todos los cuatro períodos, y las anomalías de temperaturas en 1987 fueron las más altas registradas. Los caudales en las quebradas locales que se alimentan de manantiales fueron los más bajos registrados durante la estación seca y el período de recuperación. Este trastorno del clima, asociado con El Niño/Oscilación del sur de 1986–1987, estuvo más severo que el evento parecido asociado con El Niño de 1982–1983, aunque esta oscilación anterior fue la más fuerte del último siglo. Datos para una población de ranas harlequines, recolectados durante estos dos trastornos del clima, apoyan la hipótesis que en 1987, poco antes de que la población co-*

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bution within the habitat in response to desiccating conditions. The juxtaposition of these rare demographic events suggests they were causally linked yet sheds little light on mechanisms underlying the sudden decline. While desiccation or direct temperature effects may have been factors leading to high adult mortality, moisture-temperature conditions may have interacted with some other, unidentified agent. We discuss two hypotheses concerning possible synergistic effects: In the climate-linked epidemic hypothesis, microparasites are the additional agent. In the climate-linked contaminant pulse hypothesis, atmospheric contaminants scavenged by mist and cloud water in montane areas reach critical concentrations when conditions are abnormally warm and dry.

Introduction

In 1987, the golden toad (*Bufo periglenes*; Bufonidae), endemic to elfin cloud forest in Costa Rica's Cordillera de Tilarán, appeared safe in the Monteverde Cloud Forest Preserve. During April–May, more than 1500 toads gathered to mate in temporary pools at Brillante, the principal known breeding site (Fig. 1; Crump et al. 1992). This spectacle had occurred annually since at least 1972, when the preserve was founded (W. Guindon, personal communication). But in 1988 and again in 1989, only a single toad appeared at Brillante, and a few others gathered 4–5 km SE. A variety of other amphibians in the area, including the harlequin frog (*Atelopus varius*; Bufonidae) and members of six other families, became scarce at the same time. During 1990–1992, despite our intensive surveys, no golden toads or harlequin frogs were found.

Interest in this case has intensified with the recognition that it is part of a global pattern (Barinaga 1990; Blaustein & Wake 1990; Phillips 1990; Vitt et al. 1990; Wyman 1990; Wake 1991). Nevertheless, the many reports of amphibian declines have met with some skepticism. Because populations fluctuate naturally (see Bragg 1960), an apparent decline could be an artifact of short-term observations. Pechmann et al. (1991) pointed to large fluctuations in the abundance of several species at a breeding pond in lowland South Carolina over 12 years. A species was sometimes rare or absent one year and abundant the next. Many populations that have disappeared, however, including those at Monteverde, show no sign of recovery after several years. Furthermore, studies of coastal plain populations of the eastern U.S. may have limited relevance to our understanding of events in montane and high-latitude regions, where most amphibian declines have been observed (Wake 1991).

Sightings of both golden toads and harlequin frogs at Monteverde decreased by about 99% in the same year. Whereas adult golden toads had not commonly been

lapsara, las ranas cambiaron su distribución en el hábitat en respuesta a condiciones desecantes. La juxtaposición de estos raros eventos demográficos sugieren que estuvieron ligados causalmente, pero dice poco de los mecanismos de la súbita disminución. Mientras que la desecación y los efectos directos de la temperatura pudieron haber causado mortalidad de adultos, también es posible que hubiera interacción entre las condiciones climáticas y otro factor. Se discuten dos hipótesis sobre una posible interacción: En la hipótesis de epidemia ligada al clima, los microparásitos son el factor adicional. En la hipótesis de contaminación ligada al clima, contaminantes atmosféricos removidos por la llovizna y niebla alcanzan concentraciones críticas cuando las condiciones son anormalmente cálidas y secas.

seen outside their brief annual mating bouts (one to several 5–10-day periods from March through June; Jacobson & Vandenberg 1991; W. Guindon, personal communication) harlequin frogs had been abundant and conspicuous year-round since 1980, when we began our observations (Crump 1986; Pounds & Crump 1987; Crump & Pounds 1989). Because annual adult survivorship in bufonids is generally much greater than 1% (Kelleher & Tester 1969; Clarke 1977), the abrupt nature of the declines suggests high adult mortality rather than just a lack of successful breeding and recruitment.

Environmental factors that could be implicated in these declines include acid deposition or other forms of atmospheric contamination, ultraviolet radiation, microparasites, and extreme weather conditions (Pounds 1990, 1991). Although the possibility of an extraordinary event of acid precipitation in 1987 cannot be ruled out, measurements of pH in subsequent years have revealed no abnormal acidity (Crump et al. 1992; Clark, personal communication). Moreover, while acidity is known to kill aquatic embryos (Pierce 1985) and affect the distribution of terrestrial adults (Wyman 1988; Wyman & Jancola 1992), it has not been linked to high adult mortality. The possibility, however, that other kinds of atmospheric contamination were a factor in the declines remains unexplored. Ultraviolet radiation could conceivably kill adult harlequin frogs, but golden toads normally hide in retreats about 95% of the time, emerging to breed beneath the forest canopy, typically under heavy cloud cover. A variety of microparasites attack amphibians (such as viruses, bacteria, and protozoans; Hoff et al. 1984), yet it seems unlikely that they would suddenly become highly lethal unless they were interacting with some other factor.

Crump et al. (1992) focused on the possible role of unusual weather in the disappearance of the golden toad. Examining precipitation patterns, breeding pool temperatures, and the timing of pool formation, they hypothesized that warm, dry conditions since 1987 have discouraged breeding attempts and that the toads

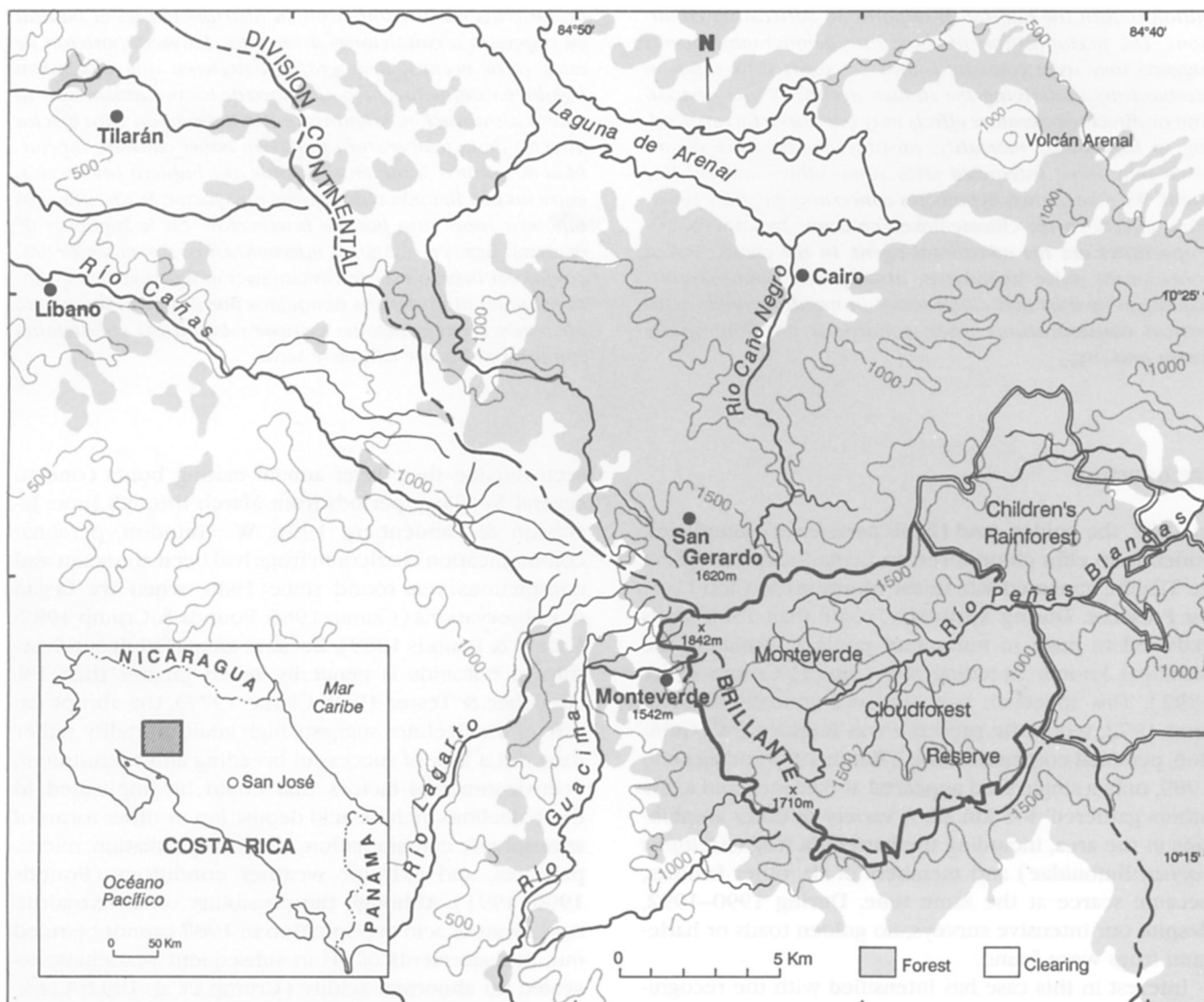


Figure 1. The Monteverde region of Costa Rica's Cordillera de Tilarán. Golden toads are known only from elfin forest along the continental divide in and near the Monteverde Cloud Forest Preserve (Savage 1966). This habitat is characterized by dwarfed, wind-sculpted trees heavily laden with epiphytes (Lawton & Dryer 1980) and belongs to the lower-montane rain-forest life zone of Holdridge (1967). Forested and deforested areas were mapped approximately from aerial photographs.

might simply be waiting in retreats for conditions to improve. In view of more recent field work, however, it seems unlikely that golden toads still survive in large numbers. In this paper, we focus on the possibility that warm, dry conditions in 1987 were a factor in high adult mortality, leading to the collapse of populations.

When golden toads and harlequin frogs were last seen in large numbers in 1987, weather at Monteverde was under the influence of the 1986–1987 El Niño/Southern Oscillation, which produced warm, dry conditions over much of Costa Rica (Manso & Ramírez 1987). After providing background on anuran moisture-temperature re-

lations and the annual weather cycle, we ask if conditions were more extreme in 1987 than in other years on record. Our analyses emphasize the potential importance of subterranean water, the source of springs and seepages that often play a role in amphibian water economy. While the data span only 24 years, they cover the 1982–1983 El Niño, the strongest of the past century (Cane 1983), and thus include some long-term extremes that are a good basis for comparisons. Afterwards, we analyze harlequin frog demographic data in light of climatic patterns and discuss possible mechanisms whereby climate disturbances could lead to amphibian declines.

Anuran Moisture-Temperature Relations

Conditions of the physical environment interact in ways that make it difficult to isolate the effect of a single factor on any species of plant or animal. The interplay of moisture availability and ambient temperature may be especially critical for amphibians. Because virtually all physiological processes are temperature-sensitive, ambient temperature is undoubtedly an important limiting factor in its own right, but its impact on water economy may also be crucial.

Most amphibians readily lose water across their moist, permeable skins, and the rate of loss is temperature-dependent (Spotila 1972). A dehydrating anuran at high temperatures may be faced with conflicting physiological demands. By increasing dermal mucous secretion, a North American bullfrog (*Rana catesbeiana*) keeps its body temperature below dangerous levels through evaporative cooling, but at the same time accelerates water loss (Lillywhite 1971). In a similar manner, a giant toad (*Bufo marinus*) in Panama maintains its body temperature below the daytime ambient temperature, yet may die from dehydration in 24–72 hours (depending on body size) unless it has access to water (Zug & Zug 1979).

To offset evaporative losses, terrestrial frogs and toads absorb water, mainly through hypervascularized skin in the ventral pelvic region (Roth 1973). In the absence of free water, they may absorb moisture bound to the substrate, but the ability to do so varies among species and depends on substrate characteristics and moisture content. In North America, xeric-adapted spadefoot toads (*Scaphiopus*), which regulate osmotic pressure of their body fluids by storing urea, can absorb water at soil moisture tensions up to 15 atm (Ruibal et al. 1969). Mesic-adapted American toads (*Bufo americanus*), on the other hand, lose water to the soil at tensions above 1.5 atm (Walker & Whitford 1970).

For terrestrial anurans in the seasonal tropics, problems with water balance are most likely to occur during the dry season, when soils may develop moisture deficits (Herrera 1985). High insolation and air temperatures, associated with reduced cloud cover and low humidity, raise evapotranspiration rates and accelerate the drying of soils. In the cloud forest at Monteverde, where the drying effect of frequent winds may also be a factor, soils can develop moisture deficits in a matter of days (N. Nadkarni, personal communication). An amphibian that vacates a drying retreat may increase its exposure to high ambient temperatures and desiccating conditions.

Where soil moisture deficits prevail, subterranean water may be an important source of moisture. During the 1983 dry season, harlequin frogs at our study site in the headwaters of the Rio Lagarto (3 km west of the Monteverde Preserve; Fig. 1) sat on wet rocks and logs

near a small aquifer-fed stream. The gallery forest along this stream became extremely dry, and the frogs seldom ventured more than 3 m from the water (Pounds & Crump 1987; Crump & Pounds 1989). These terrestrial frogs were poor swimmers and rarely entered the stream; they thus relied on moisture absorbed from wet surfaces in the stream's splash zone. Because there was little surface runoff at the time, stream flow reflected the quantity of groundwater. As flow declined and moisture availability became patchy, the dispersion pattern of the frogs became increasingly clumped as they gathered in the remaining wet areas, especially near waterfalls (Pounds & Crump 1987; Crump & Pounds 1989).

Although golden toads do not gather near aquifer-fed streams in this manner, the water table in their elfin-forest habitat often lies within 30–50 cm of the soil surface (R. Lawton, personal communication). Seepages are common. We have observed the toads coming and going from crevices that form near the roots of elfin-forest trees as they are rocked by the trade winds. The toads have also been excavated from small tunnels apparently left by the decay of tree roots (R. Law, personal communication). For toads in these subterranean retreats, groundwater might ordinarily be an important source of moisture.

The Annual Moisture-Temperature Cycle

In Costa Rica, where geographic location relative to the central axis of mountain ranges largely determines exposure to seasonal air-flow patterns, the climate regime on the Caribbean slope differs from that on the Pacific slope (Coen 1983). Because the Monteverde region straddles the continental divide (Fig. 1), its climate is a mix of these regimes.

To quantify seasonal patterns and compare them among years, we analyzed rain-gauge and stream-flow data from both the Caribbean and the Pacific slopes. Rain-gauge data were from Monteverde (20 years) and San Gerardo (14 years); stream-flow data were from Líbano (24 years) and Cairo (15 years; Fig. 1). Recording stations on each slope were those nearest the golden toad's habitat providing continuous, long-term data. Standard rain gauges underestimate windblown precipitation yet provide data that are suitable for year-to-year comparisons. Stream-flow data give a more complete, if less localized, picture of hydrological flux. We also analyzed air-temperature data (15 years) from the Monteverde recording station.

During November–April, when northeasterly trade winds dominate the weather, the Caribbean side is wetter than the Pacific side (Fig. 2a). As these moisture-laden winds meet the Cordillera de Tilarán and flow upward, they cool adiabatically, producing clouds, mist, and rain. Most of this advective precipitation falls on the

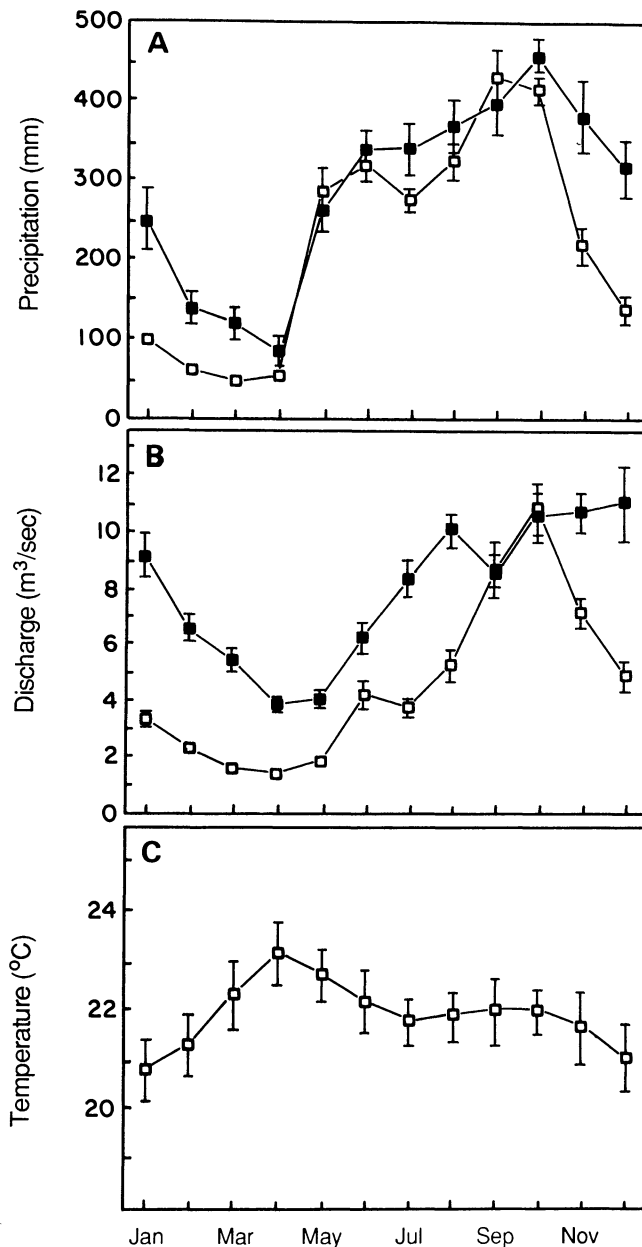


Figure 2. The annual moisture-temperature cycle in the Monteverde area. Shaded symbols are for Caribbean-slope recording stations, open ones for Pacific-slope stations (see Fig. 1 and text). Values are across-year means (of monthly totals or averages) \pm the standard error for between-year variation. (A) Total monthly precipitation. (B) Average stream flow (discharge rate). (C) Average daily maximum temperature. See text for sample sizes.

Caribbean (windward) slope and the continental divide. Some spills over to the upper Pacific (leeward) slope, but little reaches rain-shadowed areas further down-slope.

This advective Caribbean precipitation peaks in November–December with the influx of Arctic cold fronts

(Coen 1983). At many sites on the Caribbean slope, the annual peak in rainfall occurs at this time. That the peak occurs in October at San Gerardo (Fig. 2a) reflects a Pacific influence. Likewise, the high November–December precipitation at Monteverde, compared to sites further down the Pacific slope, reflects a Caribbean influence.

During January–April, as cold fronts become less frequent and the trade winds less intense, bouts of Caribbean precipitation become increasingly uncommon, resulting in relatively dry weather on both the Caribbean and the Pacific slope (Fig. 2a). Typically in April, local streams reach basal flow (Fig. 2b) and daytime temperatures reach their annual peak (Fig. 2c).

Differences in rainfall between the two slopes are least pronounced during May–October (Fig. 2a), when passage of the intertropical convergence zone generates heavy convective rains throughout the region. Also, “easterly waves” and tropical depressions produce advective precipitation sporadically during this period (Herrera 1985). Heavy advective rains in September–October (“Pacific temporals”), which occur when cyclonic winds associated with a Caribbean storm rotating near the Central American isthmus draw moisture off the Pacific, largely account for the annual rainfall peak (Coen 1983).

During the dry season, an anuran’s chances of avoiding dehydration may depend on more than just that season’s temperature and precipitation patterns. How well the preceding wet season recharged groundwater, how quickly the dry season began, and how promptly early-wet-season rains bring recovery could all be critical. To take these factors into account, we define a 12-month, July–June *amphibian moisture-temperature cycle* consisting of four periods: (1) late wet season (July–October); (2) transition into the dry season (November–December); (3) dry season (January–April); and (4) post-dry-season (early-wet-season) recovery (May–June).

El Niño and the 1986–1987 Cycle

In the wet season during a typical El Niño year, as atmospheric pressures decrease over the Pacific and increase over the Atlantic, the northeasterly trade winds become unusually intense over Costa Rica, mimicking a dry-season wind field pattern (Fernández & Ramírez 1991). These winds interfere with convective rains, especially on the Pacific slope, yet sometimes increase advective precipitation on the Caribbean slope. In the dry season during El Niño, temperatures are often unusually high, reducing condensation rates and advective precipitation while increasing rates of evapotranspiration.

During the 1986–1987 El Niño, total precipitation for

the July–June cycle in the Monteverde region was a record low on both the Caribbean and the Pacific slope (Fig. 3a). Average stream flow during the dry season and post-dry-season recovery period was likewise a record low on both slopes (Fig. 3b). Mean daily high temperature at Monteverde during March–June, the annual pe-

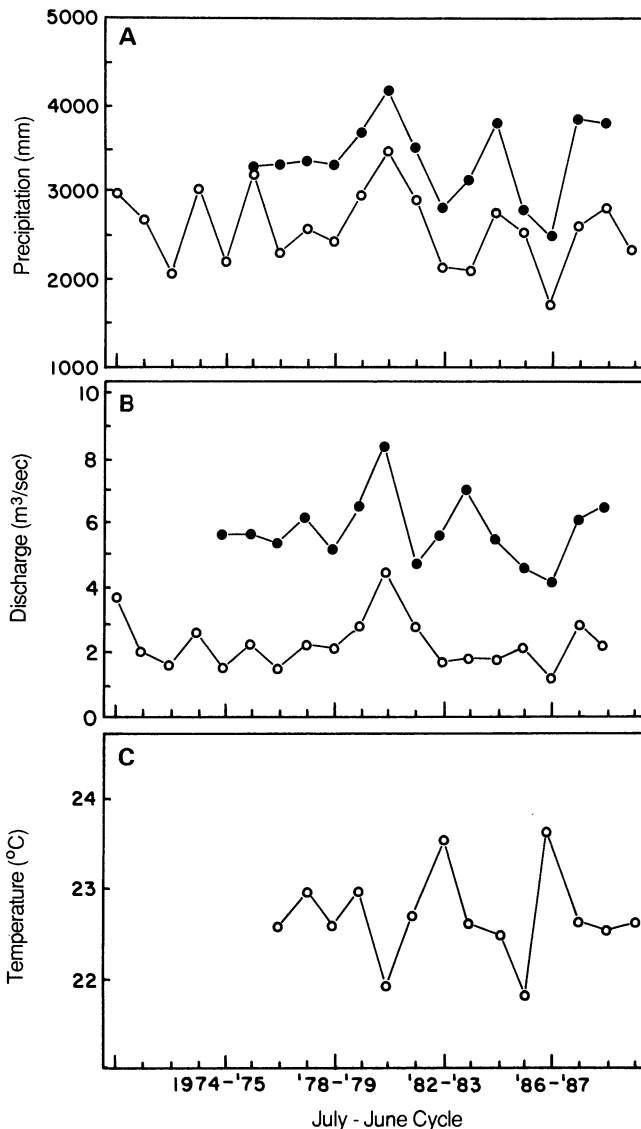


Figure 3. Variation in moisture-temperature conditions among successive amphibian moisture-temperature cycles. Each cycle is 12 months (July–June); symbols as in Figure 2. (A) Total precipitation per cycle. (B) Average stream flow (discharge rate) for the second half of the cycle (January–June), the combined dry season, and post-dry-season recovery period. Only the last 19 of the 24 years available for the Rio Cañas are shown, but these include the lowest values on record. (C) Average daily maximum temperature for March–June, the period in each cycle with the highest daytime temperatures. The average for 1991, not graphed, was 22.5°C.

riod of highest daytime temperatures, was similar to that during the 1982–1983 El Niño (Fig. 3c). Yet excluding April, which in 1987 was affected by a cold front, this period was significantly warmer than in 1983 (Mann-Whitney $U = 5396.5$; $p < 0.001$).

For a closer look at daily high temperatures, we plotted a time series of monthly mean anomalies for recent years (Fig. 4). This analysis revealed two periods of strong positive anomalies, signatures of the 1982–1983 and 1986–1987 El Niño events. The greatest positive anomalies accompanied the 1986–1987 event. They were highest in March 1987, near zero in April because of the cold front at that time, and then strongly positive through February 1988.

A more detailed analysis of precipitation patterns revealed that the 1986–1987 cycle was the only one on record with abnormally low precipitation in all four periods. This was true on both the Caribbean and the Pacific slope. On each slope, all other cycles analyzed had at least one period in which precipitation was at or above the mean (one-sample t -tests; $\alpha = 0.05$). Only in 1986–1987 did the Monteverde area experience a weak late-wet-season, followed by an abrupt transition to a harsh dry season, followed by a delayed post-dry-season recovery (Fig. 5).

Monthly rainfall and stream-flow data illustrate the development of this unusual cycle (Fig. 6). Convective rains during July–October were weak on both slopes, but more consistently so on the Pacific side. Advective Caribbean precipitation (November–April) was likewise low, except during cold fronts in January and April. Because the wet season arrived late, rainfall was low in both May and June. Basal stream flow occurred in May, rather than April as is usually the case, indicating that water tables had continued to fall at a time when groundwater is normally being replenished. Stream flow was a record low for May at both recording stations and remained significantly below average until August 1987 (one-sample t -tests; $p < 0.04$).

These analyses lead us to reject the null hypothesis that the 1987 dry season was no more severe than others on record. The timing of El Niño may have been important: the 1986–1987 event affected one complete July–June cycle, whereas others on record affected portions of one or more cycles. Nevertheless, it seems that timing alone cannot explain the severe impact of this oscillation. Given the enormous thermal signal of the 1982–1983 El Niño (Cane 1983), it is unclear why temperature anomalies at Monteverde were greater during the 1986–1987 event.

Examining temperatures of golden toad breeding pools, Crump et al. (1992) concluded that conditions after 1987 were warmer than in 1987. Our more detailed analyses, however, reveal that conditions were actually warmer in 1987 than in subsequent years (Figs. 3c and 4). Crump et al. (1992) based their conclusion on low pool temperatures recorded during the early-

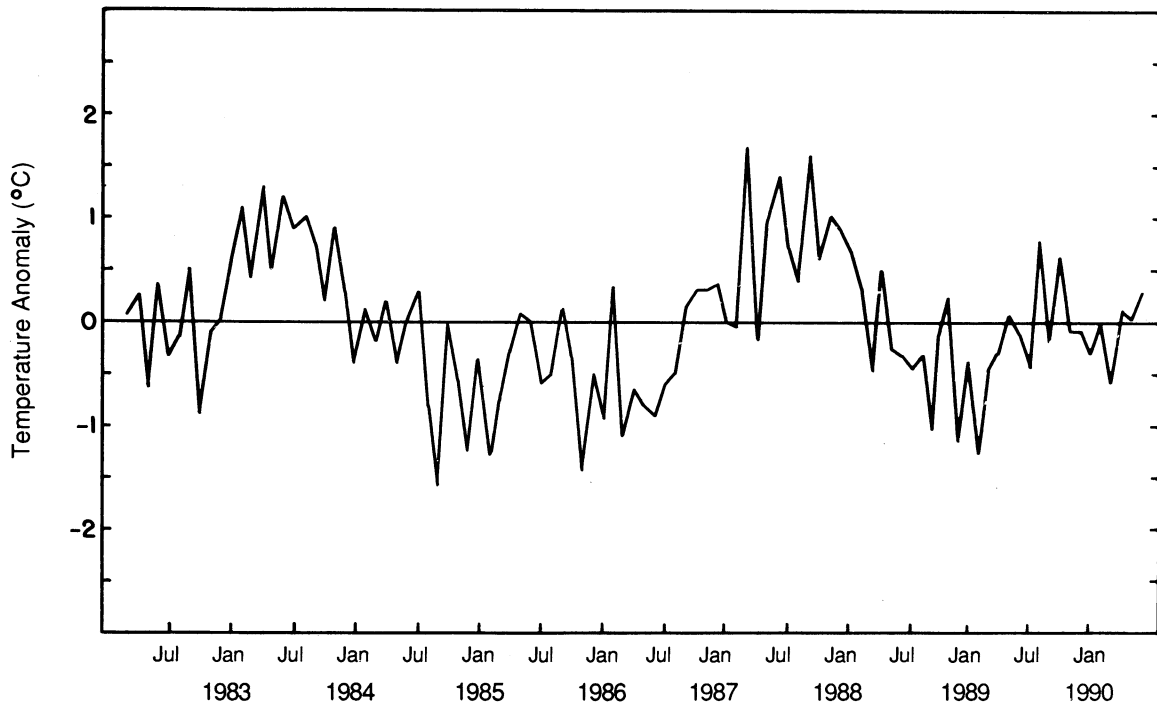


Figure 4. Anomalies of daytime air temperatures at Monteverde in recent years. Each value is the deviation of the monthly mean of daily maximum temperatures from the 15-year average of these monthly means.

April cold front in 1987, when air temperatures briefly departed from the general pattern of positive anomalies (Fig. 4). Although Crump et al. (1992) did not emphasize the point, the pool temperatures they recorded in late April and May 1987 were higher than any they re-

corded after 1987. This pattern accords with the results presented here.

Because pools filled earlier in 1987 than in the subsequent three years, Crump et al. (1992) concluded that conditions in 1987 were wetter than years after 1987.

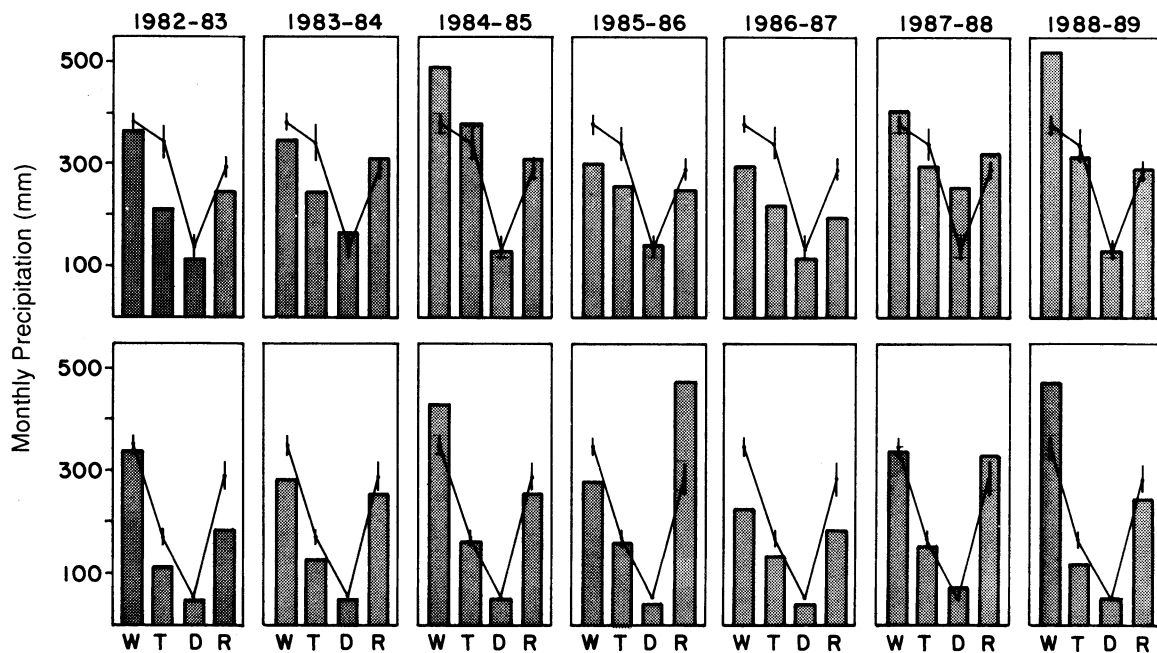


Figure 5. Precipitation by period in recent July–June amphibian moisture-temperature cycles. The upper row is for the Caribbean slope, the lower row for the Pacific slope. Bars give the average monthly rainfall for each period of each cycle. Lines give the mean (\pm standard error) across years, repeated for each cycle. W = late wet season; T = transition into the dry season; D = dry season; and R = post-dry-season recovery.

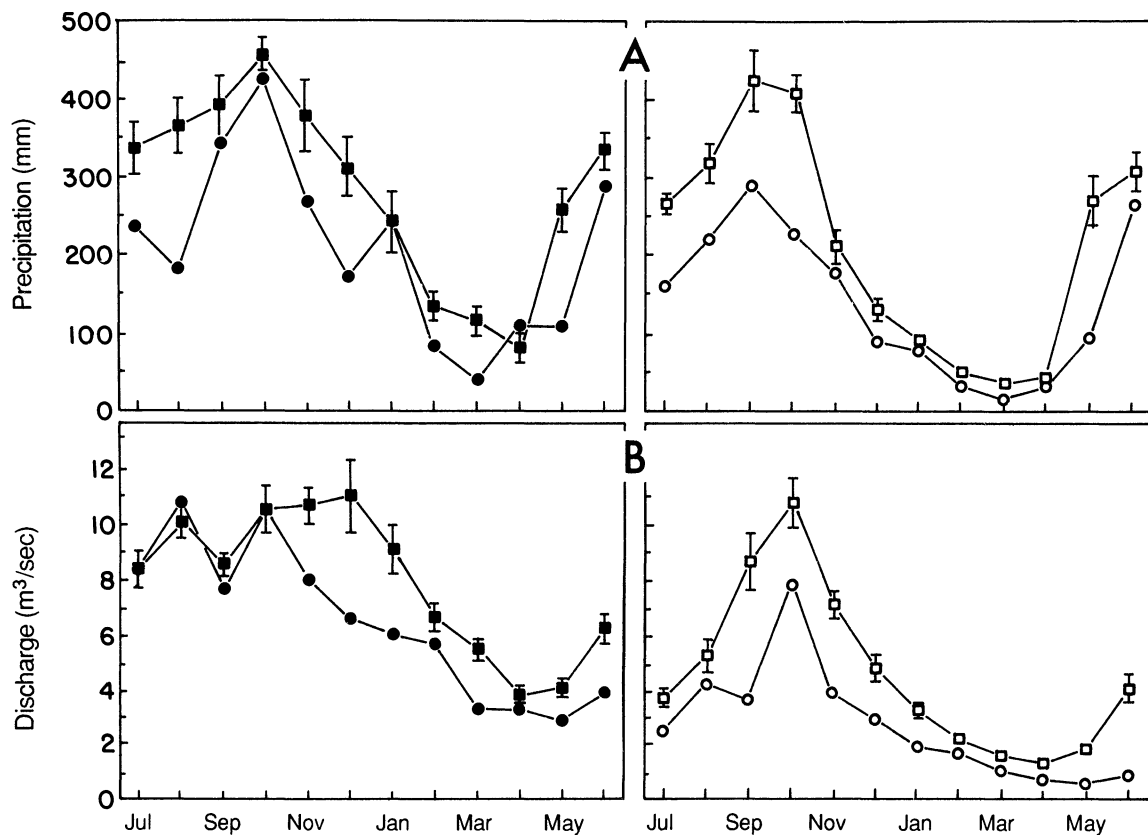


Figure 6. Month-to-month variation in precipitation and stream flow during the 1986–1987 cycle. Shaded symbols (left) are for the Caribbean slope, open ones (right) for the Pacific slope. Squares are means (\pm standard error) across years; circles are for 1986–1987. (A) Total monthly precipitation. (B) Average stream flow (discharge rate).

Our more detailed analyses, however, reveal that conditions were actually drier in 1987 than in subsequent years (Figs. 3a, 3b, and 5). The pools filled in 1987 as a result of the April cold front. This kind of extratropical disturbance, which increases condensation rates and advective precipitation, is common during the northern winter and spring but is otherwise unpredictable in time. It is not unusual for golden toad breeding pools to fill earlier or later than they did in 1987, and they often fill during convective rather than advective rains (Jacobson & Vandenberg 1991; W. Guindon, personal communication).

Biological Consequences

In 1987, golden toads emerged to breed during the temporary drop in temperatures and bout of Caribbean precipitation associated with the April cold front (Figs. 4 and 6). Because of the warm, dry conditions that followed, however, the breeding pools dried, and virtually all eggs and tadpoles died (Crump et al. 1992). As discussed earlier, this impact on early life stages probably does not explain why the population collapsed. Never-

theless, it shows that the elfin cloud forest at Monteverde, among the wettest habitats in the area, did not escape the disruption of hydrology associated with the 1986–1987 El Niño.

The effects of this climatic event on adult golden toads are unknown, yet demographic data for harlequin frogs suggest important effects on adults. Before harlequin frogs disappeared from the Monteverde area, they had been observed in the drainages of the Rios Peñas Blancas, Guacimal, and Lagartos, from 700 m on both slopes to 1700 m near the continental divide (Hayes et al. 1989). The species's geographic range is Costa Rica and western Panama (Savage 1972). At our study site in the headwaters of the Rio Lagarto, these diurnal frogs were active year-round on rocks and logs near the stream (Pounds & Crump 1987; Crump & Pounds 1989). They ranged from common to abundant (one frog per 12.5 m of stream to one frog per 0.496 m of stream) every year from 1981, when we began our observations, through 1987.

During the 1982–1983 El Niño, as the stream approached basal flow and temperatures rose above normal, the observed density of frogs declined as many took refuge in damp crevices (Crump & Pounds 1989). Be-

cause the frogs hidden in crevices included a disproportionate number of females, the operational sex ratio (in exposed areas) was highly male-biased.

In 1987, we sampled the population during March, when the warm, dry conditions associated with the 1986–1987 El Niño were near their peak. The observed density (one frog per 0.496 m of stream) was a record high, 4.4 times greater than predicted by a polynomial regression model of seasonal variation in 1982–1983 (Fig. 7a). This was the last census before the population crashed: in May 1988, density was at a record low (one frog per 40 m of stream) and by June it had fallen to zero. (Harlequin frogs disappeared at the same time from the drainages of the Rios Peñas Blancas and Guacimal; G. Bello, E. Cruz, and M. Fogden, personal communication.)

Suspecting that the high density in March 1987 might be a clue as to why the Rio Lagarto population had crashed, we considered two hypotheses. First, if recruitment were high in 1986, the population might have been unusually large in 1987. Second, if warm, dry conditions in 1987 caused individuals to leave drying crevices and gather in remaining wet areas closer to the stream, observability might have been unusually high.

Although we have no data on 1986 recruitment, these hypotheses differ in their predictions concerning sex ratio. The first predicts a normal, male-biased operational sex ratio, while the second predicts one that is less male-biased. To arrive at quantitative null predictions, we again used a polynomial regression model of seasonal variation in 1982–1983 (Fig. 7b). In March 1987, the proportion of male frogs (0.293) was 60% lower than that predicted by this model. For the first time on record, females outnumbered males.

These analyses support the hypothesis that harlequin frogs near the Rio Lagarto were responding in an unprecedented fashion to the extreme moisture-temperature conditions shortly before the population crashed and disappeared. The juxtaposition of these rare events suggest they were causally linked yet sheds little light on possible underlying mechanisms. Likewise, the simultaneous crash of golden toads and the local populations of other amphibian species suggests that all the declines were part of a single phenomenon.

Discussion

The El Niño/Southern Oscillation affects weather on a planetary scale, sometimes with devastating biological consequences (Barber & Chavez 1983), yet its impact on terrestrial and freshwater ecosystems are only beginning to be understood (Foster 1982; Grant & Grant 1989). Different El Niño events could, depending on their timing and magnitude, affect amphibians in different parts of the world. Osborne (1989) hypothesized

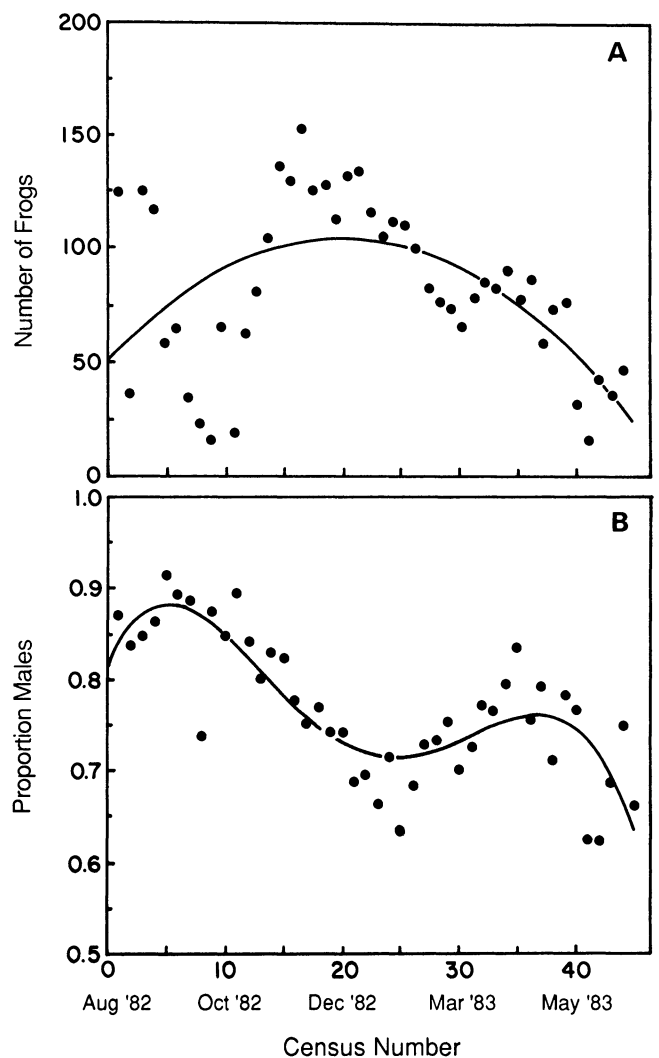


Figure 7. Seasonal variation in observed density and operational sex ratio of harlequin frog population during the El Niño/Southern Oscillation. Data are from weekly surveys conducted in 1982–1983 at the Rio Lagarto site. (A) Number of frogs per 200 m of stream. The computer-generated curve is for a quadratic regression. The number of frogs observed in late March 1987 (403) was too high to fit on this graph. (B) Proportion that were males. The computer-generated curve is for a 4th polynomial regression. The proportion of males in late March 1987 (0.293) was too low to fit on this graph.

that several years of dry weather culminating in a 1982–1983 drought (attributed to El Niño; Rasmusson & Wallace 1983) were responsible for various declines in Australia. More case studies are needed to evaluate the impact of these climate oscillations on amphibian communities.

Many reported declines of amphibian populations have taken place on mountains (Corn & Fogleman 1984; Heyer et al. 1988; Czechura & Ingram 1990; Bradford

1991), where climate is especially vulnerable to atmospheric disturbances. At middle latitudes, precipitation increases with elevation; in the tropics, it peaks at middle elevations on windward slopes (Coen 1983). Disturbances that reduce rainfall or increase temperatures in montane areas where amphibians are adapted to cool, wet conditions could have severe consequences.

Many but not all such areas have been affected. On Costa Rica's Cerro Chompipe (2200 m elevation), *Ateolopus senex* and *Bufo holdridgei* disappeared at about the same time as *A. varius* and *B. periglenes* at Monteverde, yet at Las Tablas (1800 m elevation) *A. chiriquiensis* and *B. fastidiosus* appear to be thriving (Bolaños & Barahona, personal communication). One possible explanation is that small differences in topography can translate into big differences in local climate and its vulnerability to disturbance. Turbulence in montane areas, for example, can produce local reversals in wind direction (rotor effects); hence, prevailing wind direction can differ between sites separated by only a few kilometers (Coen 1983).

The decline of amphibians at Monteverde could be a repeat of history. In the case of the golden toad, perhaps a series of climate-induced extinctions, combined with a low potential for recolonization, had left the single relic population. On the other hand, deforestation (Fig. 1) or other human activities could be increasing the impact of these disturbances. Although there are no detectable trends of decreasing annual precipitation or mean stream flow (Spearman rank correlations; $p > 0.05$), minimum stream flow in May has decreased significantly since 1966 in the Rio Cañas (Spearman rank correlation, $r_s = -0.73$; $n = 24$; $p < 0.0001$). There is a similar but statistically nonsignificant trend for the Rio Caño Negro ($r_s = -0.42$; $n = 15$; $p = 0.07$). A deterioration of local hydrology could be reducing the capacity of ecosystems to buffer natural climate disturbances.

Global warming could also be increasing the impact of these disturbances (Wyman 1991). Models of atmospheric circulation predict that regional precipitation patterns will change with warming, though the spatial resolution of these predictions is poor (Schneider 1987; Houghton & Woodwell 1989). El Niño superimposed on higher global temperatures or altered hydrological cycles could result in moisture-temperature extremes that are unprecedented in recent times. Also, by changing sea-surface temperatures and atmospheric circulation, global warming could change the frequency, timing, or intensity of El Niño events.

Hypotheses Concerning Mechanisms

As discussed earlier, the abrupt nature of the amphibian declines at Monteverde suggests high adult mortality rather than just a lack of successful breeding and recruit-

ment. Hypotheses concerning the role of moisture-temperature conditions in this mortality may invoke direct causation such as death due to desiccation or temperature stress, or indirect causation involving an interaction with an additional factor.

MOISTURE STRESS HYPOTHESIS

It is possible that high rates of anuran water loss associated with warm, dry conditions in 1987 directly caused high adult mortality. Several observations, however, cast doubt on this hypothesis. First, the Caribbean slope, although affected by El Niño, remained significantly wetter than the Pacific slope (Figs. 3 and 6), yet harlequin frogs disappeared from there as well (M. Fogden, personal communication). Compared with their Pacific-slope counterparts, harlequin frogs along the Rio Peñas Blancas (Fig. 1) should have had more opportunities to avoid dehydration. Why did these populations not show a graded response? Furthermore, with the onset of wet-season rains in Peñas Blancas Valley in 1987, red-eyed leaf frogs (*Agalychnis callidryas*; Hylidae) appeared at traditional breeding sites but disappeared shortly thereafter (M. Fogden, personal communication). If these frogs had survived the worst desiccating conditions, why did they disappear afterwards?

TEMPERATURE STRESS HYPOTHESIS

While desiccating conditions were presumably uncommon after the onset of rains in 1987, strong positive temperature anomalies continued through February 1988 (Fig. 4). Unfortunately, little is known of the thermal tolerances of golden toads and harlequin frogs. It is known, however, that the glass frog *Centrolenella fleischmanni*, which also declined sharply at Monteverde, has little ability to acclimate to temperature changes (Brattstrom 1968). Narrowly adapted montane populations—especially small, genetically homogeneous ones restricted in altitudinal range—could be particularly lacking in this kind of physiological plasticity (Brattstrom 1970). Such populations might be relatively common on low tropical mountains such as the Cordillera de Tilarán, where life zones are highly compressed (the massenerhebung effect; Flenley 1974).

CLIMATE-LINKED EPIDEMIC HYPOTHESIS

In constructing hypotheses concerning adult mortality, a natural tendency is to focus on physiologically lethal conditions. Nevertheless, nonlethal but suboptimal conditions, which may affect behavior, energy budgets, and general vitality (including immune system response), could also lead to high adult mortality by altering the outcome of critical biological interactions. Canning et al. (1964) observed this sort of interplay in captive European toads (*Bufo bufo*) maintained under crowded

conditions in England. Parasites, including the microsporidian protozoan *Plistophora myotrophica*, caused high adult mortality, especially during warm summers. Likewise, Brodtkin et al. (1992) found that the bacterium *Pseudomonas aeruginosa* caused high mortality in leopard frogs (*Rana pipiens*) maintained under suboptimal conditions, including crowding and high temperatures.

Harlequin frogs illustrate how habitat patchiness resulting from warm, dry conditions can cause a population to shift to a highly clumped dispersion pattern. To a microparasite, such a shift could represent a decrease in interhost distance, facilitating an epidemic (Dobson & May 1986). Crump et al. (1992) speculated that a "non-species-specific pathogen" might have caused the decline of amphibians at Monteverde. Alternatively, if the warm, dry conditions were a coupling factor, different microparasite species could have affected the different amphibian populations.

CLIMATE-LINKED CONTAMINANT PULSE HYPOTHESIS

The possibility of a transient increase in the concentration of toxic environmental contaminants has not been ruled out. It is clear that human activity in the lowlands of Costa Rica affects atmospheric chemistry in the highlands. Each year in March–April, turbidity of the atmosphere increases, resulting in a visible haze at Monteverde. This condition has been attributed to temperature inversions at 2000–3000 m, combined with wind erosion of soils and agricultural burning in the lowlands (Herrera 1985). Recent data from Monteverde show that cloud water collected during these months contains abnormally high concentrations of nitrates and phosphates (Clark & Nadkarni, personal communication). While this input of inorganic compounds probably does not explain Monteverde's amphibian declines, it illustrates that long-range contamination does occur. Precipitation at Monteverde might contain other, more toxic, compounds, detectable only through specific assays.

A potential source of long-range contamination in Costa Rica is the massive and indiscriminate use of pesticides (insecticides, herbicides, fungicides), which are pervasive contaminants of air and water (Hartshorn et al. 1982; Hilje et al. 1987). Pesticides enter the atmosphere by drift during application, wind erosion of deposited residues, and volatilization (Seiber et al. 1989). Once in the atmosphere, they are removed chemically, by photolysis or reaction with atmospheric oxidants, or physically, by dry deposition, adsorption onto aerosols, or rainfall (Glotsfelty 1978; Cupitt 1980).

A climate disturbance like that of 1986–1987 could interact with atmospheric contamination in several ways to produce transiently lethal conditions for amphibians. First, warm, dry conditions increase the rates

at which agrochemicals volatilize from exposed surfaces, increasing rates of input into the atmosphere (Hoff et al. 1992). Drying of soils may also create a suction gradient that draws soil contaminants to the surface (the wick effect), where they can then make their way into the atmosphere (Spencer & Cliath 1973). Second, long periods with little or no precipitation to remove toxic compounds from the air would allow more time for atmospheric concentrations to build (Glotsfelty 1978). Atmospheric residence times of organic contaminants (assuming only chemical removal) might range up to 70 days (Cupitt 1980). Third, bouts of fine mist and cloud water deposition punctuating a dry period could effectively scavenge these contaminants from the atmosphere and deposit them with minimal dilution in montane areas. Fog is much more efficient than rainwater at concentrating pesticides; for reasons still poorly understood, droplets may contain residue levels up to several thousand times greater than predicted by Henry's law, which describes the dissolution of airborne compounds in an ideal liquid (Glotsfelty et al. 1987). Fourth, moisture deficits in cloud-forest soils and epiphyte mats could diminish the extent to which these toxic compounds are diluted once they arrive. Furthermore, between sporadic events of cloud water deposition, organic residues might become highly concentrated on soil and plant surfaces as moisture evaporates during cloud dissipation (Glotsfelty et al. 1987). Fifth, partially dehydrated amphibians that rehydrate when toxic compounds are prevalent might have relatively low volumes of body fluids to dilute them. A rehydrating anuran may absorb a volume of water equal to 60–70% of its normal body water content (Putnam & Hillman 1977).

Because of the prevalence of mist and cloud water deposition at high altitudes, this *climate-linked contaminant pulse hypothesis* is consistent with the montane pattern of amphibian declines. The patchy nature of amphibian declines in montane areas could relate to the location of contaminant sources and the effects of topography on wind currents and cloud-flow patterns. During a normal dry season, airborne contaminants might arrive at sublethal background levels. During an unusually severe dry season, a deadly pulse might occur. If target compounds can be identified, their behavior in the atmosphere can be modeled and their effects on amphibians can be analyzed. Studies of this kind of possible synergism between climate disturbance and environmental contamination might be an important key to understanding the global amphibian crisis.

Coda

Since the completion of analyses for this paper, conditions at Monteverde have continued to be cooler and

wetter than in 1987. El Niño revisited in 1991–1992 (and is still with us in April 1993), but with significantly milder effects than in 1986–1987. There is still no sign, however, of either golden toads or harlequin frogs.

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