

Catastrophic Population Declines and Extinctions in Neotropical Harlequin Frogs (*Bufo*: *Atelopus*)¹

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ABSTRACT

We surveyed the population status of the Neotropical toad genus *A*, 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 *B* 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 *A* 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 *A* 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

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rangos altitudinales de 1000 m o superiores han sufrido disminuciones poblacionales, el 75 por ciento de estas ha desaparecido del todo. El 58 por ciento de las especies de bajura han sufrido disminuciones, mientras que el 38 por ciento ha desaparecido del todo. La pérdida de hábitat, no fue relacionada con las disminuciones una vez que se controló el

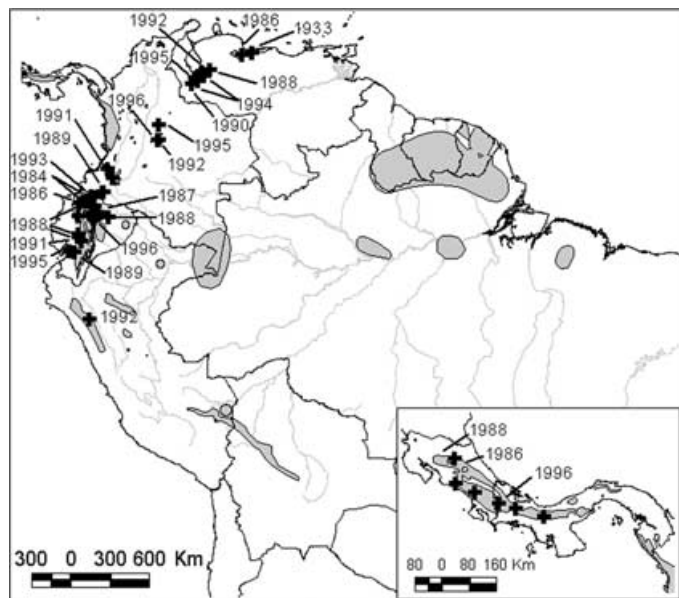


FIGURE 1. Range of the genus *A.*, with localities and dates of last records indicated for species that have disappeared. Range data compiled from IUCN (2004) and modified according to Lescure and Marty (2000) and R. Ibáñez (pers. comm.).

Many *A.* 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). *A.* 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.*, *A.*, *A.*, and *A.*, 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 & Reinthaler 1991, Pounds & Crump 1994, Lips 1998, Ron 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 *A.* population declines are available for a few species from a small number of sites (Pounds & Crump 1994, La Marca & Lötters 1997, Lips 1998, Ron 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 (*A.*, *A.*, and *A.*); 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 (*A.*, eastern Andean slopes), or unsafe (*A.*, 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 *declining* populations 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 *unknown* 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 *A.* 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 (*A.*, 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 *B* to declines, we compiled records of the disease in the entire genus. Because of the temperature sensitivity of *B*, 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 *B* 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 *A* on the presence of *B* infections (Berger 1998, Lips 2003a, Puschendorf 2003). One sample was of all *A* specimens housed in the herpetological collection of the Universidad de Costa Rica collected after 1978 (Puschendorf 2003). The second sample was of *A* and *A* collected in southeastern Costa Rica and western Panama in the late 1980s and late 1990s (Berger 1998, Lips 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 *A* 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 *A*. 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*, 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

TABLE 1. *Atelopus*

	Number of species (% of country total)		
	Declining	Stable	Data deficient
Costa Rica (CR)	4 (100)	0 (0)	0 (0)
Panama (PA)	3 (50)	3 (50)	0 (0)
Colombia (CO)	12 (27)	3 (7)	30 (67)
Ecuador (EC)	15 (58)	0 (0)	11 (42)
Peru (PE)	3 (11)	2 (7)	23 (82)
Bolivia (BO)	0 (0)	1 (100)	0 (0)
Venezuela (VE)	9 (90)	0 (0)	1 (10)
Suriname (SR)	0 (0)	1 (100)	0 (0)
Guyana (GU)	0 (0)	1 (100)	0 (0)
Brazil (BR)	0 (0)	2 (100)	0 (0)
French Guiana (FG)	1 (25)	3 (75)	0 (0)
Total for genus	42 (37)	10 (9)	61 (54)

populations of *A* species are known to persist only in Panama, Colombia, Peru, Brazil, and the Guyanas. 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 = 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 *A* 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* populations, *A* sp. 1, and *A*), 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 *A* 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* (Table 3).

Nevertheless, habitat loss was not a major factor associated with declines of *A* 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

TABLE 2. *C* 10 Atelopus 11 . *F* ()
E : , . *E. D*
 (.); , *B* (2002) . (2003); : (1991), *D* *A* (1995),
 (1997), (2004), . *E. G* *E* (.); *C* : , *C* (1994); , (1998,
 .) *C* 1.

Species	Locality (Country)	Relative abundance (first sample)	Relative abundance (second sample)	Date(s) of first sample	Date(s) of second sample
<i>A.</i>	Las Tablas (CR)	348 ind marked 800 m, 234 replicates	0 ind/pers/h 800 m, 36 replicates	1991–1993	1997, 1998, 2001
<i>A.</i>	Río Faisanes (EC)	0.03 ind/pers/h (32 h)	0 ind/pers/h (39 h)	1975	2001
<i>A.</i>	Páramo de Guamaní (EC)	23.5 ind/pers/h (2 h)	0 ind/pers/h (19 h)	1967	2000
<i>A.</i>	Páramo del Antisana (EC)	89–234 ind/400 m ² (2 replicates)	0 ind/400–1000 m ² (22 replicates)	1981	1999–2001
<i>A.</i>	Río Faisanes (EC)	0.25 ind/pers/h (32 h)	0 ind/pers/h (39 h)	1975	2001
<i>A.</i>	Quebrada Zapadores (EC)	3.2 ind/pers/h (40 h)	0 ind/pers/h (58 h)	1975	2000–2001
<i>A.</i>	La Corcovada (VE)	37 ind/pers/h (81 h)	0 ind/pers/hr (72 h)	1994–1995	1996–2004
<i>A.</i>	Río Azuela (EC)	0.125 ind/pers/h (72 h)	0 ind/pers/h (90.8 h)	1971	2000–2001
<i>A.</i>	Piñango (VE)	0.15 ind/pers/h (3 h)	0 ind/pers/hr (7 h)	1992	1998
<i>A.</i>	Río Lagarto headwaters (CR)	13–151 ind/200 m ² (45 replicates)	0 ind/200 m ² (68 replicates)	1982–1983	1990–2002

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 *B* was detected in 29 individuals of 14 species of *A*, including 9 of the 42 species in decline. These cases include populations from Costa Rica, Panama, Ecuador, Venezuela, and Peru (Fig. 2). *B* 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 *B* 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 from a *A.* collected in 1980 in Cañar Province, Ecuador. The first country records were from 1986 for Venezuela (Bonaccorso 2003) and Costa Rica (Puschendorf 2003), 1994 for Panama (Berger 1998), and 2002 for Peru (Schulte, pers. comm.).

A species have declined at all elevations, but species at higher elevations were more likely to decline than species in lower elevation habitats ($\chi^2 = 14.44$, $df = 1$, $P = 0.001$). In fact, all 28 species with sufficient data inhabiting higher elevations (those with minimum elevations above 1000 m) declined and 75 percent have disappeared. Of the 24 lowland species, 58 percent of species declined and 38 percent disappeared. We were unable to identify any apparently healthy populations at the highest elevations (i.e., above 2500 m). Most species with stable populations occurred in lowland habitats. At the highest elevations, in paramo and puna habitats, only two species, *A.* and *A.*, are known to have any remaining individuals in the wild, and both populations have been reduced to a handful of individuals (E. Toral, pers. comm.; Barrio-Amorós 2004).

Compiling *A* data from previous work in Costa Rica and western Panama revealed a total of 11 *B* 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 *A* 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 *A* 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 *A* 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 *A*. 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.* occurred within the city limits of Quito, Ecuador (Ron 2003). Only two disappearances are strongly linked to habitat loss. The only

TABLE 3. - 5- 137 24

Atelopus *E* : (1) .

10 ; (2) . 11

; (3) . 12

; (4) . 13 ; (5) . 19

C *I* .

<i>A</i> species	Natural vegetation	Fragmented	Agriculture and pastures
<i>D</i>	15.4	21.7	62.9
	51.6	3.3	45.1
	54.7	11.2	34.1
	18.4	26.3	55.3
	23.9	15.6	60.5
	53.6	1.8	44.6
	19.8	8.9	71.3
	47.9	4.1	48.0
	12.3	37.1	50.6
	89.9	0	10.1
	0	59.7	40.3
	92.0	1.1	6.9
	78.6	18.7	27.7
	53.5	34.5	12.0
sp. 19	45.5	6.6	47.9
<i>D</i>	57.2	18.3	24.5
	82.7	9.9	7.4
	64.0	0	36.0
	45.9	24.8	29.3
	99.1	0	0.9
sp. 10	99.5	0	0.5
sp. 11	15.1	84.8	0.1
sp. 12	94.7	5.3	0
sp. 13	31.3	13.2	55.5

known population of *A.* disappeared following habitat destruction of a humid seasonal forest near Maracay, Venezuela, and has not been seen since 1933 (Lötters . 2004). The type locality of *A.* was completely deforested by the mid-1980s and the last individuals were seen in 1992 (E. La Marca, pers. comm.).

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 *A.* species; additional species-specific efforts will be needed to effectively conserve the remaining species. Below, we discuss five possible additional causes of *A.* declines: disease, climate change, trade, introduced predators, and environmental contamination.

Infection by *B.* has been clearly linked with declining amphibian populations at numerous Latin America sites. Most species of *A.* have not been examined for the presence of *B.*, although most of those examined have been found to be infected.

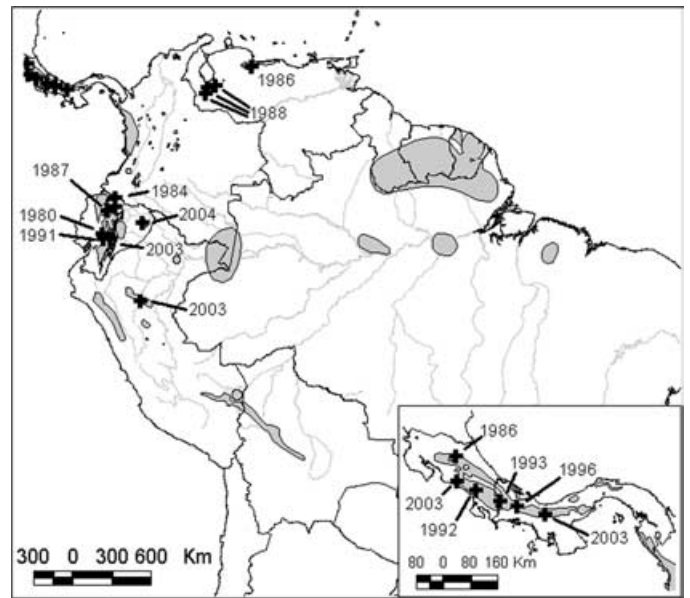


FIGURE 2. Known locations and dates of *B.* infections in *A.* superimposed on the range of the genus.

The first report of infection by *B.* was in an *A.* collected in 1980, in Ecuador, years before population declines were noticed (Ron . 2003). Our sample indicates that when detected, *B.* 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 *A.* (Table 4). The disease may occur widely and may only be virulent at cooler, higher elevation sites as laboratory studies of *B.* physiology suggest. The observation that *A.* 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 *B.* can cause mortality in most tested species of frogs (Berger . 1998, Daszak . 2003), although some amphibians may be resistant (. , Davidson . 2003). No species of *A.* has yet been tested, although dead individuals of several species had levels of infection thought to be lethal. These animals were hT64tha243.j(a)us(at)-284.pri1(or)-284.1o4tha24362(population)85.3(decli4

TABLE 5. *Atelopus* species, 1970–2002.

Species	Country of origin	Number of lots
Declining		
<i>A.</i>	Venezuela	1
<i>A.</i>	Venezuela	> 20
<i>A.</i>	Ecuador	> 20 (from different localities)
<i>A.</i>	Peru	< 15
<i>A.</i>	Peru	> 15
<i>A.</i>	Costa Rica, Panama	> 20
<i>A.</i>	Panama	5
Stable		
<i>A.</i>	French Guiana	> 20 (from different localities)
<i>A.</i>	Panama	1
<i>A.</i>	complex French Guiana, Suriname	< 10 (from different localities)
<i>A.</i>	Colombia	1
Data deficient		
<i>A.</i>	Peru	2

^ait includes the suggested junior synonym *A.*

(Lips 2003a, Ron 2003). The presence of *B.* in ten declining species of *A.* in five Central and South American countries is consistent with the hypothesis that this fungus is an important factor in population declines throughout much of the Neotropics.

Climate change has been correlated with amphibian population declines in some *A.* populations in Costa Rica, Ecuador, and Venezuela (Pounds 1999, Ron 2003, Pounds & Pushendorf 2004, E. La Marca, pers. comm.). Evidence from various systems has shown that global warming can cause diverse biotic changes (Walther 2002, Parmesan & Yohe 2003, Root 2003). Some data indicate an indirect effect of climate change on breeding activities and perhaps infectious disease (reviewed in Carey & Alexander 2003), but only further research will clarify what role climate change plays in declines of *A.* species.

Recent work with *B.* has increased our understanding of its relationship to the physical environment, but much remains to be learned. In laboratory experiments with *A.* and *D.*, *B.* grew best and was most lethal under cool (22°C), moist conditions (Woodhams 2003, Piotrowski 2004). Maintaining the Australian frog at 37°C for prolonged periods cleared them of infection (Woodhams 2003). Exposure to low humidity may also be beneficial, as an infection may not be lethal unless there is enough moisture for zoospores to survive and re-infect their host (R. A. Alford, pers. comm.). Mesocosm experiments with tadpoles of the Panamanian frog indicate that warmer temperatures decrease infection of *B.* (P. Murphy and K. Lips, pers. comm.). Together these results suggest that an amphibian may be able to avoid or survive infection by *B.* in particular microhabitats or by performing particular behaviors such as basking in the sun to raise their body temperatures.

Legal and illegal trading is suspected to have caused declines in some amphibian populations (Gorzula 1996). Hundreds of *A.* were collected in the 1960s for the pharmaceutical industry of Europe and

North America (Fuhrman 1986), and a number of species are popular in the pet trade (Schulte 1980, Heselhaus & Schmidt 1994; Table 5). Because individuals are generally difficult to maintain or reproduce in captivity (Mebs 1980, Haas 1995), and usually die shortly after being captured (Schulte 1980, Staniszewski 1995), all *A.* traded are probably wild-caught. Although several illegal shipments of *A.* have been confiscated at U.S. ports of entry (K. Zippel, pers. comm.), gauging the volume of this clandestine traffic is difficult. The pressure on some populations, however, could be important. La Marca and Reinhaller (1991) suggested overcollecting as a cause of declines in Venezuelan Andean *A.*, although the most striking example could be that of *A.*, which was collected by the thousands, year after year, in the 1970s in Costa Rica and exported to Germany (S. Lötters, pers. comm.). Evidence of overcollection in other countries is rare, although yearly collection of a few specimens of *A.* in Peru has apparently contributed to the decline of one population near Tarapoto (R. Schulte, pers. comm.). Nevertheless, there is no evidence that overcollecting has been so intense that it contributed to widespread extirpation of populations of any species. For example, populations of *A.* began to decline long after they were heavily collected.

Introduced predators such as trout (*Oncorhynchus mykiss*) and the American bullfrog (*Rana catesbeiana*) may also play a role. Some researchers have blamed declines in Venezuela and Ecuador on these species (La Marca & Reinhaller 1991, Ordoñez 1996, Ron 2003), although it is unclear whether these predators feed on *A.* (Hayes & Jennings 1986, Hanselmann 2004), or whether they might serve as disease vectors (Hanselmann 2004). In addition to direct effects, introduced predators can have indirect effects by affecting nutrient cycles and algae production (Schindler 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 *A.* 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, *A.* coexisted with trout for at least three decades before noticeable declines occurred (Ron 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 *A.* 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 2000, Lajmanovich 2003). Contamination from gold mining is suspected in the loss of a population of *A.*, near Cajamarca, Peru, in the last decade (R. Schulte, pers. comm.). Targeted research on the effects of contaminants on *A.* 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 *A.* 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 *A.* many years

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, *B* 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 *B* infection and the potential for evolved resistance. Examples include a population of *A*

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* 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 *A* 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 *B* in extant populations of lowland species of *A*, because the interaction among lowland frogs, the environment, and *B* 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 *A* that have declined for the presence of *B*.

CAPTIVE BREEDING.—Captive breeding programs have begun for *A* in Peru (D. Bernauer, pers. comm.), *A* sp. 13 from Ecuador, *A* and *A* from Panama (Zippel 2002), and *A* 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* and *A* (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, *B* and climate change, cannot be counteracted in wild populations. The only conservation tool available when either of these two factors is present is captive breeding programs.

CONCLUSIONS

Our findings point to *A* 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 *B* 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 *A* and accounts for the decline of a few species, it cannot explain widespread declines and extinctions in the genus.

A species are generally easy to detect and census, and may reflect the population status of other co-occurring 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 *A* species have been reported from some well-studied localities (Pounds . 1997; Lips 1998, 1999; Lips . 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 . 1999, Poulin . 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 . 1999, Ranvestel . 2004).

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Appendix. *Atelopus* *A*; *C*; *I*; *A*, (*=*, *=*); *Bd*: *B* (*H*); *D*: *D*; *DD*: (*>50*; *D*: *>50*; *DD*: *>50*).

<i>A</i>	species	Country	Elevational range (m)	Prot. areas	Last record	<i>B</i>	Hab. destr.	Status
		PE	1000–2000	Y	2001	—	N	Stable
		CO	2900–3000	Y	2000	—	N	DD
		CO	2000–3500	Y	1991	—	Y	DD
		EC	2200–3000	Y	1988	—	Y	Decline*

species. AbbreviatedhuriCO -710 1 T2.9(Y-7081. TD(L)-9 0 TD 0.0001 T);-96.48 Sstatus).

Appendix. C

A	species	Country	Elevational range (m)	Prot. areas	Last record	B	Hab. destr.	Status
		EC	800–2000	N	1984	—	Y	DD
		CO	1300–2000	Y	1973	—	Y	DD
		VE	2300–2600	Y	1995	1988	Y	Decline*
		CO	2350–4800	Y	1991	—	Y	DD
		PA	50–1150	Y	2003	—	N	Stable
		CR, PA	1400–2100	Y	1996	1993, 1994	Y	Decline*
		CO	1900–2200	Y	1998	—	Y	DD
		VE	2200	N	1988	—	Y	Decline*
		EC	600–1380	Y	1984	—	Y	Decline*
		VE	30–2200	Y	2004	1986	Y	Decline
		PE	1650–1800	N	1980	—	N	DD
		CO	2500–4700	Y	1992	—	Y	DD
		CO	2600–3650	N	1995	—	Y	Decline*
		EC	300–1140	Y	1994	—	Y	Decline*
		PE	1800–2500	N	1903	—	N	DD
		CO	2820–3250	Y	2004	—	Y	Decline
		EC	3150–3850	Y	2004	—	Y	Decline
		CO	1300–1580	Y	1993	—	Y	DD
		CO	2090	N	1992	—	Y	Decline*
		FG, BR	0–300	Y	2000	—	Y	Stable
		FG	5–200	Y	2000	—	Y	Stable
		CO	1500	Y	?	—	N	DD
		CO, PA	884–1500	Y	2002	—	N	Stable
		CO	70–90	Y	2002	—	N	Stable
		EC	2600–2923	N	1988	—	Y	Decline*
		CO	3400	Y	1990	—	Y	DD
		EC	1975	N	1984	—	Y	DD
		EC	2800–4200	Y	1988	—	Y	Decline*
		CO	1900–2880	Y	1992	—	Y	DD
		PA	10–730	Y	2002	—	Y	Stable
		CO	800	Y	?	—	N	DD
		CO, EC	200–2500	Y	1989	—	Y	Decline*
		CO	3000–3300	Y	1993	—	Y	Decline*
		EC, CO	800–1410	Y	1984	—	Y	Decline*
		CO	2900–3350	Y	1992	—	N	DD
		EC	700–2200	Y	1989	—	Y	Decline*
		CO	1370–1560	N	1985	—	Y	DD
		CO	1700–2000	Y	1982	—	N	DD
		VE	2300–3500	Y	2004	1988	Y	Decline
		CO	2900–3350	Y	1994	—	Y	Decline*
		CO	1900–2800	Y	1992	—	Y	DD
		EC	4000	Y	1989	—	Y	Decline*
		EC	2000–3450	N	1985	—	Y	DD
		CO	1800–2670	N	?	—	Y	DD
		VE	2100–3350	Y	1994	—	Y	Decline*
		EC	2755–3300	Y	1996	—	Y	Decline*
		EC	1000	N	1937	—	N	DD
		CO	2600–3100	N	1950	—	Y	DD
		PE	2800–4200	Y	1992	—	Y	Decline*
		CO	1750–2500	Y	1998	—	Y	DD
		CO	2600	Y	1996	—	N	Decline*
		VE	2300–2920	N	1992	—	Y	Decline*
		EC	1000–2000	Y	1987	—	Y	Decline*
		PE	600–900	Y	2004	2003	N	Decline

Appendix. C

A	species	Country	Elevational range (m)	Prot. areas	Last record	B	Hab. destr.	Status
		CO	2200–2900	Y	1992	—	N	Decline*
		PE	1600	N	?	—	Y	DD
		CO	450	N	1988	—	Y	DD
		PE	1000–2000	Y	2004	—	N	DD
		CR	1100–2200	Y	1986	—	N	Decline*
		CO	2800–3100	N	2000	—	N	Decline
		CO	2500–3000	Y	2001	—	Y	Decline
		PE	2400	Y	1988	—	N	DD
		CO	1500	N	1996	—	Y	DD
		VE	2400	N	1990	1988	Y	Decline*
		CO, EC, PE	<300	Y	2004	2004	N	DD
		FG	10–300	N	2003	—	N	Decline
		PE, BR, FG, SR, GU	0–600	Y	2002	—	N	Stable
		CO	50–500	Y	2001	—	Y	Stable
		CO	2000–2800	N	1993	—	Y	DD
		VE	2950	Y	1987	—	N	DD
		PE, BO	600–2500	Y	2003	—	Y	Stable
		CR, PA	16–2000	Y	2003	1986, 90, 92, 97	Y	Decline
		VE	600	N	1933	—	Y	Decline*
		CO	1500–2900	N	1992	—	Y	DD
		PA	335–1315	Y	2004	—	Y	Decline
sp. 1		CR	700–1700	Y	1988	—	N	Decline*
sp. 2		CO	2100	N	1990	—	Y	DD
sp. 3		CO	2200–3720	Y	1989	—	Y	Decline*
sp. 4		CO	800–1410	Y	1981	—	Y	DD
sp. 5		CO	1700	N	1994	—	N	DD
sp. 6		CO	2090	N	1992	—	N	DD
sp. 7		CO	<1000	N	?	—	N	DD
sp. 8		CO	2400–2600	Y	2004	—	N	DD
sp. 9		CO, EC	2900–3900	Y	1993	1992, 1993	Y	Decline*
sp. 10		EC	2800	N	1994	—	Y	DD
sp. 11		EC	3300	N	1987	1987	N	DD
sp. 12		EC	220	N	1996	—	Y	DD
sp. 13		EC, PE	700–1700	Y	2004	2003	N	DD
sp. 14		EC	1100–1400	N	1990	—	Y	DD
sp. 15		EC	2000–2200	N	?	—	Y	DD
sp. 16		PE	?	N	1987	—	N	DD
sp. 17		PE	?	N	1993	—	Y	DD
sp. 18		PE	1400	N	2003	—	N	DD
sp. 19		PE	1400	N	2003	—	N	DD
sp. 20		PE	2010	N	1989	—	Y	DD
sp. 21		PE	1500–2000	N	1993	—	N	DD
sp. 22		PE	1700–2000	N	1989	—	N	DD
sp. 23		PE	3000	N	2003	—	N	DD
sp. 24		PE	<1500	N	1984	—	N	DD
sp. 25		PE	3000–4300	N	?	—	N	DD
sp. 26		PE	250–800	N	?	—	N	DD
sp. 27		PE	>1500	N	?	—	N	DD
sp. 28		PE	200–500	N	1998	—	N	DD
sp. 29		PE	1700–2000	N	1982	—	N	DD
sp. 30		PE	1500	N	2003	—	N	DD
sp. 31		PE	?	N	2004	—	N	DD
sp. 32		VE	2400	Y	2004	—	Y	Decline