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Catastrophic Population Declines and Extinctions in Neotropical Harlequin Frogs (Bufonidae: *Atelopus*)[1]

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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

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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 efecto de altura en los análisis. De hecho, unas 22 especies que tienen poblaciones dentro de áreas protegidas han desaparecido. El hongo quítrido *Batrachochytrium dendrobatidis* estuvo presente en nueve especies que han experimentado disminuciones y puede explicar desapariciones en especies que ocupan hábitats no perturbados a mayores elevaciones. El cambio climático puede jugar un papel, pero es improbable que otros factores como la contaminación ambiental, el comercio ilegal, así como las especies introducidas, tengan un efecto en más que unas pocas especies. Las disminuciones a gran escala y las extinciones en *Atelopus* pueden reflejar disminuciones en otros anfibios neotropicales que son más difíciles de estudiar, y la pérdida de este grupo trófico puede traer efectos en cascada para otras especies de ecosistemas tropicales.

Key words: amphibians; Atelopus*; climate change; declines; disease; extinction; Neotropics, population; trade.*

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 (Heyer *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 multitaxa 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.).

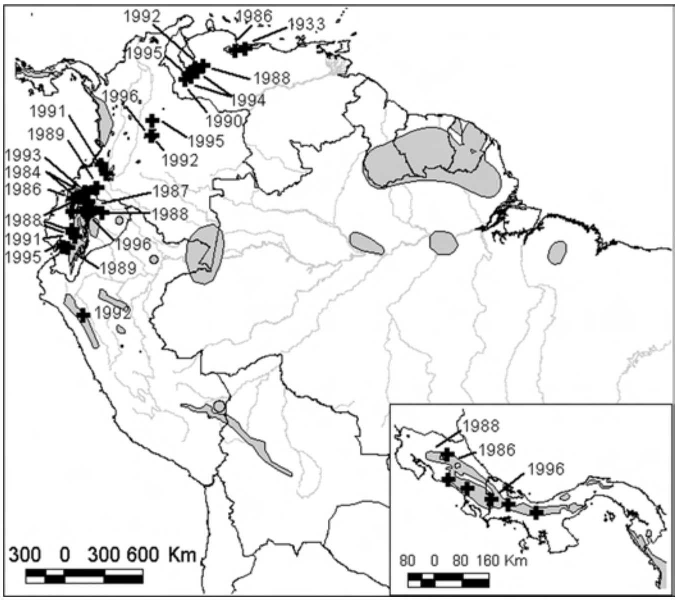

FIGURE 1. Range of the genus *Atelopus*, with localities and dates of last records indicated for species that have disappeared. Range data compiled from IUCN *et al.* (2004) and modified according to Lescure and Marty (2000) and R. Ibáñez (pers. comm.).

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 & Reinthaler 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 Guyanas. The number of data-deficient species is highest for Colombia (30), followed by Peru (23) and Ecuador (11).

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

	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)

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

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 Reinthaler (1991), Durant and Arellano (1995), La Marca and Lötters (1997), Manzanilla and La Marca (2004), J. E. García 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.*

Species	Locality (Country)	Relative abundance (first sample)	Relative abundance (second sample)	Date(s) of first sample	Date(s) of second sample
A. chiriquiensis	Las Tablas (CR)	348 ind marked 800 m, 234 replicates	0 ind/pers/h 800 m, 36 replicates	1991–1993	1997, 1998, 2001
A. coynei	Río Faisanes (EC)	0.03 ind/pers/h (32 h)	0 ind/pers/h (39 h)	1975	2001
A. ignescens	Páramo de Guamaní (EC)	23.5 ind/pers/h (2 h)	0 ind/pers/h (19 h)	1967	2000
A. ignescens	Páramo del Antisana (EC)	89–234 ind/400 m^2 (2 replicates)	0 ind/400–1000 m^2 (22 replicates)	1981	1999–2001
A. longirostris	Río Faisanes (EC)	0.25 ind/pers/h (32 h)	0 ind/pers/h (39 h)	1975	2001
A. mindoensis	Quebrada Zapadores (EC)	3.2 ind/pers/h (40 h)	0 ind/pers/h (58 h)	1975	2000–2001
A. mucubajiensis	La Corcovada (VE)	37 ind/pers/h (81 h)	0 ind/pers/hr (72 h)	1994–1995	1996–2004
A. planispina	Río Azuela (EC)	0.125 ind/pers/h (72 h)	0 ind/pers/h (90.8 h)	1971	2000–2001
A. pinangoi	Piñango (VE)	0.15 ind/pers/h (3 h)	0 ind/pers/hr (7 h)	1992	1998
A. varius	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 *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 from a *A. bomolochus* collected in 1980 in Cañar Province, Ecuador. The first country records were from 1986 for Venezuela (Bonaccorso *et al.* 2003) and Costa Rica (Puschendorf 2003), 1994 for Panama (Berger *et al.* 1998), and 2002 for Peru (Schulte, pers. comm.).

Atelopus 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. exiguus and A. mucubajiensis*, 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 *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.*

Atelopus species	Natural vegetation	Fragmented	Agriculture and pastures
Declining			
arthuri	15.4	21.7	62.9
balios	51.6	3.3	45.1
bomolochos	54.7	11.2	34.1
coynei	18.4	26.3	55.3
elegans	23.9	15.6	60.5
exiguus	53.6	1.8	44.6
guanujo	19.8	8.9	71.3
ignesens	47.9	4.1	48.0
longirostris	12.3	37.1	50.6
lynchi	89.9	0	10.1
mindoensis	0	59.7	40.3
nanay	92.0	1.1	6.9
pachydermus	78.6	18.7	27.7
planispina	53.5	34.5	12.0
sp. 19	45.5	6.6	47.9
Data deficient			
boulengeri	57.2	18.3	24.5
halihelos	82.7	9.9	7.4
nepiozomus	64.0	0	36.0
palmatus	45.9	24.8	29.3
spumarius spumarius	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. vogli* disappeared following habitat destruction of a humid seasonal forest near Maracay, Venezuela, and has not been seen since 1933 (Lötters *et al.* 2004). The type locality of *A. pinangoi* 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 *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.

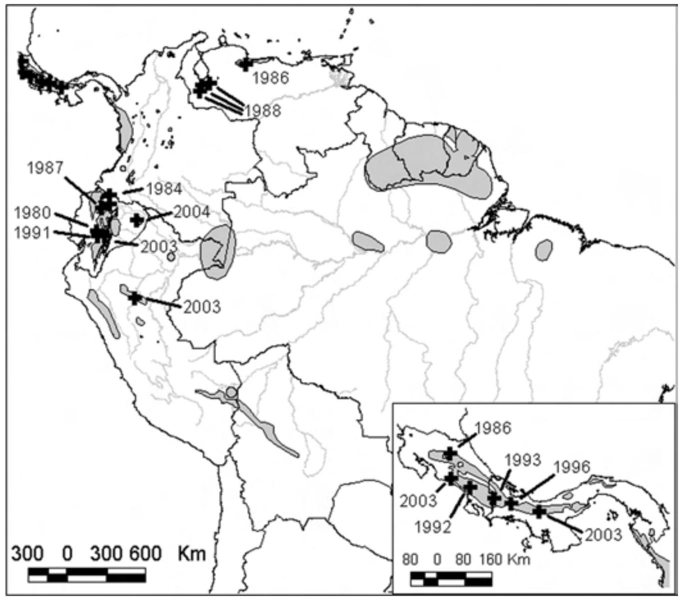

FIGURE 2. Known locations and dates of *Bd* infections in *Atelopus* superimposed on the range of the genus.

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

TABLE 4. *Occurrence of Bd among elevations in Costa Rican species of* Atelopus.

Elevational range (m)	Number of specimens: Negative	Positive	Total
0–500	1	0	1
500–1000	19	2	21
1000–1500	13	3	16
1500–2000	32	2	34
2000–2500	18	4	22
Total	83	11	95

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.*

Species	Country of origin	Number of lots
Declining		
A. carbonerensis	Venezuela	1
A. cruciger	Venezuela	> 20
A. ignescens	Ecuador	> 20 (from different localities)
A. peruensis	Peru	< 15
A. pulcher	Peru	> 15
A. varius	Costa Rica, Panama	> 20
A. zeteki	Panama	5
Stable		
A. flavescens[a]	French Guiana	> 20 (from different localities)
A. glyphus	Panama	1
A. spumarius complex	French Guiana, Suriname	< 10 (from different localities)
A. spurrelli	Colombia	1
Data deficient		
A. reticulatus	Peru	2

[a]it includes the suggested junior synonym *Atelopus spumarius barbotini.*

(*e.g.,* Lips *et al.* 2003a, Ron *et al.* 2003). The presence of *Bd* in ten declining species of *Atelopus* 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 *Atelopus* populations in Costa Rica, Ecuador, and Venezuela (Pounds *et al.* 1999, Ron *et al.* 2003, Pounds & Pushendorf 2004, E. La Marca, pers. comm.). Evidence from various systems has shown that global warming can cause diverse biotic changes (*e.g.,* Walther *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 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 *Atelopus* species.

Recent work with *Bd* has increased our understanding of its relationship to the physical environment, but much remains to be learned. In laboratory experiments with *Litoria chloris* and *Dendrobates tinctorius*, *Bd* grew best and was most lethal under cool (22°C), moist conditions (Woodhams *et al.* 2003, Piotrowski *et al.* 2004). Maintaining the Australian frog *Litoria chloris* at 37°C for prolonged periods cleared them of infection (Woodhams *et al.* 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 *Smilisca phaeota* indicate that warmer temperatures decrease infection of *Bd* (P. Murphy and K. Lips, pers. comm.). Together these results suggest that an amphibian may be able to avoid or survive infection by *Bd* 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 (*e.g.*, Gorzula 1996). Hundreds of *A. zeteki* 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 *Atelopus* traded are probably wild-caught. Although several illegal shipments of *A. zeteki* 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 Reinthaler (1991) suggested overcollecting as a cause of declines in Venezuelan Andean *Atelopus*, although the most striking example could be that of *A. varius,* 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. pulcher* 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. varius* began to decline long after they were heavily collected.

Introduced predators such as trout (*e.g.*, *Onchorhynchus* and *Salmo)* 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 & Reinthaler 1991, Ordoñez 1996, Ron *et al.* 2003), although it is unclear whether these predators feed on *Atelopus* (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. peruensis,* 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 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. mucubajiensis* 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 spumarius 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-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 *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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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	Country	Elevational range (m)	Prot. areas	Last record	*Bd*	Hab. destr.	Status
andinus	PE	1000–2000	Y	2001	—	N	Stable
angelito	CO	2900–3000	Y	2000	—	N	DD
arsyecue	CO	2000–3500	Y	1991	—	Y	DD
arthuri	EC	2200–3000	Y	1988	—	Y	Decline*
balios	EC	200–460	N	1995	—	Y	Decline*
bomolochos	EC	2500–2800	Y	2002	1980, 1991	Y	Decline

Appendix. *Continued.*

Atelopus species	Country	Elevational range (m)	Prot. areas	Last record	*Bd*	Hab. destr.	Status
boulengeri	EC	800–2000	N	1984	—	Y	DD
carauta	CO	1300–2000	Y	1973	—	Y	DD
carbonerensis	VE	2300–2600	Y	1995	1988	Y	Decline*
carrikeri	CO	2350–4800	Y	1991	—	Y	DD
certus	PA	50–1150	Y	2003	—	N	Stable
chiriquiensis	CR, PA	1400–2100	Y	1996	1993, 1994	Y	Decline*
chocoensis	CO	1900–2200	Y	1998	—	Y	DD
chrysocorallus	VE	2200	N	1988	—	Y	Decline*
coynei	EC	600–1380	Y	1984	—	Y	Decline*
cruciger	VE	30–2200	Y	2004	1986	Y	Decline
dimorphus	PE	1650–1800	N	1980	—	N	DD
ebenoides ebenoides	CO	2500–4700	Y	1992	—	Y	DD
ebenoides marinkellei	CO	2600–3650	N	1995	—	Y	Decline*
elegans	EC	300–1140	Y	1994	—	Y	Decline*
erythropus	PE	1800–2500	N	1903	—	N	DD
eusebianus	CO	2820–3250	Y	2004	—	Y	Decline
exiguus	EC	3150–3850	Y	2004	—	Y	Decline
famelicus	CO	1300–1580	Y	1993	—	Y	DD
farci	CO	2090	N	1992	—	Y	Decline*
flavescens	FG, BR	0–300	Y	2000	—	Y	Stable
franciscus	FG	5–200	Y	2000	—	Y	Stable
galactogaster	CO	1500	Y	?	—	N	DD
glyphus	CO, PA	884–1500	Y	2002	—	N	Stable
gracilis	CO	70–90	Y	2002	—	N	Stable
guanujo	EC	2600–2923	N	1988	—	Y	Decline*
guitarraensis	CO	3400	Y	1990	—	Y	DD
halihelos	EC	1975	N	1984	—	Y	DD
ignescens	EC	2800–4200	Y	1988	—	Y	Decline*
laetissimus	CO	1900–2880	Y	1992	—	Y	DD
limosus	PA	10–730	Y	2002	—	Y	Stable
longibrachius	CO	800	Y	?	—	N	DD
longirostris	CO, EC	200–2500	Y	1989	—	Y	Decline*
lozanoi	CO	3000–3300	Y	1993	—	Y	Decline*
lynchi	EC, CO	800–1410	Y	1984	—	Y	Decline*
mandingues	CO	2900–3350	Y	1992	—	N	DD
mindoensis	EC	700–2200	Y	1989	—	Y	Decline*
minutulus	CO	1370–1560	N	1985	—	Y	DD
mono-hernandezi	CO	1700–2000	Y	1982	—	N	DD
mucubajiensis	VE	2300–3500	Y	2004	1988	Y	Decline
muisca	CO	2900–3350	Y	1994	—	Y	Decline*
nahumae	CO	1900–2800	Y	1992	—	Y	DD
nanay	EC	4000	Y	1989	—	Y	Decline*
nepiozomus	EC	2000–3450	N	1985	—	Y	DD
nicefori	CO	1800–2670	N	?	—	Y	DD
oxyrhynchus	VE	2100–3350	Y	1994	—	Y	Decline*
pachydermus	EC	2755–3300	Y	1996	—	Y	Decline*
palmatus	EC	1000	N	1937	—	N	DD
pedimarmoratus	CO	2600–3100	N	1950	—	Y	DD
peruensis	PE	2800–4200	Y	1992	—	Y	Decline*
petriruizi	CO	1750–2500	Y	1998	—	Y	DD
pictiventris	CO	2600	Y	1996	—	N	Decline*
pinangoi	VE	2300–2920	N	1992	—	Y	Decline*
planispina	EC	1000–2000	Y	1987	—	Y	Decline*
pulcher	PE	600–900	Y	2004	2003	N	Decline

Appendix. *Continued.*

Atelopus species	Country	Elevational range (m)	Prot. areas	Last record	*Bd*	Hab. destr.	Status
quimbaya	CO	2200–2900	Y	1992	—	N	Decline*
reticulatus	PE	1600	N	?	—	Y	DD
sanjosei	CO	450	N	1988	—	Y	DD
seminiferus	PE	1000–2000	Y	2004	—	N	DD
senex	CR	1100–2200	Y	1986	—	N	Decline*
sernai	CO	2800–3100	N	2000	—	N	Decline
simulatus	CO	2500–3000	Y	2001	—	Y	Decline
siranus	PE	2400	Y	1988	—	N	DD
sonsonensis	CO	1500	N	1996	—	Y	DD
sorianoi	VE	2400	N	1990	1988	Y	Decline*
spumarius spumarius	CO, EC, PE	<300	Y	2004	2004	N	DD
spumarius barbotini	FG	10–300	N	2003	—	N	Decline
spumarius hoogmoedi	PE, BR, FG, SR, GU	0–600	Y	2002	—	N	Stable
spurrelli	CO	50–500	Y	2001	—	Y	Stable
subornatus	CO	2000–2800	N	1993	—	Y	DD
tamaense	VE	2950	Y	1987	—	N	DD
tricolor	PE, BO	600–2500	Y	2003	—	Y	Stable
varius	CR, PA	16–2000	Y	2003	1986, 90, 92, 97	Y	Decline
vogli	VE	600	N	1933	—	Y	Decline*
walkeri	CO	1500–2900	N	1992	—	Y	DD
zeteki	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