Catastrophic Population Declines and Extinctions in Neotropical Harlequin Frogs (Bufonidae: *Atelopus*)

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ABSTRACT

We surveyed the population status of the Neotropical toad genus *Atelopus*, and document recent catastrophic declines that are more severe than previously reported for any amphibian genus. Of 113 species that have been described or are candidates for description, data indicate that in 42 species, population sizes have been reduced by at least half and only ten species have stable populations. The status of the remaining taxa is unknown. At least 30 species have been missing from all known localities for at least 8 yr and are feared extinct. Most of these species were last seen between 1984 and 1996. All species restricted to elevations of above 1000 m have declined and 75 percent have disappeared, while 58 percent of lowland species have declined and 38 percent have disappeared. Habitat loss was not related to declines once we controlled for the effects of elevation. In fact, 22 species that occur in protected areas have disappeared. The fungal disease *Batrachochytrium dendrobatidis* has been documented from nine species that have declined, and may explain declines in higher elevation species that occur in undisturbed habitats. Climate change may also play a role, but other potential factors such as environmental contamination, trade, and introduced species are unlikely to have affected more than a handful of species. Widespread declines and extinctions in *Atelopus* may reflect population changes in other Neotropical amphibians that are more difficult to survey, and the loss of this trophic group may have cascading effects on other species in tropical ecosystems.

RESUMEN

Examinamos el estado poblacional de las ranas neotropicales del género *Atelopus* y documentamos disminuciones catastróficas recientes, las más drásticas señaladas para cualquier género de anfibios. De las 113 especies que han sido descritas o son candidatas para ser descritas, los datos poblacionales indican que en 42 especies, las poblaciones han sido reducidas por lo menos a la mitad y solamente diez especies tienen poblaciones estables. El estado de los taxa restantes es desconocido. Por lo menos 30 especies no han sido vistas en al menos ocho años de todas las localidades conocidas, y se teme que se hayan extinguido. La mayoría de estas especies desaparecieron entre 1984 y 1996. Todas las especies con...
The scientific community is well aware that amphibian populations are declining worldwide (Houlahan et al. 2000, Young et al. 2001, Stuart et al. 2004). Like other elements of biodiversity, many amphibians are threatened by habitat destruction, but a significant number have suffered unexplained declines, in which populations have substantially declined or disappeared from seemingly pristine habitats (Lips 1998, 1999; Hilton-Taylor 2000; Collins & Storfer 2003). These cases pose the greatest challenge to researchers who must sort through historical evidence to find clues about why species have declined and what can be done to reduce the chance of future declines.

To date, most reports of declines in the Neotropics have focused on individual localities or individual species (Heyes et al. 1988; La Marca & Reinthaler 1991; Pounds et al. 1997; Lips 1998, 1999; McCranie & Wilson 2002; Ron et al. 2003; Burrowes et al. 2004; Lips et al. 2004). These studies provide evidence about the patterns of declines, but do not provide a detailed picture of the geographic extent of declines. Have declines occurred only at these well-studied sites or are they characteristic of amphibian communities over broad geographical areas? The most recent multitaxon summary available for the Neotropics lists 30 genera in which at least one species has declined (Young et al. 2001). To document the breadth of declines, we follow a different approach by surveying a single species-rich genus with a wide distribution in the Neotropics.

Here we describe the results of a study of declines in Atelopus, the harlequin frogs, a species-rich genus of toads (Lötters 1996, Frost 2004). Atelopus is an appropriate taxon for such a survey for several reasons. First, most species are readily identified as belonging to this genus because of their colorful and, in some cases, aposematic coloration (Lötters 1996). Second, most species are diurnally active along streams, are typically abundant where they occur, breed over long reproductive seasons, and are slow to attempt escape from approaching humans (Lötters 1996). Because of these characteristics, Atelopus are among the easiest amphibians to detect throughout their range, even by nonspecialists. Population declines in these species are, therefore, much more likely to be detected than in taxa that are more cryptically colored or harder to find. Third, the genus is broadly distributed in 11 Neotropical countries so that factors affecting the genus as a whole represent widespread threats in the region. Fourth, most species occur along mid- to high-elevation streams, a habitat commonly associated with amphibian declines in the Neotropics (Lötters 1996, Young et al. 2001, Lips et al. 2003b, Stuart et al. 2004). Fifth, previous research has confirmed declines in several Atelopus species, including some in undisturbed habitats, indicating that the genus is susceptible to whatever causes unexplained amphibian declines (La Marca & Reinthaler 1991; Pounds et al. 1997; Lips 1998, 1999; Ron et al. 2003). In short, the choice of Atelopus as a study genus enhances the breadth and quantity of the data available for analysis, and patterns in this genus may reflect trends in more cryptic taxa with similar natural histories.

Current empirical evidence supports hypotheses that a recently described fungal disease, changing climate, or a combination of both factors would explain Neotropical amphibian declines. A highly virulent fungal disease, chytridiomycosis, has been found at several sites where Atelopus occurred and in species that have suffered population declines (Berger et al. 1998, Lips 1999, Lips et al. 2003a, Ron et al. 2003). In the laboratory, the disease agent, Batrachochytrium dendrobatidis (hereafter, Bd), grows best in cool, humid environments, suggesting that montane species should be most likely to decline (Piotrowski et al. 2004). Global warming is predicted to alter precipitation and other climatic variables in tropical highlands (Still et al. 1999, Bush et al. 2004, Pounds and Pushendorf 2004). Unusually warm, dry periods coincided with declines in at least three sites (Pounds et al. 1999, Ron et al. 2003, Burrowes et al. 2004) and it has been suggested that climate change might interact with disease agents (Pounds 2001, Pounds & Pushendorf 2004). The action of environmental contaminants, legal and illegal trade, and introduced predators such as trout (Oncorhynchus and Salmo spp.) have not yet been ruled out as causal factors in declines (Young et al. 2001). Habitat loss may be a factor, but declines in undisturbed and protected habitats indicate that one or more of these other causal agents are involved. Our objectives were to document the extent of population declines among Atelopus species and to determine whether declines were correlated with those factors involved in other amphibian declines such as habitat alteration, occurrence in protected areas, Bd infection, elevation, and trade.

METHODS

STUDY SPECIES.—Atelopus is the second largest genus within the Bufonidae, with 81 recognized species (Lötters 1996, Frost 2004; see Appendix for complete list) distributed from Costa Rica south to Bolivia and eastward through the Amazon basin into the Guyanas (Fig. 1). Despite interest by systematists in these anurans, their conservative morphology and variable coloration have often obscured their taxonomy. Many species have highly variable color patterns, and different species frequently have similar color patterns. Recent genetic studies reveal a previously unappreciated genetic diversity among populations of similar appearance (Jaramillo et al. 2003; S. Lötters, pers. comm.). As a result, an additional 32 forms are being described as new species or are candidates for elevation to species rank, yielding a current total of 113 putative species (S. Lötters, pers. comm.). We base our analyses on data for these 113 taxa. We are aware that the species count may continue to rise as a result of more fieldwork and examination of museum specimens (S. Lötters, pers. comm.).
Many Atelopus are conservative in their ecology and habitat use. Most species occur along streams, although some occur terrestrially in humid forest or paramo habitats (Lötters 1996). Atelopus occur from sea level to 4800 m elevation, but the majority live in highlands above 1500 m, with a number of species restricted to elevations above 3000 m. Some species, such as *A. varius*, *A. chiriquiensis*, *A. carbonerensis*, and *A. ignescens*, have been characterized as locally abundant along streams for at least part of the year, with hundreds of animals seen in a few hundred meters, often during annual breeding events (La Marca & Reintaner 1991, Pounds & Crump 1994, Lips 1998, Ron et al. 2003). Local endemism is common in the genus, making species particularly vulnerable to extinction. At least 26 species are known from only one population and a narrow altitudinal range (La Marca 1983, Lynch 1993).

**THE DATABASE.**—Published data on *Atelopus* population declines are available for a few species from a small number of sites (Pounds & Crump 1994, La Marca & Lötters 1997, Lips 1998, Ron et al. 2003). To supplement this information, we solicited data from scientists known to have studied members of the genus in recent years. We compiled these observations in a database with information on taxonomic identification, geographic distribution, elevational range, current and past estimates of abundance, current population status, last documented records, existence of habitat loss in a species’ range, occurrence in protected areas, and sources of data. We compiled responses from the 33 respondents of the 59 scientists to whom we sent requests. We then redistributed the resulting database for additional input and, in some cases, asked follow-up questions to fill data gaps. Seventy-five people contributed to the final version.

Despite the substantial effort to gather information, variation in data availability and in data-collection methods limits the comprehensiveness of the database. Only a few species have been well studied (*e.g.*, *A. carbonerensis*, *A. cruciger*, and *A. varius*); most species are poorly known. Many species have not been collected in many years, many localities have not been visited recently, and some species are known only from decades-old collections. Information is especially limited for remote (*e.g.*, eastern Andean slopes), or unsafe (*e.g.*, parts of Colombia and Peru) areas. In many cases, the available information did not permit quantitative analyses.

**POPULATION STATUS.**—We coded species into three qualitative population-status categories. Species had *stable* populations if one or more populations were known to have persisted through 2000, and no population had declined by more than 50 percent (even if the status of one or more populations remains unknown). Species had populations in *decline* if at least one population had declined by over 50 percent. Species declined and disappeared if there were no records since 1998 or earlier despite repeated searches in appropriate habitat in appropriate seasonal and weather conditions. Finally, species were *data deficient* if insufficient population trend data were available to judge whether a decline had occurred. We did not include data-deficient species in statistical analyses. No species showed significantly increasing populations.

As a quantitative measure of population change, we gathered data on relative abundance of *Atelopus* from 11 populations belonging to 10 species from published and unpublished sources. We included all populations for which a comparison between relative abundance for two sample periods at the same locality existed, regardless of the direction of population trend (declining or stable).

Amphibian populations fluctuate naturally and as a consequence, declines in abundance between two periods can be an artifact of periodic changes. Moreover, because amphibians have higher variation in the survivorship of larvae than adults, population decreases should be more frequent than increases (Alford & Richards 1999). To test whether the frequency of decreases between two periods was different from what would be expected from a nondeclining but fluctuating population, we applied a binomial test (increase vs. decrease) on which the probability of decline was higher than the probability of increase (0.56 and 0.44, respectively) according to the theoretical model of Alford and Richards (1999).

**HABITAT LOSS.**—We analyzed the data in three ways to examine the role of habitat loss in population declines. First, we asked whether the existence of habitat destruction (defined as severe alteration of more than 20 percent of natural habitat within a species’ range) was related to the likelihood that a species declined. Second, based on the assumption that protected areas help prevent habitat loss, we asked whether the occurrence of species in protected areas was related to their likelihood of declining. Because elevation was clearly associated with declines and all high elevation species declined, we performed each of these analyses only on the 24 species occurring within the elevational range of the ten stable species (*i.e.*, those species with a minimum elevation of 1000 m or less, defined here as lowland species). Finally, for a subset of 24 species that occur in Ecuador, we used remotely sensed data (AEE 2000) to classify percentages of the area of a 5 km circle centered on the known localities.
that consist of natural vegetation, fragmented vegetation (mixes of natural vegetation and agricultural land), or agricultural land (mostly used for crops or cattle grazing). Because no species with stable populations remains in Ecuador, we could not compare percentages of natural vegetation between declining and stable species. Instead, we summarize the data for declining species to test the hypothesis that if habitat loss was the cause of declines, then all declining species should have large fractions of their native vegetation destroyed. The natural vegetation data do not provide a temporal indication of when the destruction took place, so we were unable to examine whether the timing of destruction was linked to the timing of declines.

**DISEASE.**—To assess the possible contribution of Bd to declines, we compiled records of the disease in the entire genus. Because of the temperature sensitivity of Bd, observations that (a) species at higher elevations are more likely to decline than species at lower elevations and (b) that the frequency of infected individuals increases with elevation would be consistent with the hypothesis that Bd was involved with the declines. We therefore examined whether species at higher elevations (defined as those species with minimum elevational ranges greater than 1000 m) were more likely to decline than species occurring at lower elevations. Second, we pooled results from several studies in Costa Rica and western Panama and reanalyzed data for Atelopus on the presence of Bd infections (Berger et al. 1998, Lips et al. 2003a, Puschendorf 2003). One sample was of all A. varius specimens housed in the herpetological collection of the Universidad de Costa Rica collected after 1978 (Puschendorf 2003). The second sample was of A. chiriquiensis and A. varius collected in southeastern Costa Rica and western Panama in the late 1980s and late 1990s (Berger et al. 1998, Lips et al. 2003a). We looked for an association between elevation and prevalence of the disease in the combined sample.

**TRADE.**—Data on the number of wild-caught individuals exported for the pet trade are hard to obtain. As an indication of the magnitude of this factor in Atelopus declines, we interviewed six anonymous German importers of amphibians for information about the number of lots of each species imported between 1970 and 2002.

**RESULTS**

**POPULATION STATUS.**—We found widespread declines and disappearances of Atelopus. Of the 52 species with sufficient data, 42 (81%) are in decline (Table 1; summary data for all species are given in the Appendix). Of these, 30 (56% of species with sufficient data, 71% of all declining species) have disappeared from their known localities and have not been seen since 2000 despite survey efforts to relocate them. With the exception of A. vogli, which was last seen in 1933, all of these species were last recorded between 1984 and 1996 and may be extinct.

Seven of the 11 countries within the historical range of the genus include species in decline (Table 1). The fraction of species in decline is greatest for the best-studied countries—Costa Rica, Ecuador, and Venezuela—the first two each have only one species with a confirmed remnant population, while Venezuela has three. The 30 species that have disappeared are distributed among six countries (Fig. 1). Healthy populations of Atelopus species are known to persist only in Panama, Colombia, Peru, Brazil, and the Guianas. The number of data-deficient species is highest for Colombia (30), followed by Peru (23) and Ecuador (11).

For all species and localities for which population survey data are available, there was a decrease in abundance between the first and the second sampling period (Table 2). The frequency of population decreases was greater from that expected of stable populations with periodic oscillations in abundance (binomial $P = 0.004$). Additionally, relative abundance in the second sampling period also decreased, despite among-population differences in initial abundance and survey methodologies. There was a complete absence of records of Atelopus in all populations during the second sampling period. It is unlikely that the absence of records was an artifact of low sampling effort because effort was higher during the second sampling period in 8 out of 10 populations (Table 2). In at least four of the populations (both A. ignescens populations, A. sp. 1, and A. chiriquiensis), human-mediated habitat loss was not detected. The remaining populations showed varying levels of habitat loss (see below).

**HABITAT LOSS.**—Habitat destruction has occurred within the ranges of many Atelopus species. For example, in Ecuador the average percentage of natural habitat either fragmented or destroyed within 5-km radius circles centered on 24 known localities was 49.1 percent. Most of the destroyed habitat has been converted to agriculture, including cattle grazing. Among the 15 declining species in the sample, less than half of the natural vegetation remained for eight species (Table 3), less than 20 percent remained for five species, and no natural vegetation remained for A. mindoensis (Table 3).

Nevertheless, habitat loss was not a major factor associated with declines of Atelopus species. At high elevations, all species have declined regardless of whether habitat loss occurred within their distributions. Even at low elevations, where the 10 species with stable populations

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**TABLE 1. Status of Atelopus species throughout the range of the genus. Some species occur in more than one country.**

<table>
<thead>
<tr>
<th>Number of species (% of country total)</th>
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<tbody>
<tr>
<td></td>
</tr>
<tr>
<td>Declining</td>
</tr>
<tr>
<td>Costa Rica (CR)</td>
</tr>
<tr>
<td>Panama (PA)</td>
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<tr>
<td>Colombia (CO)</td>
</tr>
<tr>
<td>Ecuador (EC)</td>
</tr>
<tr>
<td>Peru (PE)</td>
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<tr>
<td>Bolivia (BO)</td>
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<tr>
<td>Venezuela (VE)</td>
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<tr>
<td>Suriname (SR)</td>
</tr>
<tr>
<td>Guyana (GU)</td>
</tr>
<tr>
<td>Brazil (BR)</td>
</tr>
<tr>
<td>French Guiana (FG)</td>
</tr>
<tr>
<td>Total for genus</td>
</tr>
</tbody>
</table>
occur, habitat loss was not associated with declines ($\chi^2 = 2.14, df = 1, P = 0.14$). Occurrence in a protected area was also not related to declines for the same sample of species ($\chi^2 = 2.45, df = 1, P = 0.12$). Moreover, across all elevations, 22 species disappeared despite occurring in protected areas.

**DISEASE.**—The chytrid fungus *Batrachochytrium dendrobatidis* was detected in 29 individuals of 14 species of *Atelopus*, including 9 of the 42 species in decline. These cases include populations from Costa Rica, Panama, Ecuador, Venezuela, and Peru (Fig. 2). *Bd* was detected in 9 of the 10 populations for which population survey data were available (Table 2). Four of the nine species in decline with records of *Bd* are among the 30 species that have not been observed in at least the last 5 yr. The average number of years between the first record of the disease and the last sighting of wild populations is 3.3 ± 2.6 SD yr (range: 1–7 yr; N = 4). The earliest Neotropical record in Central or South America was the last sighting of wild populations in 2000 from a country record in the Venezuelan Andes (Hofstede 2003), and these forests were home to many species of *Atelopus* but it is not a factor strongly linked with declines. Deforestation of Andean forests is almost complete in the inter-Andean valleys in Ecuador, in the Cordillera Central of Colombia, and parts of the Venezuelan Andes (Hofstede 2003), and these forests were home to many species of *Atelopus*. However, much of this habitat change may have taken place well before or after declines occurred. In addition, several species can tolerate high levels of habitat loss. For example, *A. ignescens* occurred within the city limits of Quito, Ecuador (Ron et al. 2003). Only two disappearances are strongly linked to habitat loss. The only

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**TABLE 2.** Change in abundance of 10 species of *Atelopus* at 11 localities. First and second samples refer to surveys carried out before and after (or while) population declines were noticeable, respectively. Relative abundance is expressed in individuals found per survey or per hour of survey. Sources are: Ecuadorian localities: first sample, W. E. Duellman (pers. comm.); second sample, Bustamante (2002) and Ron et al. (2003); Venezuela: La Marca and Reinhart (1991), Durans and Arellano (1995), La Marca and Lötters (1997), Manzanilla and La Marca (2004), J. E. Garcia and E. La Marca (pers. comm.); Costa Rica: Río Lagarto, Pounds and Crump (1994); Las Tablas, Lips (1998, pers. comm.). Country abbreviations as in Table 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality (Country)</th>
<th>Relative abundance (first sample)</th>
<th>Relative abundance (second sample)</th>
<th>Date(s) of first sample</th>
<th>Date(s) of second sample</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>800 m, 234 replicates</td>
<td></td>
<td>800 m, 36 replicates</td>
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<td></td>
</tr>
<tr>
<td><em>A. coynei</em></td>
<td>Río Faisanes (EC)</td>
<td>0.03 ind/pers/h (32 h)</td>
<td>0 ind/pers/h (39 h)</td>
<td>1975</td>
<td>2001</td>
</tr>
<tr>
<td><em>A. ignescens</em></td>
<td>Páramo de Guamaní (EC)</td>
<td>23.5 ind/pers/h (2 h)</td>
<td>0 ind/pers/h (19 h)</td>
<td>1967</td>
<td>2000</td>
</tr>
<tr>
<td><em>A. ignescens</em></td>
<td>Páramo del Antisana (EC)</td>
<td>89–234 ind/400 m² (2 replicates)</td>
<td>0 ind/400–1000 m² (22 replicates)</td>
<td>1981</td>
<td>1999–2001</td>
</tr>
<tr>
<td><em>A. longirostris</em></td>
<td>Río Faisanes (EC)</td>
<td>0.25 ind/pers/h (32 h)</td>
<td>0 ind/pers/h (39 h)</td>
<td>1975</td>
<td>2001</td>
</tr>
<tr>
<td><em>A. mindoensis</em></td>
<td>Quebrada Zapadores (EC)</td>
<td>3.2 ind/pers/h (40 h)</td>
<td>0 ind/pers/h (58 h)</td>
<td>1975</td>
<td>2000–2001</td>
</tr>
<tr>
<td><em>A. mucuhauiensis</em></td>
<td>La Corcovada (VE)</td>
<td>37 ind/pers/h (81 h)</td>
<td>0 ind/pers/hr (72 h)</td>
<td>1994–1995</td>
<td>1996–2004</td>
</tr>
<tr>
<td><em>A. planispina</em></td>
<td>Río Azuela (EC)</td>
<td>0.125 ind/pers/h (72 h)</td>
<td>0 ind/pers/hr (90.8 h)</td>
<td>1971</td>
<td>2000–2001</td>
</tr>
<tr>
<td><em>A. pinangoi</em></td>
<td>Piñango (VE)</td>
<td>0.15 ind/pers/h (3 h)</td>
<td>0 ind/pers/hr (7 h)</td>
<td>1992</td>
<td>1998</td>
</tr>
<tr>
<td><em>A. varius</em></td>
<td>Río Lagarto headwaters (CR)</td>
<td>13–151 ind/200 m² (45 replicates)</td>
<td>0 ind/200 m² (68 replicates)</td>
<td>1982–1983</td>
<td>1990–2002</td>
</tr>
</tbody>
</table>

Compiling *Atelopus* data from previous work in Costa Rica and western Panama revealed a total of 11 *Bd* infections in 94 samples examined (Table 4). Infections occurred at all elevations sampled, and there was no pattern with elevation (data pooled into three 1000-m intervals, G-test, $G = 1.084, df = 2, P = 0.58$).

**TRADE.**—The sample of the German importers interviewed was small and therefore the figures presented here are underestimates. Nonetheless, the results show a robust trade in *Atelopus* species. At least seven species that have declined, including one that disappeared, and five others were exported for sale in the pet trade (Table 5).

**DISCUSSION**

The genus *Atelopus* is in critical condition. It is in decline throughout its geographical range and in all habitats and elevational zones it is known to inhabit. Of the species with adequate data, 81 percent show evidence of decline, and merely ten species have healthy populations. In the few populations where quantitative demographic data are available, the declines have been drastic and so uniform that the overall trend cannot be considered an artifact of normal short-term oscillations in population size, especially given the lack of recovery after several decades (this study).

Habitat degradation has occurred within the ranges of many *Atelopus* species, but it is not a factor strongly linked with declines. Deforestation of Andean forests is almost complete in the inter-Andean valley in Ecuador, in the Cordillera Central of Colombia, and parts of the Venezuelan Andes (Hofstede 2003), and these forests were home to many species of *Atelopus*. However, much of this habitat change may have taken place well before or after declines occurred. In addition, several species can tolerate high levels of habitat loss. For example, *A. ignescens* occurred within the city limits of Quito, Ecuador (Ron et al. 2003). Only two disappearances are strongly linked to habitat loss. The only...
TABLE 3. Land-use in 5-km radius circles at 137 known localities of 24 species of Atelopus in Ecuador. Undescribed species are distributed as follows: (1) sp. 10 from Provincia de Loja, Parque Nacional Podocarpus; (2) sp. 11 from Provincia de Pichincha, Otongoro; (3) sp. 12 from Provincia de Pastaza, Lorocachi; (4) sp. 13 from Provincia Morona Santiago; and (5) sp. 19 from Provincia del Carchi and Provincia de Imbabura.

<table>
<thead>
<tr>
<th>Atelopus species</th>
<th>Natural vegetation</th>
<th>Fragmented</th>
<th>Agriculture and pastures</th>
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</thead>
<tbody>
<tr>
<td>Declining</td>
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<tr>
<td>arthuri</td>
<td>15.4</td>
<td>21.7</td>
<td>62.9</td>
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<td>balios</td>
<td>51.6</td>
<td>3.3</td>
<td>45.1</td>
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<td>bomolochos</td>
<td>54.7</td>
<td>11.2</td>
<td>34.1</td>
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<td>coynei</td>
<td>18.4</td>
<td>26.3</td>
<td>55.3</td>
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<td>elegans</td>
<td>23.9</td>
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<td>60.5</td>
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<td>44.6</td>
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<td>8.9</td>
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<td>igneens</td>
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<td>48.0</td>
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<td>longimixtis</td>
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<td>lynchii</td>
<td>89.9</td>
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<td>10.1</td>
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<tr>
<td>mindoensis</td>
<td>0</td>
<td>59.7</td>
<td>40.3</td>
</tr>
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<td>nanay</td>
<td>92.0</td>
<td>1.1</td>
<td>6.9</td>
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<tr>
<td>pachydermus</td>
<td>78.6</td>
<td>18.7</td>
<td>27.7</td>
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<td>planispina</td>
<td>53.5</td>
<td>34.5</td>
<td>12.0</td>
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<tr>
<td>sp. 19</td>
<td>45.5</td>
<td>6.6</td>
<td>47.9</td>
</tr>
<tr>
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<tr>
<td>boulengeri</td>
<td>57.2</td>
<td>18.3</td>
<td>24.5</td>
</tr>
<tr>
<td>balboi</td>
<td>82.7</td>
<td>9.9</td>
<td>7.4</td>
</tr>
<tr>
<td>nepiosomaus</td>
<td>64.0</td>
<td>0</td>
<td>36.0</td>
</tr>
<tr>
<td>palmetus</td>
<td>45.9</td>
<td>24.8</td>
<td>29.3</td>
</tr>
<tr>
<td>spermarious spumarius</td>
<td>99.1</td>
<td>0</td>
<td>0.9</td>
</tr>
<tr>
<td>sp. 10</td>
<td>99.5</td>
<td>0</td>
<td>0.5</td>
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<tr>
<td>sp. 11</td>
<td>15.1</td>
<td>84.8</td>
<td>0.1</td>
</tr>
<tr>
<td>sp. 12</td>
<td>94.7</td>
<td>5.3</td>
<td>0</td>
</tr>
<tr>
<td>sp. 13</td>
<td>31.3</td>
<td>13.2</td>
<td>55.5</td>
</tr>
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</table>

The first report of infection by Bd was in an Atelopus collected in 1980, in Ecuador, years before population declines were noticed (Ron et al. 2003). Our sample indicates that when detected, Bd is present for an average of 3 yr before the complete disappearance of a species. The disease has infected species across a wide range of elevations in Costa Rican Atelopus (Table 4). The disease may occur widely and may only be virulent at cooler, higher elevation sites as laboratory studies of Bd physiology suggest. The observation that Atelopus species occurring in higher elevation habitats are more likely to decline and disappear even though they may occur in protected areas (Fig. 2) is consistent with this hypothesis.

Laboratory experiments show that Bd can cause mortality in most tested species of frogs (Berger et al. 1998, Daszak et al. 2003), although some amphibians may be resistant (e.g., Davidson et al. 2003). No species of Atelopus has yet been tested, although dead individuals of several species had levels of infection thought to be lethal. These animals were found just prior to population decline and subsequent disappearance.

FIGURE 2. Known locations and dates of Bd infections in Atelopus superimposed on the range of the genus.

The assertion that habitat loss is not a major factor in declines is supported by our observation that 32 species have declined despite ongoing protection of at least part of their ranges. Among these, 22 species have completely disappeared. Establishing protected areas is not sufficient to conserve Atelopus species; additional species-specific efforts will be needed to effectively conserve the remaining species. Below, we discuss five possible additional causes of Atelopus declines: disease, climate change, trade, introduced predators, and environmental contamination.

Infection by Batrachochytrium dendrobatidis has been clearly linked with declining amphibian populations at numerous Latin America sites. Most species of Atelopus have not been examined for the presence of Bd, although most of those examined have been found to be infected.
such as basking in the sun to raise their body temperatures.

Evidence from various systems has shown that global warming can cause diverse biotic changes (Hayes & Jennings 1986, Hanselmann et al. 2004), or whether they might serve as disease vectors (Hanselmann et al. 2004). In addition to direct effects, introduced predators can have indirect effects by affecting nutrient cycles and algae production (Schindler et al. 2001), which can alter growth and survival in some larval amphibians (Knapp & Matthews, 2000). In some regions, there is no link between introduced fish and amphibian population declines. There are no introduced predators, for example, in Costa Rica’s Monteverde Cloud Forest Preserve, yet Atelopus sp. 1 populations disappeared from there in the late 1980s. Trout were introduced to the highlands of Chiriquí, Panama in 1925 (Hildebrand 1938) but declines did not occur there until the 1990s (Lips 1999). Similarly, at some Andean localities in Ecuador and Venezuela, Atelopus coexisted with trout for at least three decades before noticeable declines occurred (Ron et al. 2003, E. La Marca, pers. comm.). It is possible that salmonids have caused reductions in population at some localities, but it is unlikely that they are related to widespread declines.

The effect of environmental contamination on Atelopus declines is largely unknown. Many chemicals are widely used in agriculture or mining in Latin America (FAO 2003), but research on their deleterious effects on amphibians is just beginning (Izaguirre et al. 2000, Lajmanovich et al. 2003). Contamination from gold mining is suspected in the loss of a population of A. peruanus, near Cajamarca, Peru, in the last decade (R. Schulte, pers. comm.). Targeted research on the effects of contaminants on Atelopus or most other Neotropical amphibians has not yet begun.

**Research Needs.**—Information is lacking about natural fluctuations and extinctions in most tropical amphibian species, although the findings of this study emphasize that many Atelopus species and populations that were formerly regularly encountered have not been seen in many years and some species are likely extinct. In the last 5 yr, field researchers have found small populations of four species of Atelopus many years

### Table 5. List of Atelopus species that have appeared in the pet market, their origin, and estimated numbers of lots imported to Europe between 1970 and 2002, based on interviews with German importers.

<table>
<thead>
<tr>
<th>Species</th>
<th>Country of origin</th>
<th>Number of lots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Declining</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. carbonerensis</em></td>
<td>Venezuela</td>
<td>1</td>
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<tr>
<td><em>A. cruciger</em></td>
<td>Venezuela</td>
<td>&gt;20</td>
</tr>
<tr>
<td><em>A. ignescens</em></td>
<td>Ecuador</td>
<td>&gt;20</td>
</tr>
<tr>
<td><em>A. peruanus</em></td>
<td>Peru</td>
<td>&lt;15</td>
</tr>
<tr>
<td><em>A. pulcher</em></td>
<td>Peru</td>
<td>&gt;15</td>
</tr>
<tr>
<td><em>A. varius</em></td>
<td>Costa Rica, Panama</td>
<td>&gt;20</td>
</tr>
<tr>
<td><em>A. zeteki</em></td>
<td>Panama</td>
<td>5</td>
</tr>
<tr>
<td>Stable</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. flavescens</em></td>
<td>French Guiana</td>
<td>&gt;20</td>
</tr>
<tr>
<td><em>A. glypha</em></td>
<td>Panama</td>
<td>1</td>
</tr>
<tr>
<td><em>A. spumarius complex</em></td>
<td>French Guiana, Suriname</td>
<td>&lt;10</td>
</tr>
<tr>
<td><em>A. spurrelli</em></td>
<td>Colombia</td>
<td>1</td>
</tr>
<tr>
<td>Data deficient</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. reticulatus</em></td>
<td>Peru</td>
<td>2</td>
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</table>

*it includes the suggested junior synonym *Atelopus spumarius barbotini.*
after historical populations were extirpated. Some of these discoveries resulted from surveys in regions of difficult access that revealed previously unknown populations, while others came after intensive monitoring. In all four cases, *Bd* has been identified in individuals of these species and was thought to be involved in the original population declines. The existence of these populations underscores the need for research into the role of microhabitat variation in *Bd* infection and the potential for evolved resistance. Examples include a population of *Atelopus cruciger* found in Venezuela 17 yr after it had been declared extirpated and after 8 yr of intensive surveys (Manzanilla & La Marca 2004), 23 individuals of *A. mucubajensis* found after intensive searches between 1990 and 1993 (La Marca & Lötters 1997, García-Pérez 1997), several tadpoles of *A. sp. 36* in Venezuela (J. E. García-Pérez, pers. comm.), and 36 individuals of *Atelopus sp. 13* found in southwestern Ecuador (S. Ron, pers. comm.). These populations require intensive study to determine how they have persisted when so many other populations have been lost.

We recommend additional research into possible causes of declines, as well as studies of taxonomy and ecology, including physiology, population dynamics, and population genetics. The alarming number of losses documented in this genus calls for extensive surveys of moderate and high elevation habitats throughout Central and South America to evaluate the population status of all species and to initiate monitoring efforts where populations persist. It is especially important to search for *Bd* in extant populations of lowland species of *Atelopus*, because the interaction among lowland frogs, the environment, and *Bd* may differ from those in upland areas.

Insufficient sampling of older museum material prevents greater precision of the timing of disease outbreaks. Few sites were resurveyed regularly, so the date of declines is rarely known precisely. The timing of these decline events in many cases is not precisely known, especially for rarely visited remote sites. We recommend the examination of museum specimens of *Atelopus* that have declined for the presence of *Bd*.

**CAPTIVE BREEDING.**—Captive breeding programs have begun for *Atelopus pulcher* in Peru (D. Bernauer, pers. comm.), *A. sp. 13* from Ecuador, *A. zeteki* and *A. varius* from Panama (Zippel 2002), and *Atelopus spumarisius sensu lato* from Suriname (R. Gagliardo, pers. comm.). The long-term feasibility of these programs remains to be determined, but as an example of short-term success the Detroit and Baltimore Zoos have maintained and bred populations of *A. varius* and *A. zeteki* (K. Zippel, pers. comm.). Because so many species have already disappeared, captive breeding will not be a means for saving the entire genus. Nonetheless, these programs may be the only strategy currently available to conserve the few remaining extant populations. At present, two likely causes for population declines, *Bd* and climate change, cannot be counteracted in wild populations. The only conservation tool available when either of these two factors is present is *ex situ* breeding programs.

**CONCLUSIONS**

Our findings point to *Atelopus* as the most striking case of catastrophic species loss ever documented for a single amphibian, or perhaps vertebrate, genus in recent history. Declines have happened recently and rapidly, with 29 species disappearing in the last 20 yr. A large number of species declined or disappeared despite occurring in areas protected from habitat destruction. Although no single factor can explain all the declines, existing data suggest two factors are most relevant. Infection by *Bd* followed by dramatic population declines in remote, protected habitats argue for an important role for disease. Climate change can affect amphibian ecology and may indirectly operate with disease in population declines. Although habitat loss has undoubtedly affected *Atelopus* and accounts for the decline of a few species, it cannot explain widespread declines and extinctions in the genus.

*Atelopus* species are generally easy to detect and census, and may reflect the population status of other co-occuring anurans that are harder to census because of their habits, activity patterns, or low abundance. Indeed, equally dramatic losses of other amphibians that co-occur with *Atelopus* species have been reported from some well-studied localities (Pounds et al. 1997; Lips 1998, 1999; Lips et al. 2003b). Because amphibians represent a significant pool of available prey in tropical ecosystems, declines in their abundance should negatively affect predator populations, such as the diverse guild of tropical frog-eating snakes and birds (Cadle & Greene 1993, Pounds et al. 1999, Poulin et al. 2001). Similarly, adult amphibians regulate insect populations while larvae determine standing stock of primary producers in many aquatic habitats. These population changes are expected to cascade through aquatic and terrestrial food webs, with often unexpected consequences (Kupferberg 1997, Flecker et al. 1999, Ranvestel et al. 2004).

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**LITERATURE CITED**


Declines and Extinctions of Atelopus


Appendix. Summary data on Atelopus species. Abbreviations are as follows: Country abbreviations as in Table 1; Prot. Areas, presence in protected areas (Y = yes, N = no); Last record: year of most recent record; Bd: presence of the chytrid fungal disease Bd (year[s] documented); Hab. destr.: occurrence of significant habitat destruction/modification in range (Y = yes, N = no); Status: Stable, ≥ 1 population persisted through 1999 and no population has declined by > 50 percent; Decline: at least one population declined by ≥ 50 percent (asterisk indicates species that have disappeared and have no records since 1998 despite repeated searches); DD: data deficient (insufficient data to judge population status).

### Atelopus species

<table>
<thead>
<tr>
<th>Atelopus species</th>
<th>Country</th>
<th>Elevational range (m)</th>
<th>Prot. areas</th>
<th>Last record</th>
<th>Bd</th>
<th>Hab. destr.</th>
<th>Status</th>
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<td>2900–3000</td>
<td>Y</td>
<td>2000</td>
<td>—</td>
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<td>DD</td>
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<tr>
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<td>CO</td>
<td>3000–3500</td>
<td>Y</td>
<td>1991</td>
<td>—</td>
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<td>DD</td>
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<tr>
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<td>1988</td>
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<tr>
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<td>N</td>
<td>1995</td>
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### Appendix. Continued.

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<th>Last record</th>
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<th>Hab. destr.</th>
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*Decline indicates a significant decrease in population size or range, DD indicates data deficient.