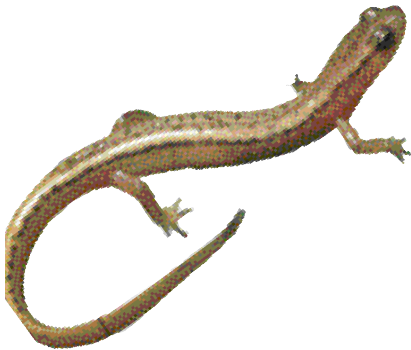




Disappearing Jewels

The Status
of New World Amphibians



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Citation:

Young, B. E., S. N. Stuart, J. S. Chanson, N. A. Cox, and T. M. Boucher.
2004. *Disappearing Jewels: The Status of New World Amphibians*.
NatureServe, Arlington, Virginia.

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ISBN 0-9711053-1-6

Primary funding for the publication of this report was provided by BP.



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The Status of New World Amphibians

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This page: *Hyalinobatrachium valerioi* (a glass frog). *Least Concern*. Costa Rica, Panama, Ecuador, and Colombia. / Photo by Piotr Naskrecki.

Front Cover

Top: *Agalychnis saltator* (a leaf frog). *Least Concern*. Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador. / Photo by Piotr Naskrecki.

Top right: *Atelopus zeteki* (a harlequin frog). *Critically Endangered*. Panama. / Photo by Forrest Brem.

Bottom left: Northern two-lined salamander (*Eurycea bislineata*). *Least Concern*. Canada and United States. / Photo by Geoff Hammerson.

Bottom right: *Phyllomedusa lemur* (a tree frog). *Endangered*. Costa Rica, Panama, and Colombia. / Photo by Forrest Brem.

Back Cover

Top: *Eleutherodactylus diastema* (a tropical rain frog). *Least Concern*. Honduras, Nicaragua, Costa Rica, Panama, and Colombia. / Photo by Piotr Naskrecki.

Bottom left: *Atelopus zeteki* (a harlequin frog). *Critically Endangered*. Panama. / Photo by Forrest Brem.

Right: *Agalychnis saltator* (a leaf frog). *Near Threatened*. Honduras, Nicaragua, Costa Rica. / Photo by Piotr Naskrecki.

Acknowledgments

We first and foremost thank the 229 scientists who contributed their time, expertise, and in many cases unpublished data to the assessments that form the basis of the Global Amphibian Assessment, of which this report presents the main findings for the New World. They are the individuals who deserve the credit for the integrity of the database. Although there are too many to mention here, all are listed in Appendix 1. We must name, however, the 23 scientists who made the extraordinary effort to fill out a draft version of the database in advance of workshop review. These included Geoffrey A. Hammerson (United States and Canada), S. Blair Hedges (Caribbean islands), Georgina Santos-Barrera (Mexico), Gustavo Cruz (Honduras), Federico Bolaños (Costa Rica), Frank Solís (Panama), Wilmar Bolívar (Colombia), Fernando Castro (Colombia), Santiago Ron (Ecuador), Luis Coloma (Ecuador), Enrique La Marca (Venezuela), Robert Reynolds (the Guianas), Débora Silvano (Brazil), Claudia Azevedo-Ramos (Brazil), Javier Icochea (Peru), Lily Rodríguez (Peru), Ariadne Angulo (Peru), Claudia Cortez (Bolivia), Esteban Lavilla (Argentina), Carmen Úbeda (Argentina), Lucy Aquino (Paraguay), Norm Scott (Paraguay), and Alberto Veloso (Chile).

Primary funding for the publication of *Disappearing Jewels* was provided by generous grants from BP and the Moriah Fund. Major support to NatureServe for its work on the New World portion of the Global Amphibian Assessment was provided by Ben and Ruth Hammett, the Regina Bauer Frankenberg Foundation for Animal Welfare, and the National Science Foundation (via grants DEB-0130273 and INT-0322375).*

The Global Amphibian Assessment (GAA) itself would not have been possible without generous financial support from a number of institutions. In particular, we thank the Moore Family Foundation and the Gordon and Betty Moore Foundation, whose extraordinary generosity through their gifts to Conservation International provided the core financial support for the Global Amphibian Assessment.

Additional major support for the New World portion of the GAA was provided by the MAVA Foundation and the U.S. State Department (to IUCN**) and by the Critical Ecosystem Partnership Fund (to Conservation International). Thanks also to those who supported the GAA in other regions, including the Chicago Zoological Society, the Columbus Zoo, the Disney Foundation, the Kadoorie Farm and Botanic Garden, George Meyer, the Society for Wildlife and Nature, the Taipei Zoological Foundation, and WWF-Australia.

Darrel Frost of the American Museum of Natural History provided a guiding hand on taxonomic and distributional information. We are deeply in debt to his service to the herpetological community for keeping us all abreast of a fast-changing field. We also thank David B. Wake for providing initial national occurrence records from the AmphibiaWeb database.

The majority of the distribution maps used for United States species were adapted from distribution data and maps assembled at Ball State University by Priya Nanjappa, M.S., Laura M. Blackburn, M.S., and Michael J. Lannoo, Ph.D. Development of the United States Amphibian Atlas Database was supported in part by grants and/or matching funds to Ball State University from the National Fish and Wildlife Foundation, the U.S. Fish and Wildlife Service, and the Disney Wildlife Conservation Fund.

The following people provided local logistical support for the GAA workshops: Enrique Lahmann and Ana Virginia Mata (Costa Rica), Adriano Paglia, Jose Maria Cardoso da Silva and Luis Paulo de Souza Pinto (Brazil), Paul and Sara Salaman (Ecuador), Esteban Lavilla and Néstor Basso (Argentina), Juan Carlos Ortiz (Chile), David Gower and Mark Wilkinson (UK), and Sixto Inchaustegui (Dominican Republic). We also thank Matt Foster, Mike Hoffmann, Penny Langhammer and Don Church for facilitating working groups during GAA workshops.

Many members of RANA (the Research and Analysis Network for Neotropical Amphibians) contributed to the development of *Disappearing Jewels*. In particular, we thank our colleagues whose names are listed on the boxed text for their contribution and careful review. They kept us focused and accurate in portraying this information. We are especially grateful to James Collins, Geoffrey Hammerson, Rafael Joglar, and Robert Puschendorf, whose comments substantially improved earlier drafts of the manuscript. Paul Robie also provided helpful review. Rob Riordan of NatureServe provided much-needed oversight in every possible way during the production and editing of this report. Clara Klimovsky and Esteban Lavilla provided a top-quality Spanish translation, and Marti Betz is responsible for the beautiful layout. Finally, thanks to the many photographers who allowed us to reproduce their images of the world's disappearing jewels.

*Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

**The designation of geographical entities in this book, and the presentation of the material, do not imply the expression of any opinion whatsoever on the part of IUCN concerning the legal status of any country, territory, or area, or of its authorities, or concerning the delimitation of its frontiers or boundaries. The views expressed in this publication do not necessarily reflect those of IUCN.

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Above: *Hyla ebraccata* (*a tree frog*). *Least Concern*. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Ecuador, and Colombia. /Photo by Piotr Naskrecki.

Executive Summary

In recent years scientists and conservationists have raised the alarm that amphibians are disappearing before our very eyes. Even in seemingly pristine habitats, more and more of these dazzling denizens of our forests, deserts, streams, and wetlands have gone missing. But reports so far have been limited in geographic and taxonomic scope. Are these declines widespread or are they limited to a few localized areas? Are amphibians suffering from the general biodiversity crisis in the same manner as other well-publicized groups such as birds or mammals, or is something fundamentally different happening to amphibians?

This report on the New World findings of the Global Amphibian Assessment (GAA) addresses these questions by providing a comprehensive analysis of the conservation status of all the amphibians of North, Central, and South America and the Caribbean. We focus on the New World because of the continuity of land masses and evolutionary relatedness of the species found there. For each species, we compiled information about taxonomy, distribution, abundance and population trend, natural history, threats, and conservation measures. These data formed the basis for applying the IUCN Red List criteria to categorize species based on their conservation status. Overall, 229 scientists contributed to the database that forms the basis of this report.

MAJOR FINDINGS

- The New World is home to more than half of the world's 5,743 known species of amphibians (frogs, toads, salamanders, and caecilians). Its 3,046 species represent 53% of the world total.
- Brazil and Colombia have the greatest diversity of amphibians in the world, with 731 and 698 species respectively. The top five countries for amphibians (including Ecuador, Peru and Mexico) are all in the New World, and Venezuela and the United States are also in the top 10. At the low end of the diversity scale, a number of Caribbean island nations have just one native amphibian species each.
- Nearly two out of five New World amphibians (1,187 species, or 39%) are threatened with extinction, including 337 species that are classified as Critically Endangered—on the brink of extinction. Nine species have gone extinct in the past 100 years. Another 117 species are “possibly extinct,” meaning that scientists are unaware of any extant population but have not performed the extensive searching required to place these species in the Extinct category. Many of these declines are recent: since approximately 1980, four species have gone extinct, and 109 additional species possibly have become extinct.
- From a regional perspective, amphibians in the Caribbean are most threatened (84% of the region's 171 species), followed by Mesoamerica (Mexico through Panama) with 52% of its 685 species, South America (31% of its 2,065 species), and North America (21% of its 262 species). The global average is 32.5%.
- With 39% of the species threatened, the risk facing New World amphibians is considerably higher than for either birds (10%) or mammals (16%) in the same region.





- While threatened amphibians occur nearly everywhere, they are concentrated in several places: Haiti; montane southeastern Chiapas, Mexico through central Guatemala; montane Costa Rica and western Panama; the Andes of Colombia and Ecuador; and the central portion of the Atlantic Forest in eastern Brazil.
- Amphibians occurring at high elevations, having restricted distributions, and characterized by terrestrial life cycles (rather than those using a mix of aquatic and terrestrial habitats) are more likely to be threatened than are species with other characteristics.
- Two major and several minor threats face amphibians. *Habitat loss* causes a gradual contracting and fragmentation of populations and is by far the most prevalent threat, affecting 89% of all threatened species. Habitat loss is primarily caused by expanding agriculture, logging, and infrastructure development (for example, industrialization, road building, and housing developments). A second factor, a recently discovered chytrid fungal *disease*, has caused or is suspected to have caused precipitous declines in many species, including nearly half (47%) of all Critically Endangered and one-quarter of all threatened species. Other important threats include *environmental contaminants* (26% of species) and intrinsic factors such as *restricted range size* (23%). *Climate change* has already begun to affect some species; a separate analysis predicts that it will become a major threat to amphibians during the 21st century.
- The Western Hemisphere's existing system of public and private parks and reserves provides no protection for more than one-third (37%) of threatened amphibians, emphasizing the incomplete nature of the protected area system. Even for species that are found in protected areas, management is often not effective at stemming habitat loss. Moreover, threats like climate change or disease transcend park and reserve boundaries.



RECOMMENDATIONS:

1. *Protected Areas:* Strengthen management and protection at existing reserves, and expand protected areas to cover the ranges of threatened species that are currently unprotected.
2. *Public Policy:* Revise and keep updated existing national and subnational lists of threatened species, and strengthen legislation protecting listed species.
3. *Captive Breeding:* Implement captive breeding for species that face a high probability of extinction in the wild, especially those threatened by the chytrid disease.
4. *Education:* Educate the public, including schoolchildren, about the plight of amphibians, especially species of local concern.
5. *Research:* Accelerate research on the biology of the chytrid disease with an aim toward being able to control it in the wild. Expand population monitoring and increase research on poorly known species and the effects of contaminants on amphibians.

This report leaves no doubt that amphibians are the most threatened animal group in the New World so far examined using IUCN Red List criteria. Extinctions are happening now. They will continue unless policy makers, conservationists, land managers, and the public take urgent, directed conservation action to save these disappearing jewels.

Facing page: *Agalychnis saltator* (a leaf frog). *Least Concern.* Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador. / Photo by Piotr Naskrecki.

This page, top: *Spotted salamander* (*Ambystoma maculatum*). *Least Concern.* United States and Canada. / Photo by Geoff Hammerson.

This page, bottom: *Bullfrog* (*Rana catesbeiana*). *Least Concern.* Native to Canada, United States, and Mexico. / Photo by Geoff Hammerson.

FIGURE 1

REGIONAL OVERVIEW MAP OF THE NEW WORLD



Introduction



Amphibians occupy an enigmatic position in the public consciousness, even among the environmentally aware. While we know that frogs, toads, and salamanders are all around us, we rarely see them. In contrast, birds regale us with their song even in the most urban of settings. Mammals live with us as household pets and companions. Even fish may brighten our aquariums or serve as the quarry of a weekend fishing expedition. Yet we simply do not encounter amphibians in our everyday lives as we do other animals. Amphibians rarely enter human habitations, with the notable exception of bathrooms in a certain class of tropical seaside hotels. Amphibians prefer bogs and swamps whereas humans, when they are outside, prefer sidewalks and dry trails. When it rains, people scurry for cover just as amphibians come out into the open. While many male frogs and toads fill the night air with their chirping, croaking, trilling, or bellowing love calls, most people are asleep. Although frogs are common in a few places, for most of us our impressions of amphibians are heavily influenced by cultural interpretations such as Kermit the Frog or talking toads in television commercials.

But if we peek into the world of real amphibians, we find some astonishing things.

- Scientists have tallied 5,743 species of amphibians around the world, about the same as the number of mammals and more than half the number of birds. However, it is clear that many more amphibian species remain to be discovered compared with birds and mammals, with the Guianas and Peru being particularly poorly known.
- Some species exhibit spectacular color patterns—they are the jewels of the forest. Few tropical birds can rival the colorful markings of, for example, the red-eyed leaf frog (*Agalychnis callidryas*) of Central America.
- Amphibians display behaviors that defy imagination. Male Darwin's frogs (genus *Rhinoderma*) from Chile and Argentina ingest their mate's eggs and incubate them in their vocal sacs. After a few weeks, the young emerge fully formed from the father's mouth.
- Female strawberry poison frogs (*Dendrobates pumilio*) in Costa Rica carry their young from the forest floor where they hatch to tiny arboreal pools of water that form in the axils of bromeliad leaves. These miniature nurseries are free of predators, but also devoid of food for the developing tadpoles. To solve this problem, the female returns regularly to lay unfertilized eggs that become food for her young.
- Spadefoots (genus *Scaphiopus*) in arid southwestern North America may spend more than 99 percent of their lives burrowed in the soil. After heavy rains finally fall, they quickly emerge for an "explosive" breeding session in which newly laid eggs develop into fully formed toadlets in as few as eight days.

The deeper we look, the more we find to challenge our preconceptions about how amphibians make a living.

WHAT ARE AMPHIBIANS?

Amphibians are distinguished from other four-legged vertebrates by characteristics that include moist, scale-less skin, a lack of true claws, and a remarkable retractor muscle that allows them to use their eyeballs to assist in swallowing. Although we learn as children that amphibians live part of their lives in water and part on land, a number of amphibians do not follow this pattern. Many tropical rain frogs (genus *Eleutherodactylus*), for example, live entirely on land, never seeing a body of water larger than what collects in a fallen palm frond. Others, such as the huge river-dwelling hellbender (*Cryptobranchus alleganiensis*) and permanently gilled waterdogs (genus *Necturus*) in the United States and the Suriname toad (*Pipa pipa*) of South America, never leave the water. Although humans have their own coming-of-age troubles during teenage years, most amphibians undergo a dramatic metamorphosis in which they transform from a finned creature that respire in water using gills into a four-legged, air-breathing adult.

Taxonomists recognize three major living groups of amphibians: the salamanders, the frogs and toads, and the caecilians (see *Box 1*). Most groups of plants and animals are very diverse in the tropics, becoming less so as one travels away from the equator. This pattern holds for frogs, toads, and caecilians, but not for salamanders. Salamanders are most diverse in the southeastern United States and Mesoamerica, well north of the equator. Only 28 species of salamanders occur in all of South America.

Top: *Gastrotheca* sp. (a marsupial frog). Panama. / Photo by Ross Alford.

Caecilians: Amphibian Enigmas

(with Roberto Ibáñez)



If it is unusual for us to bump into frogs, toads, and salamanders in our everyday lives, it is even far more unlikely that we would encounter a caecilian, or even know what one was if we were to stumble across one in a tropical forest or an unmarked terrarium in a zoo. Caecilians owe their obscurity to their habit of burrowing underground and remaining out of sight. They are limbless creatures that look like a cross between a snake and an earthworm. Their long cylindrical bodies are clearly snakelike, but upon close examination they lack surface scales and seem to have encircling rings, much like an earthworm. Yet anatomical inspection shows they have a backbone (eliminating any close relation with the earthworms) and the same eye retractor muscle found in other amphibians.

Caecilians diverged from other amphibians well over 200 million years ago¹, and now occur worldwide in tropical habitats. One hundred sixty-eight species are known, but this number will surely increase as more specimens are unearthed. A few South American species are entirely aquatic, but the rest live underground. They have well-developed bony skulls that allow them to push dirt aside as they burrow. Their eyes are generally covered by a layer of skin or even bone, suggesting that vision is not the primary way in which they sense their subterranean world. They share a unique tentacle located on each side of the head partway between the nostril and eye that presumably allows them to detect prey. Some caecilians lay eggs; others bear live young. In some species, females guard their eggs.

How do scientists find these underground denizens? In tropical rainforests, the enterprising naturalist can sometimes find caecilians deep in the leaf litter or upper soil layers at the base of tree buttresses. Another place to hunt for caecilians is in shade coffee plantations adjacent to forest. They are attracted to the high insect densities found in rotting piles of pulp discarded during the refining process. The terrestrial species cannot withstand saturated soils, so animals can be found on the forest floor after heavy rains or even swimming during floods. Their secretive habits ensure that we still have much to learn about these enigmatic cousins of our more familiar amphibians.

Above: *Gymnopsis multiplicata* (a caecilian). Least Concern. Honduras, Nicaragua, Costa Rica, and Panama. Evolutionary anomalies, the little-known caecilians live mostly underground and resemble a cross between a snake and an earthworm. / Photo by Piotr Naskrecki.

AMPHIBIANS IN THEIR ECOSYSTEMS

Although often hidden, amphibians can be very important components of their ecosystems. For example, 132 species of frogs, toads, salamanders, and caecilians co-occur at a single site, Leticia, in southeastern Columbia⁵. In a well-studied forest in New Hampshire, United States, salamanders are the most abundant vertebrate in terms of both numbers and biomass⁶. The common coqui (*Eleutherodactylus coqui*), the emblematic frog of Puerto Rico, is so abundant that it can reach densities of up to 24,800 individuals per hectare* in prime habitat⁷. All of these adult amphibians eat large quantities of insects and help keep prey populations in check. Even tadpoles in tropical streams control algal growth and facilitate populations of mayflies, which are then consumed by other aquatic organisms⁸.

Amphibians comprise three major groups of animals: the salamanders, the frogs and toads, and the little-known caecilians.

Not only are amphibians important because they eat, they are also important because they are eaten. Many birds, mammals, fish, reptiles, insects, and even spiders include amphibians in their diet. The tropical fringe-lipped bat (*Trachops cirrhosus*) specializes on eating frogs and has even learned to differentiate the calls of palatable and poisonous species⁹. A remarkable number of snakes also prey heavily on amphibians. The false fer-de-lance (*Xenodon rabdocephalus*) specializes even further on toads¹. Wading birds such as herons are well-known predators of frogs and tadpoles, but a surprising number of tropical understory birds, including woodcreepers and antbirds, also consume significant quantities of frogs¹⁰. Amphibians therefore play important roles in their ecosystems, performing services such as nutrient cycling and insect population control while at the same time supporting diverse predator communities.

The skin of amphibians is much more permeable to their environment than that of other vertebrate animals. All amphibians use their moist, vascular skin to obtain oxygen from their surroundings. Plethodontid salamanders, a large group of 341 species in the Americas, have no lungs at all. Because of the permeability of amphibian skin, waterborne contaminants readily enter the body and accumulate in tissue quicker than in other animals. For this reason, amphibians are exceptional indicators of environmental quality.

* One hectare equals about 2.5 acres.

THE PROBLEM: DECLINING POPULATIONS

Until the late 1980s, conservationists lumped the fate of amphibians with that of other wildlife. As long as we could conserve habitats in sufficient quantities, the reasoning went, we could conserve the wildlife that depended on those habitats. But then scientists began to make a puzzling observation. Even in seemingly pristine habitats, amphibian populations were mysteriously declining and disappearing. This phenomenon was not limited to a few species or a small geographic area. Declines were documented in Australia, in North, Central, and South America, in the Caribbean, and more recently in Africa and Asia^{11,12,13}. In Latin America alone, nine families and 30 genera of amphibians had been affected by the late 1990s¹⁴.

At first, some scientists were skeptical that the declines were real because amphibian populations are notorious for fluctuating widely¹⁵. Once powerful statistical tests showed that the declines were far more widespread than would reasonably be expected by chance, most researchers eventually agreed that something was seriously amiss¹⁶. Reports of declines and extinctions accelerated during the 1990s, and the mass media latched onto the story.

These observations indicated that something specific and troubling was happening to amphibians. At one site in Costa Rica, 40% of the amphibian fauna disappeared over a short period in the late 1980s¹⁶. Similar stories can be told about other sites¹⁴. The loss of amphibian species not only contributes to the world's biodiversity crisis, but also has important implications for the ecosystems where they occur. Without amphibians, links in food webs are broken and other organisms are influenced in often unpredictable ways.

PURPOSE OF THE GLOBAL AMPHIBIAN ASSESSMENT

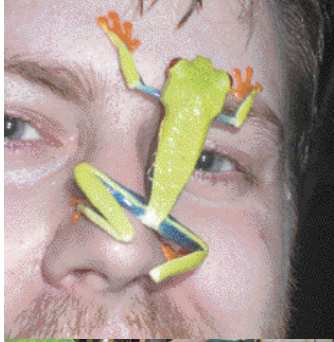
Clearly much research is needed to understand why amphibians are declining (*see Box 2*). But scientists now have new insights into the diversity and natural history of amphibians, and are now able to tell important parts of the story. Knowing the current conservation status of amphibian species is a major step in identifying important areas for research and in knowing where management and protection are most needed.

The Red List criteria developed by the Species Survival Commission of IUCN (the World Conservation Union) provide a widely accepted method for categorizing imperiled plants and animals^{18,19,20}. Over the past 15 years, conservationists have refined these categories and criteria to reflect just how close to extinction a species finds itself. Although scientists

BOX 2

RANA: Catalyzing Amphibian Research

(with Karen R. Lips)



When amphibians began mysteriously disappearing from their habitats in the late 1980s, most field herpetologists were unprepared to study the phenomenon. At the time, most herpetologists concentrated more on studying taxonomy and behavior than demography. Few people thought amphibian diseases were interesting or deserving of much study.

But during the 1990s, it became clear that amphibians in many parts of the world and especially Latin America were in trouble¹⁴. Potential explanations for the declines included disease, climate change, environmental contaminants, and the effects of introduced species. To sort out these explanations, scientists needed to monitor populations, perform autopsies on dead animals, and analyze weather data in addition to their other studies. The challenge demanded new collaborations with colleagues working in other countries and in other fields¹⁷.

To catalyze this sea change and better coordinate their research, in 2002 a group of biologists founded the Research and Analysis Network for Neotropical Amphibians—RANA for short. Funded by the U.S. National Science Foundation, RANA's goals are to promote international collaboration on amphibian decline research and to develop a database on the status of amphibian populations throughout Latin America. To date, over 80 scientists working in 14 Latin American countries have joined the network.

RANA has allowed scientists to examine similarities in how periods of drought correlate with population declines in such distant places as Ecuador, Costa Rica, Venezuela, and Puerto Rico. Another group of RANA scientists is examining the near extinction of harlequin toads, a tropical group in which most of the 77 known species have disappeared from across their range over the last 20 years. And finally, numerous RANA members contributed to this report on the current status of New World amphibian populations. Through these efforts, RANA hopes to hasten the day when we can explain why amphibians are disappearing from pristine habitats and determine what we can do about it.

For more information, visit RANA's website at <http://rana.biologia.ucr.ac.cr>.

Top: A RANA scientist gets to know a red-eyed leaf frog (*Agalychnis callidryas*). / Photo by Ross Alford.

Bottom: Researcher Cesar Jaramillo of Panama is one of more than 80 scientists collaborating on amphibian research in Latin America through RANA. / Photo by Bruce Young.

have assessed all known bird and mammal species against these criteria, until recently no one has systematically examined amphibians. Because they now appear to have unique conservation problems, are often strongly tied to aquatic habitats (as opposed to most birds and mammals), and have strong sensitivity to environmental pollution, amphibians are clearly in need of a similarly exhaustive conservation assessment.

This report provides a summary of the New World portion of the Global Amphibian Assessment, an effort to assess amphibians worldwide against the IUCN criteria. Amphibians in the New World are united by evolutionary history, geography, and the economies and cultures of the people managing their habitats. By writing this report, we hope to highlight the diversity and imperiled status of the New World

amphibians. We show which amphibians are most threatened and describe what threatens them. We evaluate the effectiveness of national systems of protected areas in helping to conserve amphibian faunas. Finally, we present an agenda for the conservation of amphibians. The results can be used by governments and environmental organizations to set priorities for conservation actions at regional, national, and local levels.

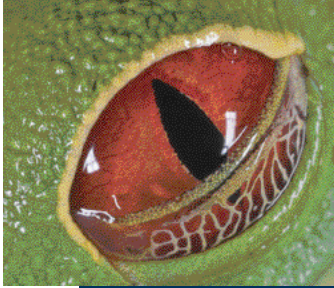
By highlighting the plight of amphibians, we hope to stir resource managers and the public into action so that these glittering jewels of our wild fauna receive the same long-term protection as any masterpiece painting hanging in a museum. The need is urgent, for these brilliant gems are fast disappearing. Unless we take rapid action, many will be gone forever.

TABLE 1
IUCN RED LIST CATEGORIES

Threatened species are listed in one of the three categories printed in RED.

CATEGORY	ABBREVIATION	DEFINITION
EXTINCT	EX	Species for which extensive surveys show that there is no reasonable doubt that the last individual has died.
EXTINCT IN THE WILD	EW	Species that survive only in captivity and/or as naturalized populations.
CRITICALLY ENDANGERED	CR	Species that are facing an extremely high risk of extinction.
ENDANGERED	EN	Species that are considered to be facing a very high risk of extinction in the wild.
VULNERABLE	VU	Species that are considered to be facing a high risk of extinction in the wild.
NEAR THREATENED	NT	Species that do not qualify for Critically Endangered, Endangered or Vulnerable now, but are close to qualifying for or likely to qualify for a threatened category in the near future.
LEAST CONCERN	LC	Species that do not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened. Widespread and abundant taxa are included in this category.
DATA DEFICIENT	DD	Species for which there is inadequate information to make an assessment of extinction risk based on distribution and/or population status. A taxon in this category may be well studied, and its biology well known, but appropriate data on abundance and/or distribution are lacking. Data Deficient is therefore not a category of threat.

The IUCN Red List Criteria



The IUCN Species Survival Commission has identified five criteria by which a species can be classified as threatened. For each criterion, species with more severe conditions qualify for higher threat categories. The five criteria are:

A. *Declining population size.* Even abundant species can qualify if their populations are declining fast enough.

B. *Small, declining geographic range.* Geographic ranges typically contract when suitable habitat is systematically destroyed.

C. *Small and declining population size.* Species with small and declining populations are endangered because a single disease or catastrophic climatic event such as a flood could quickly wipe them out.

D. *Small population size (with no decline).* Even stable, small populations are still vulnerable single catastrophic events.

E. *Quantitative analysis indicating a high probability of extinction in the near future.* These analyses typically use mathematical predictions of population trajectories based on demographic information.

Each criterion is accompanied by guidelines specifying the characteristics a species must display to be classified in a specific threat category. Assessors painstakingly compile all known information about a species before determining which of these criteria apply. The actual criteria are available in English, French, and Spanish on the web at <http://www.iucn.org/themes/ssc/redlists/RLcats2001booklet.html>, and guidelines for using the criteria are posted (in English only) at <http://www.iucn.org/themes/ssc/redlists/RedListGuidelines.pdf>.

Above: Designed by evolution: closeup of the eye of a red-eyed leaf frog (Agalychnis callidryas). / Photo by Piotr Naskrecki.

METHODS

Our analyses are based upon the application of the Red List criteria²⁰ to the 3,046 species of amphibians occurring in the New World. Table 1 lists the categories and their definitions (see also Box 3). We define the New World as continental North, Central, and South America, all near-shore islands, and the Caribbean. Much of the analysis is by regions of the New World (Figure 1):

South America: All countries in continental South America plus the near-shore islands of the Netherlands Antilles and Trinidad and Tobago.

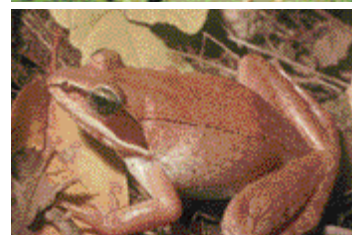
Mesoamerica: Mexico through Panama.

Caribbean: All countries and territories of the Greater and Lesser Antilles plus associated islands such as Turks and Caicos, the Bahamas, and the Cayman Islands.

North America: Canada and the United States (exclusive of Hawaii and overseas possessions).

To apply the criteria, compile the supporting information, and draw range maps, we enlisted the help of numerous herpetologists from throughout the region. In most cases, a single scientist filled out a draft database, including information on distribution, abundance and population trends, natural history, threats, and conservation measures, for all species in a region. Then, in a workshop setting, other experts updated the information based on recent literature and unpublished information. Overall, 229 scientists participated in some stage of the development of the database (see Appendix 1).

Once the entire database was compiled, we reviewed the Red List category assignments for all species to ensure that the criteria were applied evenly across all regions of the New World. Spatial analyses are based on the number of species fulfilling the criteria being analyzed that occur in each quarter-degree block of latitude and longitude. Unless noted otherwise, the analyses pertain to extant native species. Native species are those that have arrived at their current distribution unaided by humans. Our analyses do not include data from 11 species that were described in previous centuries and for which type specimens have been lost or information about country of origin is in doubt. For a more detailed description of our methods, including a list of the



Top: Female strawberry poison frog (*Dendrobates pumilio*). Least Concern. Nicaragua, Costa Rica, and Panama. / Photo by Ross Alford.

Second from top: *Hyla polytaenia* (a tree frog). Least Concern. Brazil. With 731 species, Brazil has the world's greatest amphibian diversity. / Photo by Martha C. Lange.

Third from top: Wood frog (*Rana sylvatica*). Least Concern. Canada and United States. Thriving from the Appalachians to the Arctic Circle, the wood frog is the northernmost-ranging amphibian in the hemisphere. / Photo by Geoff Hammerson.

Bottom: *Oedipina collaris* (a salamander). Data Deficient. Nicaragua, Costa Rica, Panama. For one in five New World amphibians, including this salamander, sufficient data is lacking to properly assess conservation status. / Photo by Roberto Brenes.

The Southeastern United States: Hotbed of Salamander Diversity

(with Geoffrey A. Hammerson and David B. Wake)



The United States is the world's third-largest country, but due to its position well north of the equator it rarely rates so high for biological diversity². Even small tropical countries such as Ecuador typically have many more kinds of virtually every group of organism. Not so for salamanders. With 168 species of salamanders, the United States is tops in the world. Only Mexico, with 127 species, is close.

The southern Appalachian Mountains of western North Carolina and eastern Tennessee is the most salamander-rich area on Earth. Thirty-one species occur within the boundaries of Great Smoky Mountains National Park alone³. And on a good day in northeastern Mississippi you could find members of seven of the world's ten families of salamanders: four aquatic families (Amphiumidae – amphiumas, Cryptobranchidae – hellbenders, Proteidae – waterdogs and mud-puppies, Sirenidae – sirens), two largely terrestrial families (Ambystomatidae – mole salamanders, Plethodontidae – lungless salamanders), and one amphibious family (Salamandridae – newts). Only southern Mexico and Central America, with their great diversity of terrestrial species, rival the diversity in the southeastern United States.

Due to the broad ranges of some of these salamanders and their frequent occurrence in remote mountains, relatively few species are threatened with extinction. Seventeen (16%) of the 106 species that occur in a 13-state region bounded by Virginia, Missouri, Louisiana, and Florida are threatened, but none critically so. The threatened species tend to have small ranges, such as the black warrior waterdog (*Necturus alabamensis*), which is restricted to a few counties in Alabama's Black Warrior River drainage. As a group, U.S. salamanders are threatened by habitat loss and degradation caused by logging⁴, atmospheric pollution, and reduced water quality from agricultural, industrial, and residential runoff. Public and private land managers in this extraordinary area shoulder an important responsibility in safeguarding the world's richest salamander fauna.

Top: Black warrior waterdog (*Necturus alabamensis*). Endangered. United States. Waterdogs, like their cousins the sirens, amphiumas, and hellbenders, are aquatic salamanders, often giant in size and bizarre in form. This species is found only in a few streams of Alabama's Black Warrior River drainage, and nowhere else in the world. / Photo by Wayne Van Devender.

Bottom: Weller's salamander (*Plethodon welleri*). Endangered. United States. Restricted to Virginia, North Carolina, and Tennessee. Weller's salamander lives chiefly in high-elevation spruce forests. / Photo by Wayne Van Devender.

The Status of New World Amphibians



The diversity of New World amphibians, in both numbers and habitats, is remarkable. Although incapable of generating their own body heat to withstand extreme cold, amphibians nevertheless inhabit the New World continuously across 123 degrees of latitude. Wood frogs (*Rana sylvatica*) gather each spring for their mating ritual in barely thawed bogs just a stone's throw from the Arctic Ocean in Alaska. At 70° north latitude, these are the northernmost lands in the New World graced by amphibians. Honors at the other end of the globe go to the toad *Bufo variegatus* that ranges to the Strait of Magellan in southern Chile at 53° south. In between lay countless landforms ranging from the wettest rainforests to the driest deserts, with all but the remotest islands and tallest mountain peaks inhabited by amphibians.

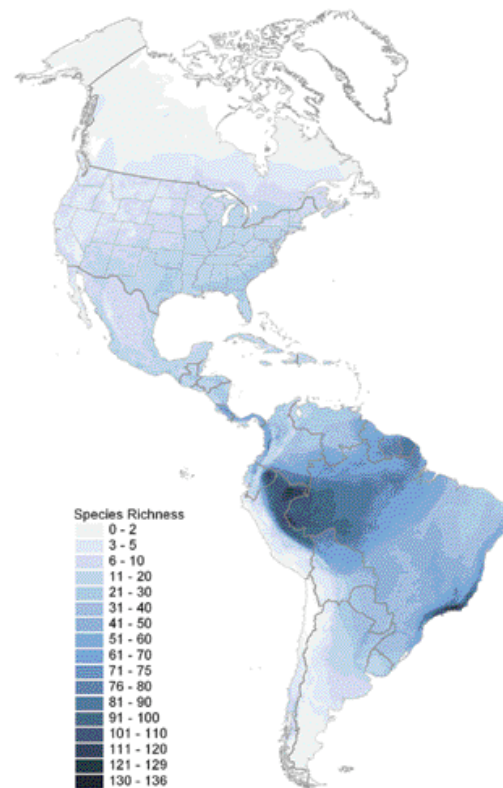
OVERVIEW OF DISTRIBUTION AND ABUNDANCE

Many amphibian families are restricted to the New World. Half of the world's salamander families (Ambystomatidae, Amphiumidae, Dicamptodontidae, Rhyacotritonidae, and Sirenidae) occur here and nowhere else. One caecilian family (Rhinatrematidae) and nine frog families (Allophrynidae, Ascaphidae, Brachycephalidae, Centrolenidae, Dendrobatidae, Leptodactylidae, Rhinodermatidae, Rhinophrynidae, and Scaphiopodidae) are similarly restricted to the New World. With 1,124 species in North, Central, and South America as well as the Caribbean, the Leptodactylidae is the most species-rich family of amphibians on Earth.

The New World (North, Central, and South America and the Caribbean) is home to 3,046 amphibians—over half of the world's known species.

Patterns of amphibian diversity are a result of the complex interactions of several variables: geological history, topography, current environmental conditions, and competition among species themselves. Salamanders are most diverse in the southeastern United States and Mesoamerica (see Box 4). Frogs and toads are most diverse in the upper Amazon Basin and eastern Brazil. The less numerous caecilians are most diverse in the Amazon basin (Figures 2-4). What follows is a brief south to north overview of amphibian diversity in the major regions of this hemisphere, home to 3,046 species, over half (53%) of the world's known amphibians. Tables 2 and 3 show summary data for the hemisphere. A complete species list is available online at www.natureserve.org/publications/disappearingjewels.jsp.

FIGURE 2
DIVERSITY OF NEW WORLD FROGS AND TOADS



Above: Red-eyed leaf frog (*Agalychnis callidryas*). *Least Concern.* Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and Colombia. One of the most widespread and colorful of tropical amphibians, the red-eyed leaf frog is also favored in the pet trade. / Photo by Ross Alford.

FIGURE 3
DIVERSITY OF NEW WORLD SALAMANDERS



FIGURE 4
DIVERSITY OF NEW WORLD CAECILIANS



TABLE 2
OVERALL AMPHIBIAN DIVERSITY—
TOP TEN NEW WORLD COUNTRIES

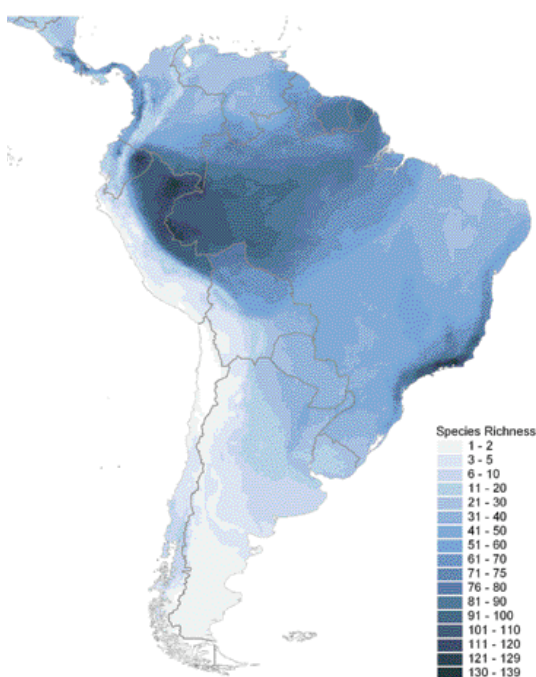
COUNTRY	NO. OF SPECIES
BRAZIL	731
COLUMBIA	698
ECUADOR	447
PERU	398
MEXICO	351
VENEZUELA	293
UNITED STATES	262
BOLIVIA	201
PANAMA	189
COSTA RICA	179

Left: Couch's spadefoot (*Scaphiopus couchii*). *Least Concern.* United States and Mexico. Like other spadefoots, this mainly desert species spends months in underground burrows, then emerges to breed only after heavy rains. /Photo by Geoff Hammerson.

Center: American toad (*Bufo americanus*). *Least Concern.* Canada and United States. The musical trill of these and other common toads is among the welcome signs of spring in North America. /Photo by Geoff Hammerson.

Right: *Bufo atacamensis* (a toad). *Least Concern.* Chile. Shown in amplexus (mating), this toad lives in oases scattered through Chile's Atacama Desert, the driest place on Earth. /Photo by Alberto Veloso.

FIGURE 5
AMPHIBIAN DIVERSITY IN SOUTH AMERICA



SOUTH AMERICA

In terms of amphibian diversity, South America is second to none. An astonishing 2,065 species occur within its continental landmass, more than anywhere else on Earth. And this total is far from complete. Taxonomists are discovering and naming new species faster today than ever before²¹. By contrast, birds were mostly discovered and named in the nineteenth century, with just a trickle of new species still being found today.

South America owes its diversity to geological history, extensive moist areas, diversity of habitats, and its current fortuitous position straddling the equator. The major groups of amphibians had dispersed into South America before it separated from other Southern Hemisphere continents 30 to 35 million years ago²². The Andes, one of the largest mountain ranges on earth, began to uplift 70-80 million years ago as South America drifted west from Africa²¹. The rugged slopes of this 7,500-kilometer-long cordillera created numerous barriers to amphibian dispersal, fostering speciation as populations developed in local isolation. The topographical relief of the other major mountain ranges, the ancient Guianan tepuis and the highlands of eastern Brazil, also provided numerous opportunities for speciation. Finally, the climatic effects of cold ocean currents interacting with these mountain ranges has led to complex patterns of wet and dry habitats on the continent.

Amphibians, with their dependence on water (or at least humid microhabitats) and avoidance of temperature extremes, are more abundant in mild, wet climates. Montane species tend to have small distributional ranges whereas lowland species, with less severe barriers to dispersal, tend to be broadly distributed. Not surprisingly, amphibian diversity is highest in moist tropical highlands and lowest in dry temperate lowlands of southeastern Bolivia south through Argentina (Figure 5). The highest diversity of amphibians occurs in the upper Amazon basin and in the Atlantic Forest of eastern Brazil. The narrow ranges of some Andean and (to a lesser degree) Atlantic Forest species are remarkable. Numerous species are restricted to single watersheds; some are still only known from the site where scientists first spotted them.

The greatest diversity of amphibians on Earth is found in the upper Amazon basin and in the Atlantic Forest of eastern Brazil.

The salamanders of South America are conspicuous by their rarity, with just 28 species in two genera occurring here. Ancestors of these species appear to have dispersed from North America into a previously salamander-free South America during the last three to five million years since the Isthmus of Panama formed. Caecilians, though inconspicuous, are in fact fairly diverse in South America, where varied habitats support fully half of the Earth's species.

But the real show in South America is the frogs and toads, responsible for 95% of the continent's amphibian fauna (1,959 species). These creatures live in nearly every conceivable habitat. For example, the toad *Bufo atacamensis* occurs in oases in the middle of Chile's Atacama Desert, the driest place on Earth. The frog *Telmatobius marmoratus* occurs in streams at up to 5,000 meters elevation, high above the tree line in the Andes. The family Leptodactylidae has diversified into 834 species, including 421 species in the genus *Eleutherodactylus*, the world's most diverse vertebrate genus. Many more leptodactylid species have dispersed to and diversified in the Caribbean and Mesoamerica, even reaching the southern United States. South America is the only place you can find the Tukeit-Hill frog (*Allophryne ruthveni*), a frog so different from all others that it was placed in its own family (Allophrynidae). Other unique South American families include the gold frogs (Brachycephalidae), a group of six minute, often brightly colored species, and the two species of Darwin's frogs (Rhinodermatidae).

TABLE 3

THREAT STATUS OF NEW WORLD AMPHIBIANS BY COUNTRY OR TERRITORY

COUNTRY	TOTAL	EX	EW	CR	EN	VU	NT	LC	DD	PERCENT EXTINCT OR THREATENED*
SOUTH AMERICA	2,065	4	0	151	247	231	100	791	529	31
Argentina	155			2	15	13	9	106	10	19
Bolivia	201			5	6	10	6	161	13	10
Brazil**	731	1		20	38	52	21	440	159	15
Chile	53			9	4	7	3	13	17	38
Colombia	698			50	78	80	43	326	121	30
Ecuador	447	2		32	73	58	22	201	59	37
French Guiana	101					3		95	3	3
Guyana	115					6		97	12	5
Netherlands Antilles	1							1		0
Paraguay	78			1			3	71	3	1
Peru	398			19	31	28	11	213	96	20
Suriname	101					2		93	6	2
Trinidad and Tobago	33			2	2	5		24		27
Uruguay	43				2	2	3	36		9
Venezuela	293	1		18	24	26	7	142	75	24
MESOAMERICA	685	3	0	120	158	77	38	197	92	52
Belize	39			1	3	2	6	26	1	15
Costa Rica	179	1		20	22	19	9	88	20	35
El Salvador	31			3	3	2	1	21	1	26
Guatemala	135			19	34	21	12	38	11	55
Honduras	116	2		27	23	3	8	50	3	47
Mexico	351			57	90	44	21	94	45	54
Nicaragua	68			1	4	5	1	55	2	15
Panama	189			18	22	12	7	107	23	28
CARIBBEAN	171	0	0	63	62	18	7	21	0	84
Anguilla	1							1		0
Antigua and Barbuda	2						1	1		0
Bahamas	2							2		0
Barbados	1							1		0
British Virgin Islands	5			1	1			3		40
Cayman Islands	2							2		0
Cuba	58			15	23	9	2	9		81
Dominica	4			1	1		1	1		50
Dominican Republic	36			10	16	5	1	4		86
Grenada	3				1			2		33
Guadeloupe	5			1	2		1	1		60
Haiti	50			31	10	5		4		92
Jamaica	21			7	8	2	2	2		81
Martinique	4			1		1	1	1		50
Montserrat	2			1				1		50
Puerto Rico	18			7	5	1	1	4		72
Saint Kitts and Nevis	2			1				1		50
Saint Lucia	2						1	1		0
St. Vincent & the Grenadines	3				1			2		33
U.S. Virgin Islands	5				2			3		40
NORTH AMERICA	262	2	1	2	15	34	32	162	14	21
Canada	44					1	3	40		2
United States	262	2	1	2	15	34	32	162	14	21
NEW WORLD	3,046	9	1	337	482	358	169	1,057	633	39

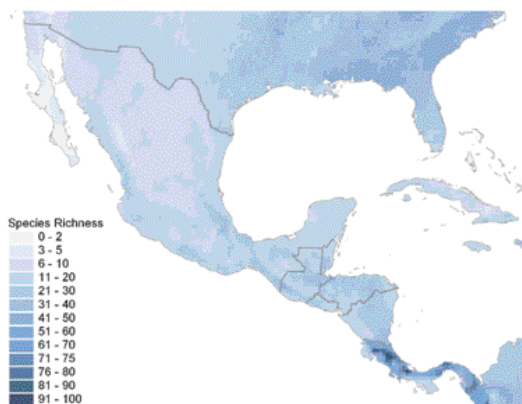
* Includes Extinct, Extinct in the Wild, Critically Endangered, Endangered, and Vulnerable.

** For the purposes of this report, we modified the categories assigned to some Brazilian species to reflect consistent application of the Red List criteria.

NOTE: Columns do not add up to regional totals due to species that are found in more than one country. A complete species list is available online at www.natureserve.org/publications/disappearingjewels.jsp.

When it comes to frog diversity, nature's imagination goes far beyond the homogeneous green creatures of television animations or the stuffed toys that accumulate in our children's bedrooms. In South America, these animals are remarkably variable in size, shape, color, and pattern. Poison dart frogs (family Dendrobatidae), named for a species in Colombia that was used by indigenous peoples to anoint hunting darts, can have blotches on their skin of every color in the rainbow. These tiny gems can be very common along tropical streams and on the forest floor. Monkey treefrogs in the genus *Phyllomedusa* wear Cheshire-cat smiles that never go away. Harlequin toads (genus *Atelopus*) display every conceivable pattern of black and yellow, with a little red or orange thrown in on occasion for variety. South America indeed hosts an astonishing assemblage of frogs with forms and colors that seemingly could exist only in an artist's imagination.

FIGURE 6
AMPHIBIAN DIVERSITY IN MESOAMERICA



MESOAMERICA

Considering that the land mass of Mesoamerica is dwarfed by neighboring continents to the north and south, amphibian diversity in the region—685 species—is extraordinary. Like South America, Mesoamerica owes its diversity to complex topographical relief and consequent variety of habitats, moist climate regimes, and location in the tropics. In addition, Mesoamerican diversity has benefited from dispersal into the region from both North and South America.

The geological history of Mesoamerica is far too complex and controversial to describe in detail here. Briefly, the land north of the Isthmus of Tehuantepec (the narrow constriction in Mexico in Veracruz and Oaxaca states) is historically part of



Top: *Brachycephalus nodoterga* (a gold frog). Data Deficient. Brazil. One of the gold frogs, a family of six species found only in Brazil. / Photo by Martha C. Lange.

Second from top: Tukeit-Hill frog (*Allophryne ruthveni*). Least Concern. Venezuela, Guyana, Suriname, French Guiana, and Brazil. This taxonomically unusual frog comprises its own family, *Allophrynidae*. / Photo by Christian Marty.

Third from top: *Phyllomedusa lemur* (a monkey treefrog). Endangered. Costa Rica, Panama, Colombia. Recent population declines of more than 50% are suspected to be due to the chytrid disease Bd. / Photo by Ross Alford.

Bottom: Green poison frog (*Dendrobates auratus*). Least Concern. Nicaragua, Costa Rica, Panama, Colombia. A member of the kaleidoscopically-colored family *Dendrobatidae*, the poison dart frogs. / Photo by Forrest Brem.

the North American continent. The land south of the Isthmus to the southern Nicaragua lowlands is a mosaic of plates that have rearranged themselves and alternately been submerged and exposed by the ocean several times during the last 65 million years. The region encompassed by Panama, Costa Rica, and southern Nicaragua formed over the last three to ten million years through a combination of volcanic activity and uplift²³. The result is a jumble of mountain ranges interrupted by valleys and lowlands. Like South America, humid mountain slopes rise above both dry (generally on the Pacific side) and wet (Caribbean side) lowland habitats.

The presence of moist tropical highlands has again led to extensive diversification of amphibian forms. Unlike in South America, salamander diversification here is substantial, with 213 salamander species known. South of central Mexico, all salamanders belong to the family Plethodontidae (the lungless salamanders), a group that is also widespread in North America. This observation suggests that salamanders dispersed into Mesoamerica from the north. Salamander diversity is concentrated in the highland areas of southern Mexico and Guatemala. Diversity is highest in cool, humid, montane forests and lowest in dry lowlands. In fact, the salamander *Pseudoeurycea gadovii* occurs at elevations as high as 5,000 meters on the upper slopes of the Pico de Orizaba volcano, the highest point in Mexico. The highest elevation recorded in Mesoamerica for a frog, by contrast, is just 3,600 meters for the ridged treefrog (*Hyla plicata*) in central Mexico.

Frogs and toads have also diversified into myriad species in Mesoamerica. The taxonomic affinities clearly indicate that the ancestors of these species dispersed into Mesoamerica from both the south and north. For example, the frog genus *Rana* has 26 members in the United States, dwindling southward to four species in Panama. The poison dart frogs (family Dendrobatidae), glass frogs (family Centrolenidae), and harlequin toads (genus *Atelopus*) are groups that have dispersed in the other direction from South America.

Although no families are endemic to Mesoamerica, several genera (e.g., *Anotheca*, *Atelophryniscus*, *Bradytriton*, *Chiropterotriton*, *Crepidophryne*, *Cryptotriton*, *Dendrotriton*, *Duellmanohyla*, *Ixalotriton*, *Lineatriton*, *Nototriton*, *Nyctanolis*, *Oedipina*, *Parvimolge*, *Plectrohyla*, *Ptychohyla*, *Thorius*, and *Triprion*) appear to have originated in Mexico, the mountains of Guatemala and Honduras, and the Cordillera de Talamanca in Costa Rica and Panama. In most cases, the species in these genera are restricted to highlands.

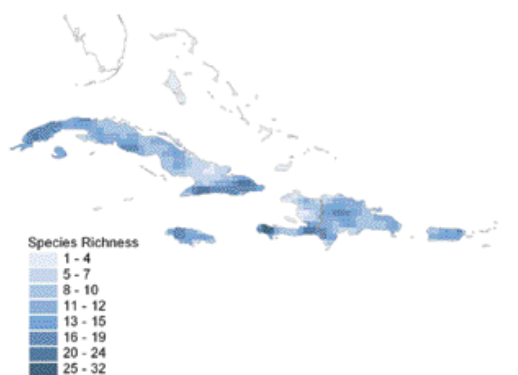
The highest concentrations of frog and toad species occur in the Caribbean lowlands of Costa Rica and Panama and the Pacific lowlands of southern Costa Rica and Panama (Figure 6). There we find remarkable numbers of species. For example, La Selva Biological Station, a 1,600-hectare mixture of old growth and second-growth forest in the

Caribbean lowlands of Costa Rica, has 44 species of frogs and toads²⁴. Farther south, this number increases to 59 species in the slightly larger area of Soberanía National Park along the Panama Canal²⁵. The origin of much of this diversity is the closing of the Isthmus of Panama, which allowed South American species to spread northward and give rise to new forms. Unlike salamanders, frog and toad diversity does not increase appreciably with elevation. Above 1,600 meters elevation, diversity drops steadily.

Nearly two out of every five amphibians in the New World are already threatened with extinction—a rate far higher than that for birds or mammals.

Scientists have identified 16 species of caecilians in Mesoamerica, ranging as far north as southern Mexico. With so few species (that have likely colonized from South America since the closure of the isthmus in Panama) it is inappropriate to talk of “hot spots” of diversity. In our current state of knowledge, Panama is home to ten caecilian species, Costa Rica has seven, and no other country has more than two species. Caecilians are creatures of the lowland moist forests, rarely occurring as high as 1,400 meters elevation. All species in the region are terrestrial.

FIGURE 7
AMPHIBIAN DIVERSITY IN THE CARIBBEAN



CARIBBEAN

Like Mesoamerica, the Caribbean islands are located midway between North and South America. But because amphibians, with no ability to swim in salt water or fly, have such a hard time dispersing to the islands, we find very different patterns of amphibian diversity in the Caribbean. The most striking difference is that no salamanders or caecilians occur on any of the islands. The other obvious contrast with Mesoamerica is that few genera or families of amphibians occur in the Caribbean. Whereas there are 15 families and 67 genera in Mesoamerica, just four families and five genera occur in the Caribbean. The vast majority (88%) of the Caribbean's 171 amphibian species belong to just one genus of frog, *Eleutherodactylus*.

The geological history of the Caribbean can explain some of these patterns. Although the subject remains under intense study, most geologists agree that the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico) are geological cousins of the plates that make up northern Central America. When dinosaurs still rumbled across the landscape, these islands were lined up more or less between North and South America in approximately the location of present day Central America. Over the last 70 million years, these islands have drifted east to their current positions. The trailing edge of this parade of islands has fused to North American and now makes up northern Central America. Some of the Greater Antilles may have had temporary land connections with North and/or South America as they drifted eastward²⁶.

The Lesser Antilles formed in a completely different manner. As the Caribbean Plate was pushing the Greater Antilles northward and eastward, it ran up on top of the oceanic Atlantic Plate. Periods of volcanic activity along the arc of this collision zone created the many small islands known collectively as the Lesser Antilles, which today include such idyllic tourist destinations as the Virgin Islands and Barbados²⁶.

How did amphibians get onto these islands? Two scenarios seem plausible. First, some ancestral amphibians may have hopped onto the islands of the Greater Antilles long ago when they had temporary land connections with North or South America²⁶. However, the presence throughout much of the islands of limestone—a rock that only forms under salt water—suggests that they were submerged 30 million years ago. Any frogs present at that time would have met certain extinction.

The second, more likely origin of amphibians in the Caribbean is the dispersal of animals via rafting. During violent storms, large tangled masses of trees and other vegetation can float out to sea and be carried to distant shores on ocean currents. In rare cases, frogs and toads can survive on these natural rafts to colonize islands. Once established, frogs

disperse across the island and, through the age-old process of natural selection, diversify and adapt to local habitats over the course of millions of years. Ocean currents in the Caribbean flow generally from south to north, so it is not surprising that most Caribbean amphibians are more closely related to those in South America than elsewhere. The few genera in the Caribbean suggest that the fauna we see today is derived from very few colonization events²⁶.

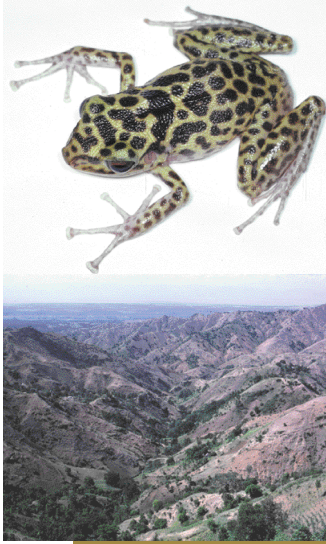
We therefore have a fauna that was founded by a very few amphibian colonists, which then diversified in their new homes (see Box 5). Virtually all Caribbean amphibians (94%) are endemic to single islands, indicating that dispersal events between islands are rare. Species have diversified to occur on high mountain ranges such as the Cordillera Central in the Dominican Republic and sea-level mangrove swamps in Haiti. The highest densities of species occur in moist mountain ranges, such as the Sierra Maestra and Macizo de Sagua-Baracoa in eastern Cuba, the Cockpit Country of western Jamaica, the Massif de la Hotte in Haiti, the Massif de la Selle / Sierra de Baoruco on the Haitian-Dominican Republic border, and El Yunque in Puerto Rico (Figure 7). Species diversity is low on the islands of the Lesser Antilles, a consequence of their small land area and their isolation from potential founding populations.



Above: Common coqui (*Eleutherodactylus coqui*). Near Threatened. Puerto Rico. Amphibians disperse from the mainland to Caribbean islands with difficulty, then evolve there in isolation. The Caribbean islands are home to 171 species of frogs and toads, but not a single species of salamander or caecilian. / Photo by Forrest Brem.

Haiti: A Megadiverse Caribbean Country

(with S. Blair Hedges)



Known internationally mainly for its political turmoil, Haiti and biodiversity are rarely mentioned in the same breath. Stories about enchanting Haitian wild areas never appear in the nature magazines we read. With its political instability, overcrowding, and few natural attractions, why should conservationists pay attention to Haiti?

The answer is its amphibian diversity. Haiti is home to 50 native amphibian species, second in the Caribbean only to Cuba, which has 58 species in four times the land area. Of Haiti's total, 26, or more than half, occur in no other country, not even the neighboring Dominican Republic. The largest concentration of amphibian species anywhere in the Caribbean occurs in the Massif de la Hotte, on the tip of the long Tiburon Peninsula that juts westward into the Caribbean Sea in southern Haiti. This small area is home to 32 frog species²⁶.

This diversity is all the more remarkable when we consider that Haiti has no taxonomists actively describing species. All Haitian species that have been discovered in the last 50 years have been described by U.S. herpetologists, including Blair Hedges, Albert Schwartz, Richard Thomas, and Ernest Williams, who have visited the country infrequently. So Haiti likely holds (or held) a number of undiscovered species.

Unfortunately, the future for many of these species is grim. Widespread rural poverty has led to the dismantling of natural habitats for firewood and charcoal production. Hillsides are denuded and streams have dried up. The Haitian government has set up an extensive system of protected areas, but park personnel are either nonexistent or powerless to stop rampant extraction of natural resources. Many amphibians have been found only in the tiniest remnants of vegetation that will likely disappear shortly if they have not already. Although establishing effective conservation programs in unstable countries is a challenge, Haiti's remarkable and unsung diversity merits the effort.

Top: *Eleutherodactylus counouspeus* (a tropical rain frog). Endangered. Haiti. This frog occurs only in the limestone caves and forests of the Massif de la Hotte in southwestern Haiti. / Photo by S. Blair Hedges, Pennsylvania State University.

Bottom: Denuded hillsides in southern Haiti that once supported rainforest. Clearing of hillside forests for charcoal production is causing an environmental and human disaster in Haiti. / Photo by S. Blair Hedges, Pennsylvania State University.

NORTH AMERICA

Although North America, with its 262 species, does not have the megadiversity of neighboring tropical regions, the continent's amphibian fauna is nevertheless impressive. Take the tiger salamander (*Ambystoma tigrinum*), for example. This adaptable species can be found in the western portion of its range from sea level all the way up to 3,660 meters elevation. Few tropical salamanders span more than 1,200 meters of elevation and none come close to the tiger salamander's adaptability. Distributions of many North American species are enormous compared with their more southerly cousins. For example, the wood frog, our arctic hero, has a cross-continental range that abuts the shores of three oceans—Atlantic, Pacific, and Arctic.

Other noteworthy North American amphibians include the hellbender (*Cryptobranchus alleganiensis*) and the unique eel-like sirens and amphiumas that are nearly restricted to the southeastern United States. Some of these thoroughly aquatic salamanders reach lengths of 75 to 100 centimeters or more, placing them among the New World's largest amphibians. North America also hosts a diverse group of cave-adapted salamanders. Some of these species, which are typically endemic to single cave systems, have greatly reduced eyes that may be rather useless in the eternal darkness of their habitats. Also worthy of mention are the two species of tailed frogs (genus *Ascaphus*), the only frogs that sport a tail-like appendage when fully adult.

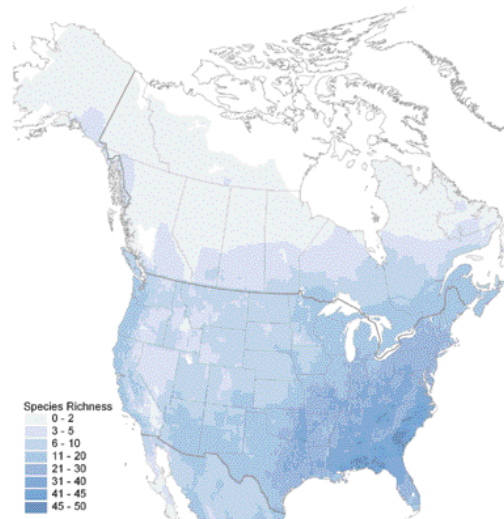
North America currently has a land connection only to South America, but that was not always the case. Over the past 60 million years, North America has also had land connections with both Asia and Europe²⁷. This observation may explain why members of the salamander family Cryptobranchidae (including the hellbender) occur only in eastern Asia and North America, and how a few species of the Plethodontidae, a family of salamanders restricted primarily to the New World, arrived in Europe.

The Appalachian Mountains began to uplift before the first amphibian crawled or hopped, and have been gradually eroding ever since. The moist temperate forests that cover these mountains today grow on severely eroded remnants of a formerly towering cordillera. These mountains, especially their southern extreme, are home today to the most diverse salamander fauna in the world (see Box 4).

Although North American salamander diversity peaks in the Southern Appalachians, frog and toad diversity peaks on the coastal plain that slopes gradually from these mountains to the Atlantic Ocean and Gulf of Mexico. There a visit to a pond in good habitat on a warm, drizzly spring night can yield over a dozen species of amphibians, including treefrogs, spadefoots, cricket frogs, chorus frogs, true frogs, and toads. Most males will be squawking, beeping, and trilling away, while a fortunate few will cling to females about to lay eggs.

FIGURE 8

AMPHIBIAN DIVERSITY IN NORTH AMERICA



Top: Hellbender (*Cryptobranchus alleganiensis*). Near Threatened. United States. A denizen of fast-flowing streams and rivers of the Appalachians, the surreal-looking hellbender is completely aquatic and can reach more than two feet in length. / Photo by Wayne Van Devender.

Bottom: Tiger salamander (*Ambystoma tigrinum*). Least Concern. Canada, United States, Mexico. The adaptable and widespread tiger salamander is one of 168 species of salamanders in the United States—the world center for salamander diversity. / Photo by Geoff Hammerson.

Another concentration of North American amphibian diversity occurs in the Pacific states of California, Oregon, and Washington (Figure 8). This region is home to a variety of giant, mole, and lungless salamanders, as well as true frogs and toads. Some of these animals, such as the mountain yellow-legged frog (*Rana muscosa*), breed in alpine lakes at elevations up to 3,600 meters in the Sierra Nevada. The soggy rainforests of the Pacific Northwest provide good habitats for salamanders. Many species, such as the Pacific giant salamander (*Dicamptodon tenebrosus*, one of the largest terrestrial salamanders on Earth), occur in damp mats of moss or under rotting tree trunks. Others, such as the Olympic torrent salamander (*Rhyacotriton olympicus*), inhabit cold springs and streams in old growth forests. By contrast, the extensive arid regions of most of western North America hold few amphibians, although interesting drought-adapted species have evolved in these habitats.

CONSERVATION STATUS AND IMPERILMENT

This first-ever compilation of assessments for all New World species indicates that 39%, or two out of every five amphibians are extinct or threatened with extinction (Table 3). Fully 14% of all reliably assessed species (i.e., excluding Data Deficient species) are listed as Critically Endangered, or facing an imminent threat of extinction. With more research, scientists will likely reclassify some of the Data Deficient species to a threatened category. Thus the figure of 39% of New World species being threatened or extinct is probably an underestimate.

A total of 1,057 species falls into the Least Concern category (35%), indicating that they are widespread, common, and have good chances of surviving under current conditions. Many of these species adapt well to human modifications to habitat, or occur in environments that are not immediately threatened by human activities. It is sobering to realize, however, that these secure species are fewer in number than those that are threatened.

A substantial portion of the species, one-fifth of the total, is too poorly known scientifically to be assigned a threat category with confidence (the “Data Deficient” species). The largest numbers of Data Deficient species occur in tropical countries where remote rainforests remain poorly explored by herpetologists. Even the United States has species too poorly known to assess, although this situation is largely a result of recent taxonomic changes.

STATUS BY TAXONOMIC GROUP

Of the major groups of amphibians, salamanders are slightly more threatened than are frogs and toads (Table 4, Figure 9). Caecilians are so poorly known that over three-fifths of all species fall into the Data Deficient category. With the exception of *Typhlonectes compressicauda* and *Chthonerpeton indistinctum*, no one has studied the population trends of caecilians well enough to be able to state that species are increasing or decreasing or deserving of threatened status. Of the taxonomic families that have at least 10 species, the toads (Bufonidae), tropical frogs (Leptodactylidae), mole salamanders (Ambystomatidae), and lungless salamanders (Plethodontidae) are faring the worst, with 45 to 55% of species assessed as threatened. Treefrogs (Hylidae), narrow-mouth toads (Microhylidae), and true frogs (Ranidae) have the smallest fraction of threatened species (Table 4). Of special concern are the Darwin's frogs (family Rhinodermatidae), a Chilean/Argentinean family of which one species (*Rhinoderma rufum*) has not been seen since 1978 and the other (*Rhinoderma darwini*) has declined throughout much of its range. If the trend continues, we will lose an entire family with a unique breeding system (see Introduction).

The frogs and toads of North America are significantly less diverse and generally less threatened than those of Central and South America.

EXTINCTION

Nine New World species are currently classified as extinct, including four frogs, four toads, and one salamander (Table 5). Five of these extinctions have taken place since 1980. The extinct species are all endemic to single countries, including the United States, Honduras, Costa Rica, Venezuela, Ecuador, and Brazil. All of these species had restricted ranges in which extensive searching has failed to turn up any individuals. Several species seen as recently as the 1980s or even the early 1990s, have not been found in more recent surveys.

Unfortunately, these nine species may soon have some company. Scientists flagged 117 species as “possibly extinct,” meaning that they are unaware of any extant population but have not performed the extensive searching required to place these species confidently in the Extinct category. In 109 of

TABLE 4

THREAT STATUS OF NEW WORLD AMPHIBIANS BY TAXONOMIC GROUP

ORDER	TOTAL	EX	EW	CR	EN	VU	NT	LC	DD	PERCENT EXTINGUISHED OR THREATENED*
FROGS & TOADS	2,560	8	1	298	396	301	130	905	521	39
Allophryinae	1							1		0
Ascaphidae	2							2		0
Brachycephalidae	6					1	1	1	3	17
Bufoinae	253	4	1	72	34	29	11	77	25	55
Centrolenidae	138			6	16	29	9	29	49	37
Dendrobatidae	228			19	30	16	14	57	92	29
Hylidae	682	1		52	79	55	29	344	122	27
Leptodactylidae	1,124	2		141	231	155	55	322	218	47
Microhylidae	55				2	5	2	37	9	13
Pipidae	7				1			5	1	14
Ranidae	54	1		7	3	10	8	23	2	39
Rhinodermatidae	2			1		1				100
Rhinophryinae	1							1		0
Scaphiopodidae	7						1	6		0
Allophryinae	1							1		0
SALAMANDERS	397	1	0	39	86	57	39	119	56	46
Ambystomatidae	29			8	2	3	1	13	2	45
Amphiumidae	3						1	2		0
Cryptobranchidae	1						1			0
Dicamptodontidae	4						1	3		0
Plethodontidae	341	1		31	82	53	31	89	54	49
Proteidae	5				1		1	3		20
Rhyacotritonidae	4					1	2	1		25
Salamandridae	6				1		1	4		17
Sirenidae	4							4		0
CAECILIANS	89	0	0	0	0	0	0	33	56	0
Caeciliidae	80							29	51	0
Rhinatreumatidae	9							4	5	0

* Includes Extinct, Extinct in the Wild, Critically Endangered, Endangered, and Vulnerable.

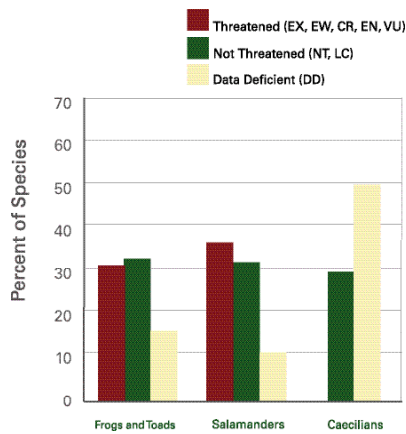
TABLE 5

EXTINCT AMPHIBIANS OF THE NEW WORLD

TAXONOMIC GROUP	SCIENTIFIC NAME	COMMON NAME(S)	COUNTRY	LAST SEEN ALIVE
FROGS & TOADS				
Bufoinae	<i>Atelopus ignescens</i>	A harlequin toad; jambato	Ecuador	1988
Bufoinae	<i>Atelopus longirostris</i>	A harlequin toad	Ecuador	1986
Bufoinae	<i>Atelopus vogli</i>	A harlequin toad	Venezuela	1933
Bufoinae	<i>Bufo periglens</i>	Golden toad; Sapo dorado	Costa Rica	1989
Hylidae	<i>Phrynomedusa fimbriata</i>	A leaf frog	Brazil	1920s
Leptodactylidae	<i>Eleutherodactylus chrysozetetes</i>	A rain frog	Honduras	1989
Leptodactylidae	<i>Eleutherodactylus milesi</i>	A rain frog	Honduras	1983
Ranidae	<i>Rana fisheri</i>	Las Vegas leopard frog	United States	1942
SALAMANDERS				
Plethodontidae	<i>Plethodon ainsworthi</i>	Ainsworth's salamander	United States	1964

these cases, the species seem to have disappeared since 1980. Outside of the New World, four species have gone extinct since 1980 and four others are possibly extinct in the same span. In sum, all but eight of the 122 amphibian species worldwide that scientists know or suspect to have gone extinct since 1980 are New World species. Extinctions are therefore a recent, ongoing, and widespread event in amphibians, and concentrated on New World species. Some of these species may turn out to have remnant populations, but further searching could well indicate that many of them are indeed gone.

FIGURE 9
COMPARISON OF MAJOR RED LIST CATEGORIES BY TAXONOMIC GROUP



COMPARISON TO BIRDS AND MAMMALS

How do the numbers of threatened species reported here for amphibians compare to those for other kinds of animals? After all, environmentalists have been sounding the extinction alarm for decades now. Are amphibians any worse off than other groups?

The only other groups available for accurate comparison are the birds and mammals. No other animal or plant group has been exhaustively assessed for IUCN status for the entire New World. This comparison shows that a far greater percentage of New World amphibians fall into each of the Red List threat categories than do species of either birds or mammals from the region (Figure 10). Amphibians are five to seven times more likely to be Critically Endangered, three to six times more likely to be Endangered, and about twice as likely to be Vulnerable as are birds or mammals. Conversely, only 61% of amphibians fall into one of the unthreatened or data deficient categories, as opposed to 84% of mammals and 90% of birds. Overall, 10% of New World birds and 16% of New World mammals are threatened, contrasting with 39% of all New World amphibians. Clearly, amphibians face risks far in excess of those experienced by other well-studied groups

Endemic species of frogs, often with ranges restricted to a single mountaintop, are especially at risk of extinction.



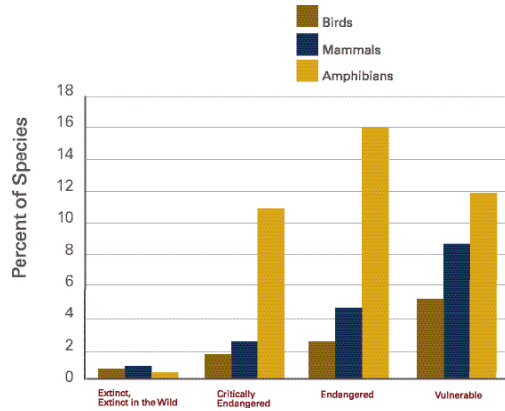
Left: *Elachistocleis ovalis* (an oval frog). *Least Concern.* Panama, Colombia, Venezuela, Trinidad and Tobago, Bolivia, Paraguay, Brazil. / Photo by Forrest Brem.

Middle: Spring salamander (*Gyrinophilus porphyriticus*). *Least Concern.* Canada and United States. Usually found in springs, seeps, and caves. / Photo by Geoff Hammerson.

Right: Darwin's frog (*Rhinoderma darwini*) with offspring. *Vulnerable.* Argentina and Chile. Male Darwin's frogs swallow their mate's eggs to incubate them in their vocal sacs. After a few weeks, the young emerge from their fathers' mouths as fully developed froglets. / Photo by Michael and Patricia Fogden.

FIGURE 10

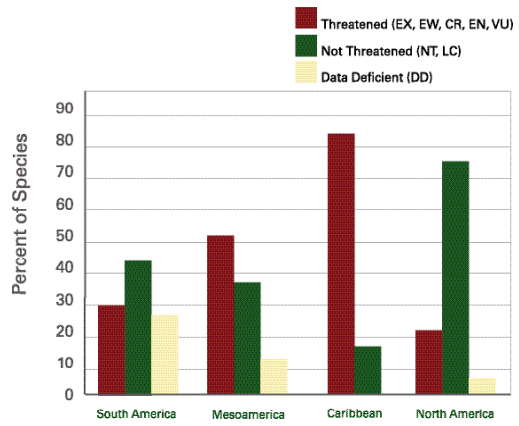
COMPARISON OF STATUS OF NATIVE NEW WORLD AMPHIBIANS, BIRDS, AND MAMMALS



Bird data from BirdLife International²⁸; mammal data from the World Conservation Union²⁹ and NatureServe^{30,31}.

FIGURE 11

COMPARISON OF MAJOR RED LIST CATEGORIES FOR AMPHIBIANS BY REGION



REGIONAL STATUS

Threat levels affecting amphibians vary widely among regions (Figure 11). In the Caribbean, where most species have small geographic ranges within single islands and habitat destruction is rampant, four-fifths of all species are threatened. On the other end of the spectrum is North America, where “only” one-quarter of the species are threatened. Half of Mesoamerican species are threatened, as are nearly a third of South American species. Scientific knowledge is best for Caribbean species, none of which fell in the Data Deficient category. The biggest challenge for scientists is South America, where a quarter of all species (532 in total) are too poorly known to classify.

SOUTH AMERICA. While threatened species occur in every South America country, they cluster in two distinct areas (Figure 12). The first includes the Cordilleras Occidental and Central in the Colombian Andes, continuing south into Ecuador on the Cordilleras Occidental and Oriental (see Box 6). The second is in the central Atlantic Forest of Brazil along the Serra do Mar, centered on Rio de Janeiro and southeastern São Paulo states (see Box 7). The Andes are considerably steeper and higher in elevation, but concentrations of threatened species are similar in the two areas. The most secure faunas occur in the Orinoco and Amazon River drainages, the caatinga-cerrado-Pantanal region of central and northeastern Brazil, the Gran Chaco of Bolivia, Paraguay, and Argentina, and the Pampean and Patagonian regions of Argentina.

FIGURE 12

DISTRIBUTION OF THREATENED AMPHIBIANS IN SOUTH AMERICA



Telmatobius: A Vanishing Genus of High Andean Frogs

(with Andrés Merino-Viteri)



Although many tropical frogs are noteworthy for their spectacular color patterns, the Lake Titicaca frog, *Telmatobius culeus*, is renowned instead for its bizarre shape. This giant frog—30 centimeters in length—has such baggy skin that it looks like it is wearing a suit three sizes too big. Its looks and restriction to the world's highest navigable lake have earned the frog attention from Jacques Cousteau and international nature magazines³². The Lake Titicaca frog, however, is but one of a group of 51 species in a genus that is threatened in ways that are emblematic of many amphibians.

Telmatobius frogs are aquatic lake and stream-dwelling frogs distributed in the Andes from Ecuador to northern Chile and Argentina at elevations usually exceeding 3,000 meters. The champion is *T. marmoratus*, which naturally occurs as high as 5,000 meters. To adapt to such elevations, these frogs use their skin to obtain oxygen from the water and highly efficient hemoglobin to bring the oxygen to their body tissues.

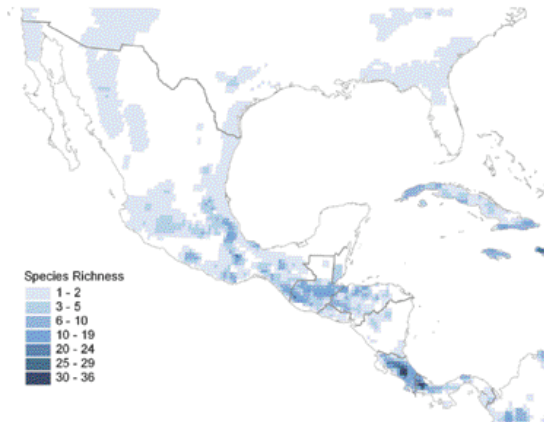
Scientists have not found any of the three Ecuadorian species for the last 10 years, despite numerous scientific expeditions to known localities. Museum specimens of *T. niger* collected before the declines show evidence of *Batrachochytrium dendrobatidis*, a disease-causing fungus that has devastated amphibian populations worldwide, including Ecuador. This disease, another fungus, and climatic abnormalities may have played a role in the Ecuadorian declines^{33,34}.

In Peru and Bolivia, large *Telmatobius* frogs from the Andean lakes of Junín, Titicaca, and others are harvested in great quantities for local consumption and to serve in restaurants to adventuresome tourists³⁵. In addition, frogs are caught and killed to produce a supposed elixir that is gaining in popularity as an alternative to Viagra. Uncontrolled commercial harvests may have caused dramatic declines in species from this region.

Herpetologists have recently described a number of *Telmatobius* species from isolated small water bodies in dry desert habitats from the Andes of Chile and Argentina³⁶. With large expanses of unsuitable habitat between populations, these species are highly vulnerable to human and agricultural uses of the water where they live. Seventy percent of *Telmatobius* species occur outside of protected areas. Considering the threat from disease and loss of habitat quality, this is a group that urgently needs habitat protection, population monitoring, and for some species, the establishment of captive populations that can be used as a source of animals for reintroduction into restored habitats.

FIGURE 13

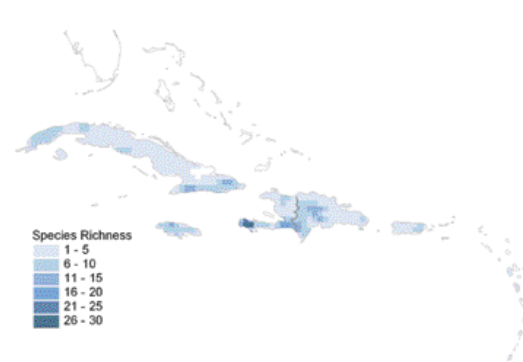
DISTRIBUTION OF THREATENED AMPHIBIANS IN MESOAMERICA



MESOAMERICA. Mesoamerica has multiple centers of threatened species (Figure 13). The greatest concentrations occur in the Chiriquí highlands of western Panama and the Cordillera Volcánica Central of Costa Rica. Many threatened amphibians also exist in the Cordilleras de Talamanca and Tilarán in Costa Rica; the northern and western highlands of Honduras; the Guatemalan highlands; and eastern Chiapas, central Oaxaca, and the eastern portion of the Central Volcanic Belt in Puebla and Veracruz, Mexico. Areas with few threatened species can be found in both mountainous (Chihuahua, Mexico) as well as lowland areas (Yucatán Peninsula-northern Belize, Honduran and Nicaraguan Mosquitia, and lowland coastal Panama).

FIGURE 14

DISTRIBUTION OF THREATENED AMPHIBIANS IN THE CARIBBEAN



CARIBBEAN. As in Mesoamerica, concentrations of threatened species are spread widely in the Caribbean (Figure 14). Each of the Greater Antilles supports at least one center of threatened species. On Cuba, these areas are in the Sierra de los Órganos in the west and the Sierra Maestra in the east. On Jamaica, threatened species are concentrated in the Cockpit Country in the western interior. On Hispaniola, which is divided into the countries of Haiti and the Dominican Republic, critical areas are the Cordillera Central and Tiburon Peninsula. And on Puerto Rico, threatened species cluster in the Cordillera Central.



Facing page, upper: Lake Titicaca frog (*Telmatobius culeus*). *Critically Endangered*. Peru and Bolivia. Endemic to Lake Titicaca, this species is in serious decline due to overharvesting for fish bait and human consumption. / Photo by © Peter Oxford/naturepl.com.

Facing page, lower: Tonico de Rana, or Frog Tonic, a drink made from *Telmatobius* frogs, is popular in some South American countries due to its supposed medicinal properties. / Photo by Bruce Young.

This page, left: *Hyla pardalis* (a tree frog). *Least Concern*. Brazil. *Hyla pardalis* is found across large portions of Brazil's Atlantic Forest, one of the two greatest centers of amphibian diversity in the New World. / Photo by Paula Cabral Eterovick.

This page, middle: *Atelopus zeteki* (a harlequin frog). *Critically Endangered*. Panama. / Photo by Forrest Brem.

This page, right: Puerto Rican crested toad (*Bufo lemur*). *Critically Endangered*. Puerto Rico and British Virgin Islands. With a very restricted range and observed population declines of 80% over the last ten years, this species is in imminent danger of extinction. / Photo by Wayne Van Devender.

FIGURE 15

DISTRIBUTION OF THREATENED AMPHIBIANS
IN NORTH AMERICA



NORTH AMERICA. North America has by far the most secure amphibian fauna of the New World. There are no concentrations of threatened species of the same scale as those found in the rest of the hemisphere (Figure 15). Instead, threatened species are scattered in coastal and southern regions from the Pacific Northwest to southern California and eastward through southeastern Arizona, southwestern New Mexico, and Texas, to southern South Carolina. Additional threatened species occur in the Great Smoky Mountains. In the rest of the continent, many species are declining locally, such as the western toad (*Bufo boreas*) in the western United States, but no species is threatened with global extinction. Only one threatened species, the Oregon spotted frog (*Rana pretiosa*), occurs as far north as Canada.

All but 8 of the 122
amphibian species worldwide
that scientists suspect to have
gone extinct since 1980 are
New World species.

STATUS BY COUNTRY

New World countries span the gamut from those that harbor virtually no threatened species (e.g., Paraguay, Suriname, and Canada) to countries in which nearly every native species is threatened (e.g., Haiti and the Dominican Republic) (Figure 16). The nations with the greatest fraction of their faunas threatened are all in the Caribbean— island nations home to species with very small ranges. If the population of a restricted range species is decreasing even moderately, Red List criteria place it in one of the “threatened” categories. Widespread tourist development, conversion of habitat to agricultural uses, and the consequences of human poverty (in some places) have caused the populations of numerous frogs to decline in the Caribbean.

On the mainland, countries in the temperate zones (e.g. U.S., Canada, Argentina, Uruguay) or those dominated by lowlands where species tend to have broad distributions (e.g. Belize, Guyana) have much more secure faunas. Mountainous tropical countries tend to harbor many species with small ranges that are much more sensitive to habitat destruction. These countries therefore have a higher portion of their fauna with threatened status (e.g. Mexico, Guatemala, Ecuador).

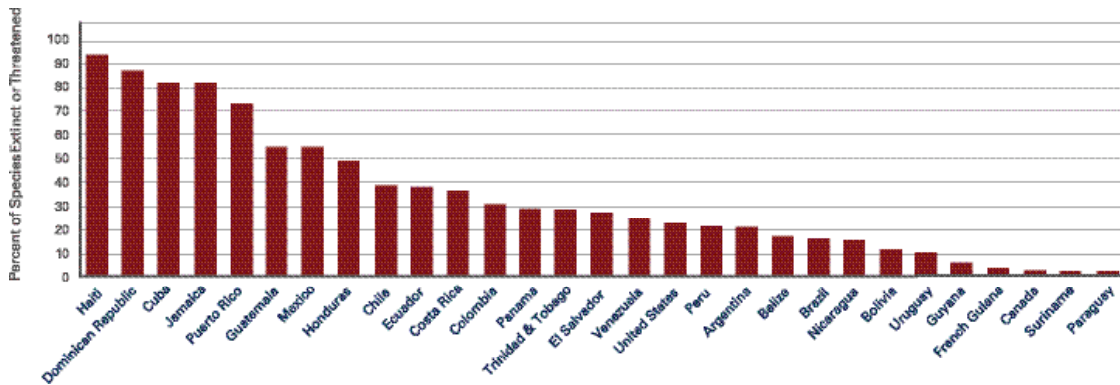
The fact that a nation has a significant portion of its species in threatened categories does not necessarily reflect on its biodiversity protection efforts. In Costa Rica, for example, despite an extensive system of protected areas in its highlands, 35% of the species are threatened. There amphibians have been devastated in montane areas even within parks, probably due to disease, climate change, or a combination of both factors. In Uruguay, conversely, just 4 of 43 species are threatened, but the country has no system of national parks or protected areas. Most of Uruguay’s species are widespread, occurring in Argentina and Brazil as well, where they find some legal habitat protection.

ECOLOGICAL FACTORS

Amphibians vary considerably in the habitats they occupy, the elevations where they occur, and their distributional extent. How do these factors correlate with threat status? First, threatened species are more likely than non-threatened species to be entirely terrestrial (47% versus 28%, respectively), and less likely to occur in both terrestrial and aquatic habitats during different life stages (50% versus 71%). Few species are entirely aquatic (4% of threatened and 2% of non-threatened species). The pattern is somewhat complicated because species that are Critically Endangered are more likely to have an aquatic phase of their life cycle than other threatened species. Second, higher elevation faunas are much more threatened than lower-elevation faunas (Figure 17). Finally, species with smaller distributional ranges are much more likely to be threatened than species with larger ranges (Figure 18), a result that is not surprising considering that small range size is part of the Red List criteria. This analysis leaves us with a picture of terrestrial, montane, range-restricted species typically being most threatened while lowland species that occur in both aquatic and terrestrial habitats over large areas are the least likely to be threatened.

FIGURE 16

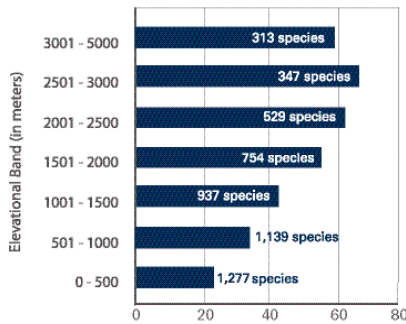
PROPORTION OF EXTINCT AND THREATENED AMPHIBIANS IN NEW WORLD COUNTRIES AND TERRITORIES



Only countries/territories with more than 15 native amphibian species are shown.

FIGURE 17

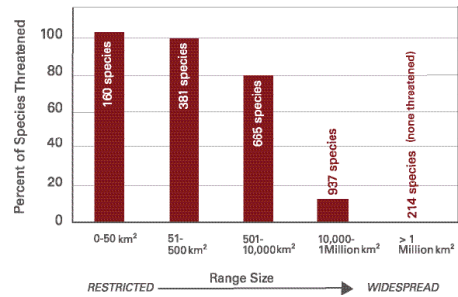
PROPORTION OF THREATENED SPECIES BY ELEVATION



Percent of Species Extinct or Threatened
Many species occur in more than one elevational band.
Data deficient species not included.

FIGURE 18

PROPORTION OF THREATENED SPECIES BY SIZE OF SPECIES RANGE



Left: *Hyalinobatrachium colymbiphellum* (a glass frog). Least Concern. Costa Rica, Panama, Colombia. While amphibian reproduction is popularly associated with ponds and streams, many frogs reproduce through direct deposit of their eggs on leaves or other vegetation. / Photo by Forrest Brem.

Middle: Tadpoles begin to form within the eggs of the red-eyed leaf frog (*Agalychnis callidryas*). / Photo by Piotr Naskrecki.

Right: *Centrolene prosoblepon* (a glass frog). Least Concern. Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador. The developing frog pictured during its metamorphosis from tadpole to adult. / Photo by Ross Alford.

Unwelcome Silence: The Lost Frogs of the Brazilian Atlantic Forest

(with W. Ronald Heyer and Sergio Potsch de Carvalho e Silva)



In 1975, Smithsonian Institution herpetologist Dr. Ron Heyer set out to understand the biogeography of frogs in the Atlantic Forest, a formerly continuous strip of rainforest extending along the coast and coastal mountains of eastern and southeastern Brazil. Biogeography is the study of how organisms have diversified, dispersed, and come to occupy the ranges where we find them today. Heyer selected a group of stream-dwelling frogs in the genus *Cycloramphus*, an obvious choice for the study because the adults are easy to find calling at night along fast-flowing streams. The tadpoles are also conspicuous because they tend to cling to rocks bathed in spray from adjacent waterfalls. At the time, taxonomists recognized 10 species in the genus, all endemic to the Atlantic Forest.

For an introduction to the frogs, Heyer enlisted the help of Rio de Janeiro herpetologist Sergio Potsch de Carvalho e Silva. Carvalho e Silva brought Heyer to a nearby stream one night where male *Cycloramphus* were calling. Over the next five years, Heyer tramped up and down streams along the length of the Atlantic Forest collecting frogs. By the time he finished, he had doubled the number of known species of the genus *Cycloramphus*³⁷.

In the early 1980s, Heyer returned to Boracéia, a site where he had reliably found two species during his sojourns of the 1970s. To his surprise, both *Cycloramphus* and several other previously common frogs were nowhere to be found³⁸. In the 1990s, Carvalho e Silva began visiting a relative's mountain retreat near Teresopolis, located in the Atlantic Forest of Rio de Janeiro state near another of Heyer's original collecting localities. Despite repeated searches of the streams at night, he never could find the populations that Heyer had found so easily two decades previously. Meanwhile, herpetologists Paulo Garcia in Santa Catarina and Magno Segalla in Paraná were revisiting Heyer's old field sites in their states, finding populations either gone entirely or greatly reduced in abundance. Although one species that disappeared, *C. fuliginosus*, has subsequently rebounded, no one has seen 13 of the 18 stream-dwelling *Cycloramphus* species in the last 20 years.

What happened to all of these frogs? Without monitoring data for any of the populations, we will never know for sure. However, the observation of montane stream-associated frogs disappearing despite no obvious loss in habitat fits the pattern recorded elsewhere in tropical America. A hypothesis that scientists are currently working on is that a combination of a trend toward dryer weather and disease may have finished off a number of these populations. A particularly harsh frost in 1979 may have caused the disappearances at Boracéia³⁸. Whatever the reason, montane streams in the Atlantic Forest are now quieter at night.

Top: *Cycloramphus izecksohni* (a tropical frog). Data Deficient. Brazil. This species is known only from isolated sites in the Atlantic Forest of southern Brazil. It and other *Cycloramphus* species from this area seem to be rapidly disappearing. / Photo by Magno Segalla.

Bottom: This waterfall in Brazil's Atlantic Forest is typical of the habitat where *Cycloramphus* frogs once were commonly found. / Photo by Bruce Young.



Threats to Amphibians

What is causing so many amphibian species throughout the New World to be threatened? Two major factors appear to be at play. First, the loss of suitable quality habitat is clearly the reason most species enter into one of the threat categories. Fully 89% of all threatened species suffer from habitat loss (Figure 19). The most important factors causing habitat loss include conversion to agriculture, timber harvesting, mining, and the development of infrastructure, including housing, industry, roads, and dams (Figure 20). Fires also degrade habitat for a number of species.

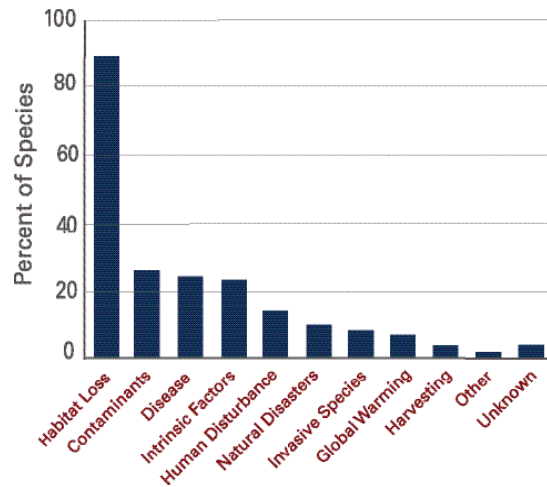
Focusing on the Critically Endangered species shows that a second factor is causing the most rapid declines and disappearances of species, outpacing habitat destruction in many cases. In 158 (47%) of the Critically Endangered species, population declines in the absence of habitat loss are linked to or show patterns associated with the effects of a newly identified fungal disease, possibly working in concert with climate change. These species tend to inhabit mid to high elevations, are often associated with streams, and tend to disappear without any obvious destruction to their habitats¹⁴. The pattern is more pronounced in the “possibly extinct” species (those with no known populations, but lacking sufficient searching to verify extinction), of which 74 species (65%) have or may have been affected by disease.

About one-fourth of all threatened species are threatened by environmental contaminants, disease, and intrinsic factors such as small range size or limited ability to disperse. Human disturbance, including tourist activities, fires, and armed conflicts, affects 13% of threatened species. Natural disasters (such as droughts, floods, and wildfires), invasive species, and global warming each affect about eight percent of species. Harvesting for consumption, the pet trade, or scientific research is a cause of decline for just three percent of threatened species.

For one set of risk factors, including habitat destruction, invasive species, and harvesting, determining that they cause amphibian declines is a straightforward process. When forests are cut down, forest-dwelling species will decline sharply or disappear. When collectors export thousands of frogs, native populations suffer. The ecological basis for these processes is well understood. For other risk factors, however, including disease, global warming, and contaminants, scientists are much more challenged to demonstrating cause and effect³⁹. A diseased frog may crawl under a rock to die and never be seen by a scientist. Especially in tropical habitats, dead animals decompose in a matter of hours leaving no trace. Pesticides can blow in on the wind and debilitate animals such that they are more susceptible to disease. Finding pesticide residues in wild

FIGURE 19

COMPARISON OF RISK FACTORS AFFECTING THREATENED AMPHIBIANS



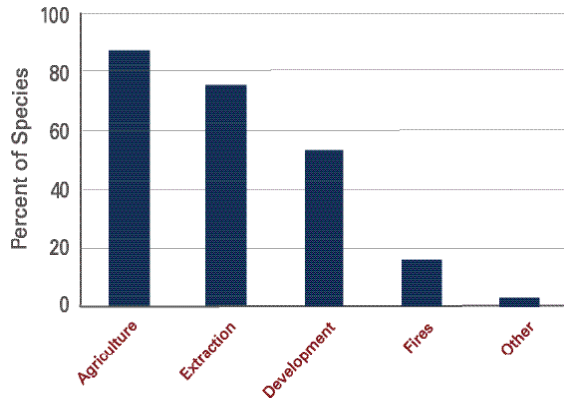
Based on analysis of 1,177 threatened (CR, EN, and VU) species. Note: more than one factor can threaten a species.

animals is a difficult task, and proving that these chemicals were the cause of death is even more challenging. For this reason, statistics on the exact number of species affected by a particular cause will always be approximate, and scientists must look at characteristic patterns of decline to infer cause.

Top: Red-eyed leaf frog (*Agalychnis callidryas*). Least Concern. Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and Colombia. /Photo by Forrest Brem.

FIGURE 20

CAUSES OF HABITAT LOSS AFFECTING THREATENED AMPHIBIANS



HABITAT LOSS

The complex habitat needs of amphibians present a special challenge for conservation. Some species are entirely terrestrial. Some are entirely aquatic. Most use both habitat types during different stages of their life cycle, meaning that land managers must protect both natural lands and waters in order to maintain amphibian diversity.

Our growing human population and its demand for food, shelter, energy, and consumer goods continue to drive the destruction of habitats throughout the hemisphere. Although population growth rates are substantially lower than they were in the 1960s and 1970s, most countries are still growing. The United Nations' mid-range estimate for Latin America and the Caribbean projects that the human population will swell 48% to 768 million people by 2050. Similarly, the UN projects the population of North America to increase 42% to 448 million people over the same period⁴⁰. All of these people will place additional burdens on our natural resources, and amphibians and other wildlife will be pushed further to the margins of their existence.

Forest cover continues to diminish. During the 1990s alone, South America lost four percent of its forest cover and the islands of the Caribbean lost a whopping ten percent. North America had essentially no net change in forest cover during the last decade⁴¹, but this seemingly favorable circumstance masks the loss of old growth and mature forest that was replaced by much younger forests, which generally are much less favorable as amphibian habitat. Our compilation of the causes of habitat loss directly affecting amphibians shows that agriculture, logging, and development are most important. In many areas, logging occurs first, then land is cultivated, and finally development

eats up farm land. The details vary with geography. For example, in Chile, native southern beech (genus *Nothofagus*) forests are being replaced directly with plantations of introduced pines where few amphibians can persist. In Colombia, coca farmers clear patches of forest in a cat and mouse game with authorities. In Honduras, subsistence farmers relentlessly push back the agricultural frontier. In the northwestern United States, pressure persists to fell more old-growth forest. Whatever the process, the result is the same for amphibians.

Wetlands are disappearing, too, but at a rate that is much more difficult to quantify. Although large wetlands are detectable in satellite imagery, the forested swamps, small creeks, springs, and temporary pools that are essential for the reproduction of many amphibians simply do not show up. Thus scientists are challenged to monitor change in the availability of wetlands. In the United States, the Fish and Wildlife Service estimates that wetlands loss has slowed sharply in recent decades to 23,700 hectares per year or 0.05% of the total wetlands area⁴². This is an encouraging sign and a tribute to the power of effective legislation.

The leading threats to amphibians are habitat loss and the chytrid disease, with pesticides, climate change, invasive species, and illegal trade also taking their toll.

In other countries, standardized data on change in the extent of wetlands are virtually nonexistent⁴³. Some of the world's most spectacular wetlands are found in South America, including the Orinoco and Amazon River drainages, the Llanos wetlands in Venezuela and Colombia, the Pantanal of Brazil, and the wet chaco of Paraguay and Argentina. But these natural wonders, together with rivers throughout the hemisphere, are threatened by dams that disrupt natural hydrological regimes. Brazil, for example, obtains 90% of its energy from hydroelectric plants⁴⁴, and power companies everywhere are regularly prospecting for new dam sites. Wetlands monitoring and the development of strategies to ameliorate the negative effects of hydroelectric projects on amphibians and other aquatic wildlife are priorities for future work.

DISEASE

Until about 15 years ago, few people who worked with amphibians paid much attention to diseases. Zookeepers of course were worried about diseases striking their animals, but field researchers rarely had any reason to suspect diseases were much of a factor in the dynamics of the populations they studied. Dr. John Lynch, the taxonomist who has discovered more new species of amphibians in the world than anyone else, recalled that prior to 1997 he “had never seen more than 2-3 dead or dying frogs in a single field season”⁴⁵. If field researchers did not see dead or dying frogs then how could disease be an important mortality factor?

Although certain natural pathogens have long been known to attack amphibians, none had been implicated in widespread declines. By the 1990s, however, scientists began to suspect that diseases might be playing a role in cases where amphibian populations were crashing in otherwise undisturbed habitats. In 1996, Dr. William Laurance and colleagues looked at the pattern of disappearances of 14 species of frogs endemic to Australia’s east coast and concluded that only an emerging, highly pathogenic disease could explain the pattern⁴⁶. By that time, several sites in Costa Rica had lost substantial numbers of species, and some frogs and toads in western North America had inexplicably declined⁴⁷⁻⁴⁹. Scientists were frustrated because examination of dead frogs revealed no known pathogen that could have caused such widespread mortality.

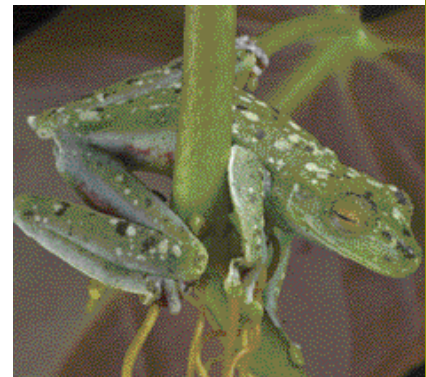
The mystery was resolved in 1998 when scientists used an electron microscope to examine skin sections of dead Central American and Australian frogs. They found a previously unknown fungus, now named *Batrachochytrium dendrobatidis*^{50,51} (see also <http://lifesciences.asu.edu/lifeceba/amphibians/>). *B. dendrobatidis*, referred to as *Bd*, belongs to a group of fungi called chytrids, which were not known to be pathogenic to vertebrates. Chytrids occur naturally in diverse ecosystems and play an important role in digesting proteins such as chitin from insect exoskeletons, cellulose from plants, keratin from hair and skin, and pollen^{52,53}. In amphibians, *Bd* appears to attack keratin in the beaks of tadpoles and the skin of adults. The exact mechanism of death is still unknown. *Bd* may produce a toxin that kills the host, or perhaps they affect the passage of moisture, nutrients, or contaminants across the permeable skin.

Three aspects of the biology of *B. dendrobatidis* help explain patterns of amphibian decline. First, this chytrid will grow in culture only in cool temperatures. This may explain why montane species are more likely to decline than lowland species⁵⁴. Second, like most chytrids, *Bd* appears to occur only in aquatic habitats, which would explain why amphibians

that spend at least part of their life cycle near streams are more likely to decline. Third, *Bd* affects primarily the keratinized beak of tadpoles, explaining why tadpoles in affected areas can be missing their beaks.

These observations raise many questions about the role of chytrid disease in amphibian declines. Have *Bd* outbreaks been occurring all along, unnoticed until now? Or is it a disease that has only recently spread to much of the world, wiping out native populations that have not evolved defenses against the disease? How does *Bd* move from place to place? How is the disease transmitted from individual to individual?

In an attempt to answer the question of origin, Erica Morehouse and colleagues looked at the genetic variation of *Bd* strains isolated from wild amphibian populations in North America, Africa, and Australia. Their DNA analysis suggested that chytrids have recently spread worldwide from a single source⁵⁵. Dr. Patricia Burrowes and colleagues examined 106 museum specimens of frogs collected on the island of Puerto Rico from 1961 to 1978. The earliest they detected chytrids was on a specimen collected in 1976, suggesting a recent arrival of the disease to that island⁵⁶. Inspection of amphibian specimens elsewhere shows that *Bd* was present in the United States as early as 1974 and in Australia as early as 1978^{57,58}.



Above: *Hyla rufitela* (a tree frog). Least Concern. Nicaragua, Costa Rica, Panama. A native of humid lowland forest, *Hyla rufitela* is a widespread species—making it more able to withstand habitat loss and habitat modification than amphibians with restricted ranges. /Photo by Piotr Naskrecki.

Malformed Frogs: Leaping to the Wrong Conclusion?

(with Stanley K. Sessions)



In 1995, a group of Minnesota schoolchildren made an unsettling discovery at a neighborhood pond. They spied a large number of leopard frogs swimming with horrible deformities, including some with extra hind limbs. The school kids contacted the Minnesota Pollution Control Agency which helped them put their observation on the Internet. The national media picked up the story and finally the Environmental Protection Agency got involved. What could be a more convincing harbinger of environmental collapse than our children finding “Frankenstein frogs” in the ponds near where we live? Could these deformities indicate toxic chemical pollution or dangerous UV irradiation? Are these deformities related to the general collapse of amphibian populations?

It turns out that the likely cause of the deformities was known. In 1990, Dr. Stanley Sessions of Hartwick College and colleague S. B. Ruth described how trematode flatworms can cause extra limbs to grow in developing tadpoles⁶⁶. Subsequent research has confirmed that trematodes are the most likely cause of amphibian malformations in North America^{67,68}. How do these little worms cause such striking changes in their hosts?

The trematode that infects frogs attacks three different hosts during its life cycle. These trematodes (the genus *Ribeiroia* appears to be the only deformity-causing trematode in North American frogs) need to infect aquatic birds in order to complete their life cycles and produce more adult worms, but they must first undergo embryonic development inside of a pond snail. To do that, the worm’s eggs enter pond water in bird excrement, and the first larval stage, called miracidia, hatches and infects snails. Each miracidium then produces numerous worms of the second larval stage, called cercariae, which develop inside the snail host. The parasite now has a problem: How does it get back into its primary host (birds) to complete its life cycle? These cercariae swim until they find a tadpole where they form cysts (called metacercariae) exactly where limbs will soon form. The cysts disrupt natural limb development causing extra legs and other limb deformities. A frog with extra or badly deformed legs cannot swim or hop well, so it falls easy prey to aquatic birds—exactly what the trematode “wants” in order to finish its life cycle.

Researchers thought at one time that pesticide runoff, particularly retinoid chemicals (such as methoprene, used for mosquito control), caused limb deformities in wild frogs. Although retinoids can cause distinctive deformities in frogs in a laboratory setting, the kinds of deformities seen in the field more closely match those caused by trematode worms.

While deformities can depress frog populations locally, they are unlikely to explain declines globally. Many amphibians that have declined reproduce in fast-flowing streams, temporary pools, or directly in moist leaf litter, all microhabitats where the snail intermediate host does not occur. Observations of mass die-offs of frogs rarely record deformed frogs among the dead. Thus deformities are more a function of local parasite and snail population dynamics (which may be influenced by human-induced degradation of wetlands) and as yet have no connection to global declines.

Details about transmission and movement of the disease are still sketchy. Certainly an uninfected animal can become infected when it enters a body of water that has been contaminated by diseased individuals⁵⁹. Outside of the water, it appears that only physical contact between animals can transmit the disease. Long-distance dispersal appears to occur only when infected frogs themselves move, usually with human help. For example, *Bd* leapfrogged from eastern to western Australia by hitchhiking on a frog that stowed away in a crate of fruit⁶⁰.

The chytrid disease—unknown a decade ago—is striking down amphibian populations even in pristine protected areas.

Does this mean that *Bd* is to blame for all amphibian declines in protected areas? Possibly, but we may never know for sure. Other factors cited here—pesticide drift, other diseases, and climate change—play a role. Most frogs die without any witnesses around to collect a specimen. For innumerable populations that simply disappeared, we will never be certain of the cause. Nevertheless, we now have enough data to conclude that *Bd* outbreaks, possibly in concert with changing climates, have contributed significantly to the decline of amphibian populations^{58,61,62}.

PESTICIDES

Beginning in the 1950s, technological advances have dramatically changed the way we grow our food crops, increasing yields substantially. A cornerstone of this “green revolution” is the cornucopia of pesticides now used by the world’s farmers to control weeds, diseases, and animal pests. Data from the Food and Agriculture Organization of the United Nations (FAO) show that pesticide use in the Americas remained high during the period 1990-2000, averaging several kilograms per hectare of cultivated land⁶³.

Pesticides vary tremendously in their toxicity and permanence in the environment. Some of the worst in terms of their effects on wildlife have been banned, but many others remain on the market. Rains and winds cause these chemicals to be washed or blown into natural habitats surrounding agricultural areas where they can harm native species^{64,65}. Amphibians, with their permeable skin and aquatic habits, might be particularly susceptible to these chemicals. Amphibians also consume large amounts of insects, including aquatic insects. If prey animals are contaminated with pesticides, then these substances can build up over time in amphibian tissues, leading in some cases to death or malformation (see *Box 8*).

Information on the effects of pesticides on amphibian populations is limited, but wind- and water-borne pesticides could potentially explain declines in sites where no obvious habitat loss has occurred. One place where the interaction between pesticide use and amphibian populations has been studied is California, one of the most intensively farmed regions of the world. In 1998 alone, California farmers used 90 million kilograms of pesticides⁶⁹. Previous work has shown that winds blow pesticides long distances from where they are applied and that wild amphibians in California can have traces of agrochemicals in their tissues, suggesting a possible causal link. Dr. Carlos Davidson and colleagues analyzed the spatial patterns of pesticide drift and declines in eight amphibian species. In four of these species—the red-legged frog (*Rana aurora*), Cascades frog (*Rana cascadae*), foothill yellow-legged frog (*Rana boylei*), and mountain yellow-legged frog (*Rana muscosa*)—declines were more likely in populations directly downwind of large agricultural areas than in populations downwind of land with relatively little agricultural activity⁶⁹. This pattern, repeated in different parts of the state and for different frog species, strongly suggests a roll for pesticides in amphibian declines in otherwise undisturbed habitat. In Latin America, studies of the effects of contaminants on amphibians are just beginning^{70,71}, but the volume of pesticides applied in agricultural areas strongly warrants further investigation.



Facing page: A malformed bullfrog (*Rana catesbeiana*). The growth of its extra legs is caused by parasitic worms. / Photo by Stanley K. Sessions.

This page, upper: Red-legged frog (*Rana aurora*). Near Threatened. Canada, United States, Mexico. Population declines of this species in California are linked to pesticides used in agriculture as well as habitat loss. / Photo by Wayne Van Devender.

This page, lower: California giant salamander (*Dicamptodon ensatus*). Near Threatened. United States. With their permeable skin and reliance on aquatic habitats, salamanders and other amphibians are especially sensitive to man-made chemicals in the environment. / Photo by Geoff Hammerson.

Fish Tale: Introduced Trout in the High Sierra

(with Roland A. Knapp)



Intrepid hikers who venture to the high peaks of the Sierra Nevada in Yosemite National Park are rewarded with vistas of pristine lakes and stunning mountain ranges apparently unchanged since the days when John Muir walked those same ridges and was inspired to pen his revolutionary wilderness philosophy. Yet a careful reading of Joseph Grinnell and Tracey Storer's 1924 classic *Animal Life in Yosemite* reveals something missing from those lakes today: frogs. Whereas Grinnell and Storer reported that frogs were abundant in many of these lakes, a visitor now is hard-pressed to find a single one.

What happened in these lakes, seemingly in one of the most unspoiled parts of western North America? In the 1990s, scientist Roland Knapp set out to find an answer. Peering into those lakes, Knapp found something that Grinnell and Storer rarely saw: trout. Over the last century, angler groups and the state of California have stocked these historically fishless lakes with trout for recreational fishermen. Following on the pioneer observations of David Bradford⁸², Knapp wondered if the fish might have eaten the frogs to local extinction. He first surveyed 1,700 lakes and ponds for fish and mountain yellow-legged frogs (*Rana muscosa*), the species historically present there. Bodies of water without fish were three times more likely to have frogs than those with fish, suggesting that Knapp's hunch was on the mark⁸³.

Next, colleague Vance Vredenburg experimentally removed all fish from selected frogless lakes. Within a short time, frogs appeared and successfully reproduced and populated the lakes. Vredenburg also confirmed that trout eat tadpoles as they hatch⁸⁴. These results strongly suggest that introduced trout are the critical factor in the disappearance of mountain yellow-legged frogs from much of the Sierra Nevada. Fortunately, remnant populations remain that can recolonize lakes where trout are removed. With thousands of lakes in the Sierra Nevada, there should be enough for both fisherman and frogs.

Top: Kaweah Basin in California's Sierra Nevada is typical habitat for the mountain yellow-legged frog. / Photo by Roland Knapp.

Bottom: Mountain yellow-legged frog (*Rana muscosa*). Vulnerable. United States. Many populations of this frog in California and Nevada have been extirpated due to introduced trout. / Photo by Roland Knapp.

CLIMATE CHANGE

Our climate is changing, and much of this change is due to carbon dioxide and other greenhouse gases released into the atmosphere by human activity⁷². Recent research has shown that climate change is not an abstract possibility, but rather an ongoing event actually happening today with measurable effects on wild organisms. In the north-temperate zone, many plants and animals are stretching their ranges northward. The dates on which some birds lay their eggs, butterflies emerge from their cocoons, and alpine wildflowers bloom are happening earlier. Amphibians are crawling out of their overwintering burrows and starting their mating choruses sooner in the spring than at any time in the last century^{73,74}. What role might these climate changes play in amphibian population declines and extinctions?

Climate change has already altered reproductive timing in temperate frogs, and is strongly linked to disappearances of some tropical species.

Like contaminants, climate change can act on amphibians in a number of ways. The ranges of many species are determined not only by favorable habitats, but by a specific set of environmental conditions such as temperature and precipitation. As climates change, the location of these “climate envelopes” moves across the landscape. Organisms adapted to a particular climate envelope have to move with the envelope to avoid extinction. For example, trees and many other organisms of North America moved back and forth, north and south, during the successive ice ages and interglacial warming periods of the past 200,000 years. Problems arise for species restricted to mountaintops or protected areas surrounded by unsuitable habitat. As the temperature warms, the climatic envelope moves away and species are left with nowhere to go. Although there are as yet no definitive cases of this phenomenon leading directly to the extinction of an amphibian species, it most likely will happen in the next 100 years⁷⁵. In fact, by the end of the century climate change may outpace habitat loss as the most important threat to biodiversity^{75,76}.

The clearest evidence that this process is underway comes from tropical cloud forests, where montane forests are constantly bathed in a cloud-borne mist. Studies have shown that either deforestation or small changes in sea surface temperature upwind can cause the cloud level to rise significantly^{77,78}. Animal distributions in at least one Central American cloud forest are already responding to this change⁷⁹.

Climate change can also have more direct effects on amphibians. A drying trend can mean that temporary pools that some species require for reproduction may dry up before tadpoles have had a chance to complete metamorphosis. Additionally, increased temperatures and/or less precipitation can stress amphibians, leading to greater susceptibility to disease⁸⁰. Thus climate change may also act indirectly by causing local biological changes that increase amphibian mortality.

To draw firm conclusions, we need sites with both comprehensive, long-term climate data as well as long-term population monitoring data. Rarely are both available for the same place. Without data pinpointing the timing of declines and showing climatic trends, documenting a relationship between climate and decline events is impossible. Yet in three tropical sites, highland Costa Rica, Andean Ecuador, and montane Puerto Rico, the requisite combination of population and climate data is available for analysis. In the Costa Rican site, 20 species of frogs and toads, including the golden toad (*Bufo periglenes*), declined or disappeared abruptly in 1988, with subsequent sharp declines of survivors in 1994 and 1998. Each of these decline events occurred during unusual dry periods when the typical cloud-borne mist failed to form⁷⁹. Andean Ecuador was home to the spectacular jambato toad (*Atelopus ignescens*), which suddenly disappeared from 47 sites in the 1980s, just after the two driest years recorded during the period 1962-1998⁸¹. Similarly, drought accompanied the disappearance of three species and the decline of six species of frogs from the genus *Eleutherodactylus* in Puerto Rico⁵⁶. In all of these cases, weather may have interacted with disease to cause the declines (see *Synergistic Effects* below).



Above: *Eleutherodactylus cruentus* (a tropical rain frog). Least Concern. Costa Rica and Panama. This lowland species is doing fairly well, illustrating a trend in which species that live at higher elevations are at higher risk from global environmental changes. /Photo by Ross Alford.

INVASIVE SPECIES

Invasive species brought to foreign lands, whether by intention or accident, are well known to cause extinctions of the native flora and fauna. How have these invasive species affected New World amphibians?

Invasive species are threatening amphibians in a number of ways. Introduced trout that prey principally on amphibian larvae have severely depressed populations of mountain yellow-legged frogs in California (see Box 9). A number of western North American pond-breeding salamanders also suffer population reductions from the presence of introduced trout. Trout have colonized mountain streams from Central America through the Andes as a result of both intentional introductions and escapes from fish farms. Comprehensive studies of the effects of trout on tropical stream amphibians have yet to be undertaken so we do not yet know the impact of this introduced predator on amphibian populations.

Invasive species such as bullfrogs often prey on native amphibians and can contribute to local population declines.

Bullfrogs (*Rana catesbeiana*) are native to eastern North America, but have invaded western North America and parts of the Caribbean and South America. Bullfrogs are widely exported to frog farms that sell frog legs for the local restaurant trade. Some animals, defying their intended fate, escape from their tanks and establish feral populations. These voracious eaters can consume prodigious quantities of food, including tadpoles and adults of native species. In some areas, introduced bullfrogs have played a role in the decline of local leopard frog species.

Even innocuous looking annual plants threaten amphibians. Purple loosestrife (*Lythrum salicaria*), native to Europe, has spread widely in eastern North America. Although its lavender flowers brighten up roadsides throughout its new range, purple loosestrife catalyzes the filling in of seasonal and permanent wetlands. As each wetland disappears, so do the spring choruses of the frogs and toads that need healthy wetlands to reproduce.

TRADE

One of the remotest places in the New World is the Gran Chaco, a dry, low-lying region at the border of Bolivia, Paraguay, and Argentina. There you can be 150 kilometers from the nearest place to buy a soft drink (farther if you want a cold one). Even here, several species of frogs, including horned frogs (genus *Ceratophrys*) and tropical bullfrogs (genus *Leptodactylus*) are starting to miss their annual singing dates that occur with the onset of seasonal rains. The reason? Their odd shapes and coloration (*Ceratophrys cranwelli* looks like a giant mouth with eyes and legs thrown on for decoration) make them prized for the pet trade. Although dealers in destination countries profit the most, the small amounts of cash paid to local collectors explain why they are willing to brave the elements and distance to collect these frogs.

Overall, trade in amphibians for pets, consumption, and scientific use is cited as a factor in the decline of only 36 threatened species (3% of the total). Harvest of frogs and salamanders as a local food source and traditional medicine has affected species such as frogs in the genus *Telmatobius* in Peru and Bolivia (see Box 6), the salamander *Ambystoma dumerili* (the skin of which is made into a medicinal syrup for respiratory ailments by nuns in a convent near Lake Pátzcuaro, Mexico, where the species occurs)⁸⁵, and the mountain chicken (*Leptodactylus fallax*), a large frog consumed on Dominica and Montserrat⁸⁶. International trade is regulated under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), a treaty that has been signed by 160 countries. The existence of a clandestine trade in these amphibians is proven by regular confiscations by customs officials in exporting and importing countries. On the balance, however, commercial trade alone has pushed relatively few amphibians into the ranks of the threatened.

Before the significant development of a global pet trade, several species were harvested for use as pickled specimens to dissect in high school or college anatomy classes. The northern leopard frog (*Rana pipiens*) in North America and the toads *Bufo chilensis* in Chile and *Bufo arenarum* in Argentina have all been collected by the thousands for educational and scientific purposes. These species are generally widespread and abundant (although the northern leopard frog has disappeared from parts of its former range in the midwestern United States) despite decades of persecution. This observation highlights the fact that while some species are threatened by over-harvesting, others can tolerate moderate levels of collecting without suffering serious population level declines.

SYNERGISTIC EFFECTS

Aside from habitat destruction, declines are rarely the result of single causes⁸⁷. Disappearances of the jambato toad in Ecuador and *Eleutherodactylus* in Puerto Rico show a relationship with both unusual climate and the appearance of the chytrid fungal disease^{56,81}. Mortality in boreal toads in the U.S. Pacific Northwest has resulted from of a combination of ultraviolet radiation and *Saprolegnia* fungus⁸⁸. Even in the case of the mountain yellow-legged frog where introduced trout seemed to be a major explanation for declines, *Bd* may also play a role⁸⁹.

Other scenarios are also possible. Bullfrogs on a Uruguayan frog farm tested positive for chytrid disease in 1999. These frogs could have infected local native frogs, or brought the disease with them when they were exported to other South American countries or the United States⁹⁰. The African clawed frog (*Xenopus laevis*) apparently tolerates *Bd* in its native Africa. Worldwide trade in the species in the mid-1900s as a pregnancy assay and later as a laboratory study animal may have spread the disease to susceptible native species⁹¹. The only known long-distance dispersal mechanism for the deadly chytrid disease involves movement on live frogs. Thus transport of frogs not only for meat but also for the pet trade has the potential to spread this disease to more parts of the world.



Top: African clawed frog (*Xenopus laevis*). *Least Concern*. Native to Africa; now introduced to the Western Hemisphere and elsewhere. International trade in this and other exotic species may be a factor in spreading chytrid disease to susceptible native populations. / Photo by Wayne Van Devender.

Second from top: Tropical bullfrog (*Leptodactylus pentadactylus*). *Least Concern*. Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Venezuela, Guyana, Suriname, French Guiana, Peru, Bolivia, and Brazil. / Photo by Piotr Naskrecki.

Third from top: Northern leopard frog (*Rana pipiens*). *Least Concern*. Canada and United States. This common species is widely used for dissection in biology classes. It remains widespread, though it has disappeared in some areas. / Photo by Geoff Hammerson.

Bottom: *Physalaemus olfersii* (a foam frog). *Least Concern*. Brazil. Found in the Atlantic Forest of Brazil, an area under enormous pressure from habitat loss. Less than 10% of the original forest remains. / Photo by Paula Cabral Eterovick.

Can Zoos Save our Frogs? The Role of Captive Breeding

(with Amy J. Lind)



With habitats rapidly disappearing and diseases threatening entire species, zoos may seem like our best option for last-ditch conservation of species on the brink of extinction. To successfully fill the roll of Noah's Ark, zoos have to be able to do two things. First, they must succeed at captive rearing: reproduce animals continually over multiple generations. Second, they must succeed at reintroduction: release animals in the wild to create self-sustaining populations. History has shown that the first task is much easier than the second.

Zoos and governmental hatcheries have been successful at inducing reproduction in a number of threatened species. In Europe, reintroductions of some species such as the Mallorcan midwife toad (*Alytes muletensis*) have been successful⁹⁶. However, New World amphibians have yet to recover from near extinction due to reintroduction efforts.

- Wild populations of Wyoming toads (*Bufo baxteri*) are now gone, but 12 zoos and two government facilities rear the species in captivity. Despite annual introductions of tadpoles and toadlets to Mortenson Lake since 1992, the population is still not self-sustaining⁹⁷.
- Western toads (*Bufo boreas*) have disappeared from many parts of their range in western North America, and they are now on the Colorado state endangered species list. Despite the investment of \$14 million on rearing metamorphs (juveniles that have recently grown their legs and absorbed their tails) and adults in captivity, reintroduction efforts failed to establish any new populations⁹⁸.
- The Puerto Rican toad (*Bufo lemur*) once occurred along the coasts of Puerto Rico as well as in the British Virgin Islands. Today it is restricted to a single population in Guánica National Forest in southwestern Puerto Rico. Although captive rearing has been successful, no reintroduced toads have survived to maturity^{99,100}.

The causes for failure are not clearly understood, but disease and predation are known contributing factors. Reintroductions cannot be successful unless the process that originally threatened a species is stopped before the release of captive-reared animals¹⁰¹. Determining what these threatening processes are is clearly a great challenge, but the midwife toad example shows that it is possible.

A less intensive technique called "head starting," in which eggs laid in the wild are collected, reared to metamorphosis in captivity, and then released in appropriate habitat, is showing some promise. Head starting of three endangered leopard frogs (genus *Rana*) in Arizona (United States) appears to be working in some areas¹⁰². Captive rearing is serving our conservation goals by maintaining living populations of gravely threatened animals. The devil is in the details of successfully reintroducing these creatures to the wild.



Conserving Amphibians: An Agenda for the Future

Given the array of threats facing New World amphibians, what actions can we take to improve their chances for survival in the decades to come? A mix of short-term and long-term actions is needed, and the challenge requires the participation of scientists, conservationists and policy-makers in dozens of countries. Stemming the tide of coming extinctions will require strengthening protected areas systems, improving legal protections and public policies, strategically using captive breeding, raising public awareness, and finding the answers to critical questions about the life history of amphibians and what threatens them.

HABITAT PROTECTION

For nine out of every ten amphibian species that are threatened by extinction, habitat loss is a risk factor. Therefore strengthening and expanding systems of public parks and private reserves must be the top priority for conservationists. Protected lands hold the line on expanding agricultural frontiers and safeguard the aquatic and terrestrial habitats needed by amphibians. Indeed, for many species, the existence of a protected natural area means the difference between survival and extinction.

An analysis of the role of protected areas shows that in most countries, existing governmental and private reserves play a potentially important role in protecting threatened species of amphibians from habitat loss and other threats. In most countries, over three-quarters of all threatened species occur in at least one protected area. Countries with relatively unprotected faunas include Mexico (33% of threatened species occur in parks), Guyana (33%), Peru (49%), and Guatemala (55%). Countries and territories in which large portions of threatened species occur in protected areas, whether by design or by accident, include Jamaica (94%), Panama (94%), Honduras (93%), and Puerto Rico (92%). Yet virtually no park was created expressly to protect amphibian fauna, and management plans rarely take into account their conservation needs. Park managers need to reevaluate whether current policies and practices are sufficient to protect habitat quality for threatened species in these parks. In many cases in the developing world, "paper parks" provide little on-the-ground protection due to the lack of funding and parks staff⁹². Support is urgently needed to convert good intentions into functioning protected areas.

HABITAT PROTECTION RECOMMENDATIONS

- **Strengthen management and protection at existing reserves, especially those harboring multiple threatened species.**
- **Include amphibians in conservation priority-setting exercises.**
- **Expand protected areas to cover the ranges of threatened species that are currently unprotected.**
- **Establish small, regional reserves to protect microendemic species.**

A number of governments and international environmental organizations use priority-setting procedures to help them decide where to invest in conservation. In tropical countries, amphibians have usually been excluded from these analyses because data on population status and distribution were not available in a comprehensive form. With the conclusion of the Global Amphibian Assessment and the publication of all results on the Internet (*see <http://www.globalamphibians.org>*), amphibians are now one of the easiest groups to include in these analyses⁹³.

Facing page: *Atelopus zeteki* (a harlequin frog). *Critically Endangered*. Panama. Endemic to Panama, this terrestrial species dwells in montane forest. Other high-altitude *Atelopus* species in the same region have experienced severe population declines, probably due to chytridiomycosis. The individual pictured was reared in captivity. / Photo by Bill Flanagan.

This page, top: *Common coqui* (*Eleutherodactylus coqui*). *Near Threatened*. Puerto Rico. / Photo by Forrest Brem.

A current conservation trend is to create large landscape-scale reserves to protect entire ecosystems. While this approach is praiseworthy, large distances usually separate these megareserves. Amphibians throughout the New World show a pattern of microendemism such that many small mountaintops or river valleys have endemic species. Without care by planners, some of these species may fall between the cracks of protected area systems. For example, the southern Mexican state of Chiapas has several large, very effective biosphere reserves, including El Triunfo and La Sepultura. Yet the state is also home to some endemic species (such as the treefrog *Plectrohyla pycnochila* and salamander *Ixalotriton niger*) that are currently unprotected. In these situations, conservation planners should create small regional reserves to protect microendemic species as well as large, landscape reserves to preserve ecosystems.

LEGAL PROTECTION AND PUBLIC POLICY

Many New World nations now have published lists of endangered species recognized by the government. Legislation creating these lists is an important start in protecting these species from extinction. Yet these lists can use two important reforms.

First, lists in many countries were drawn up without access to all available population data for the entire amphibian fauna. Thus many of these lists need to be brought up to date to reflect current knowledge of taxonomy and threat status. The information provided in our assessment can be an important input into the process. Although the Global Amphibian Assessment uses the IUCN Red List criteria for defining threat status, the supporting data for the individual species assessments are readily available on the Internet and can be used as input into other threat assessment schemes, such as one used in Argentina designed specifically for amphibians and reptiles⁹⁴. Regardless of which system is used, national lists should reflect the current state of knowledge.

Second, endangered species legislation tends to fall under wildlife law. One often finds lists of endangered species in laws regulating hunting and fishing. Specific penalties are listed for killing a threatened animal. While the situation varies by country, often the laws do nothing to prevent the loss of essential habitat, such as damming a river that is the only home for an endemic frog, or converting a diverse forest that is critical salamander habitat into a pine plantation. With input from stakeholders such as conservationists and landowners, public officials should revise endangered species legislation to protect habitats as well as safeguard species from direct persecution.

LEGAL PROTECTION AND PUBLIC POLICY RECOMMENDATIONS

- **Revise existing national and subnational lists of threatened species based on current knowledge.**
- **Rewrite endangered species legislation to provide for protection from habitat destruction as well as direct exploitation.**
- **Severely restrict or ban the importation of exotic species, especially bullfrogs and African clawed frogs.**
- **Avoid excessive exploitation of traded species by monitoring populations of potentially threatened species.**

National legislation also needs to address trade in amphibian species. As we have seen, bullfrog farms can threaten native amphibians by being a source of escaped frogs or diseases, either of which can decimate local faunas. The African clawed frog may also be an important vector of disease. Extreme safety measures should be used to prevent escape into the wild. Unrestricted exploitation and trade of native species can diminish local populations to the point of local extinction and can lead to the global spread of serious diseases. Imported animals should be quarantined and examined for all known amphibian diseases, including *Bd*. Trade in native species can be achieved in a sustainable manner, but must be regulated based on ongoing population monitoring. Finally, trade in species known to transmit diseases should be banned or severely restricted⁹⁵.

CAPTIVE BREEDING

Captive breeding is a conservation tool that can be employed in concert with habitat protection. Habitat protection is much less costly than captive rearing and often more effective, and therefore it should be the normal course of action for the conservation of small populations. In some cases, such as when disease threatens, habitat protection alone may not be sufficient. Examples include the protection of highland species of harlequin toads, *Telmatobius* frogs, stream dwelling treefrogs, *Eleutherodactylus* frogs, and glass frogs, all of which are known to be susceptible to the disease *Bd*. Currently, no management technique is available to prevent wild populations from being wiped out by the disease. When

a species is vulnerable to disease, captive breeding should be considered. Ideally, to ensure genetic diversity in breeding stock, animals should be captured before a population becomes too small. Of course, habitat protection or restoration is essential, too, so that suitable areas exist for the release of captive-reared individuals.

To be successful, captive rearing programs must make use of the best available husbandry techniques for the target species. Methods of inducing reproduction in captivity are only just being developed for many tropical species, so specialists need effective mechanisms for rapidly communicating promising new techniques to the zoo community. In some cases, hobbyists may have useful rearing techniques they can share with professional keepers. Multiple captive populations of each species should be established to maintain genetically diverse breeding stock and as a hedge against unexpected loss at any one rearing site.

Conservationists must also address the contentious issue of the captive rearing of species native to developing countries. Funding and facilities are more likely to be available in developed countries, but developing countries are understandably reluctant to surrender their dwindling biodiversity to wealthy foreign zoos. One solution is the transfer of technology and capacity to developing countries so they can rear threatened native species in their own facilities. Another possibility is negotiating ownership rights such that source countries retain ownership over frogs exported to foreign zoos for captive rearing.

CAPTIVE BREEDING RECOMMENDATIONS

- **Initiate captive breeding before populations become so reduced they are on the brink of extinction.**
- **Disseminate widely techniques for the captive rearing of amphibians.**
- **Establish breeding facilities with sustainable funding sources in developing countries with threatened fauna, and, when that is not possible, develop model agreements between countries with endangered fauna and countries with suitable rearing facilities.**
- **Focus research efforts on improving reintroduction success.**

Conservationists should be aware that although many threatened species can breed in captivity, very few have been successfully reintroduced into the wild (*see Box 10*). The added factor of the highly virulent chytrid disease in a vast geographic range further complicates reintroduction efforts. Once *Bd* becomes established in a region, reintroduction of susceptible amphibians will be futile until *Bd* can be controlled in the wild. Captive rearing can therefore maintain living animals but, at the moment, is not always a reliable method of averting amphibian extinction in the wild. Further research on reintroduction techniques may some day improve these odds.

EDUCATION AND AWARENESS RECOMMENDATIONS

- **Work with the media to highlight the plight of local species.**
- **Develop curriculum materials for schoolchildren.**
- **Sponsor outings to enhance appreciation for amphibians.**
- **Hold cultural events centered on amphibian themes.**
- **Construct ponds to attract and conserve amphibians.**

EDUCATION AND AWARENESS

Although the popular media has alerted the public to amphibian declines, we need greater penetration into the public consciousness of the message that amphibians are in big trouble almost everywhere. This report shows that amphibians are disappearing far faster than any other group of organisms that has been comprehensively assessed using the Red List criteria. The large number of critically endangered species, many of which may already be extinct, indicates that we are seeing only the tip of the extinction iceberg.

Deeper public awareness of the problem will encourage governments to put more amphibians on endangered species lists, donors to fund more conservation and research projects on amphibians, and conservationists to include amphibians in their analyses of areas in need of protection. It could also strengthen regulations protecting wetlands and other habitats used by amphibians.

To achieve this goal, both scientists and conservationists should highlight the plight of local species in the media and include amphibian conservation in outreach programs. To reach schoolchildren, educators and scientists should work together to develop classroom materials on amphibian conservation. Scientists can also help schools and nature centers by leading walks in search of amphibians in local habitats to enhance appreciation for these often overlooked creatures. Zoos, natural history museums, and art galleries can sponsor special exhibits centered on amphibians. Schools, rural hotels, nature preserves, and parks can create artificial fish-free ponds to attract amphibians and better acquaint the public with them. In addition—especially in tropical montane areas—these ponds are important conservation tools to buffer against droughts that cause natural pools to dry up before tadpoles can undergo metamorphosis.

ADDITIONAL RESEARCH

Disappearing Jewels demonstrates that scientists have come a long way toward understanding amphibian declines since reports of population crashes first began circulating in the late 1980s. Most declines are caused by habitat destruction, and no research is needed in most cases before protection of critical habitats can proceed. Over the next century, climate change will become a major threat and, again, we clearly need to protect habitats that may become favorable for threatened species as climates change. The major challenge facing field researchers today is how to prevent diseases from wiping out populations of amphibians (see *Understanding Disease* below).

The effects of contaminants on amphibian populations also remains poorly studied. How do the endocrine changes induced by pesticides such as atrazine translate into population level changes? Dozens of agrochemicals now find their way to amphibian habitats worldwide. How do these affect amphibian reproduction and survival? How does contaminant-induced stress influence the immune system? Scientists know very little about the effects of agrochemicals on amphibians in tropical environments. Are these effects any different than those measured in temperate environments? We know that wind can blow contaminants far into protected areas. How does this affect populations?

Despite major advances in recent years, amphibians remain poorly known creatures. For one-fifth of the species evaluated, scientists do not know enough to assign a threat category. Reasons cited include doubts about taxonomic status, incomplete range information, or a lack of recent abundance and population trend data. Future research should focus on filling in the gaps for these data-deficient species.

RESEARCH RECOMMENDATIONS

- **Study the effects of contaminants on a variety of species in different habitats .**
- **Improve our knowledge of the taxonomy, distribution, and abundance of data-deficient species.**
- **Monitor as many species as possible in a wide range of habitats.**
- **Reevaluate the conservation status of all species regularly.**
- **Facilitate research on threatened species.**

Finally, this analysis demonstrates the urgent need for population monitoring. Many species seem to have declined and even disappeared without anyone witnessing the event. We have no better than a vague idea when the declines occurred and have no specimens collected during the decline to give us clues to why it happened. We clearly need rigorous monitoring programs in a wide variety of habitats and on a wide variety of species to better document and understand population changes in the future. Properly designed monitoring programs should encompass not only amphibian populations but also environmental variables if we are to understand the causes of population change¹¹. Future iterations of this hemispheric amphibian assessment will provide a measure of how well we are accomplishing our conservation goal.

A danger of publishing a Red List of threatened animals is that local agencies responsible for issuing research and collecting permits may become reluctant to allow scientific research on endangered species. This behavior is counterproductive. Research is essential to improving our understanding of the natural history of and threats to endangered species. Permitting agencies should therefore strive to facilitate research on endangered species by reputable scientists.

UNDERSTANDING DISEASE

Although habitat destruction is the primary factor affecting threatened amphibians, the disease *Bd* has undoubtedly played a major role in pushing formerly common species to, if not over, the brink of extinction. These effects have

occurred recently, perhaps in the last 30 years. Understanding *Bd* better and learning how to manage it in wild populations are the most important priorities for preventing future amphibian extinctions.

Researchers face many key questions about the biology of *Bd*. Exactly how does the disease spread over short and long distances? Understanding mechanisms of disease spread will help prevent the disease from reaching unaffected populations. How does it persist in the environment? Are there animals that serve as “reservoir” hosts for which the disease is not lethal? Answering this question will explain how the disease can persist in an environment even when all susceptible frogs have disappeared. Can species that are normally solitary and do not enter the water become infected? Some species not associated with water (such as some coqui frogs in Puerto Rico) have suffered population declines but the involvement of *Bd* is still unclear. How do climate change events, especially periods of drought, interact with the disease cycle? Several studies point to a connection between droughts and disease outbreaks, but how these factors interact remains a mystery. Are other diseases also causing widespread declines? Perhaps *Bd* is not the only major killer involved.

Finally, and most importantly, how do we eliminate the disease from a habitat once it arrives? Until we answer this conundrum we will only be able to watch as populations continue to become infected and disappear. Moreover, we will have no success at reintroducing captive-reared species that are susceptible to *Bd*. Fortunately many scientists are now focusing their research on *Bd* biology. New discoveries are emerging regularly from labs all over the world, and our hope is that we will learn how to manage the disease before all susceptible populations are gone for good.



RECOMMENDATIONS FOR UNDERSTANDING DISEASE

- **Focus research questions on topics that will lead to management of *Bd* in wild populations.**
- **Learn how *Bd* spreads.**
- **Understand the relationship between climatic events such as drought and disease outbreaks.**
- **Survey for the presence of other diseases and measure their effect on amphibian populations.**

Top and second from top: Eastern newt (*Notophthalmus viridescens*). *Least Concern*. Canada and United States. During its “red eft stage” (top), the Eastern newt lives on land. After up to several years, it returns to the water and through metamorphosis becomes the aquatic adult newt (second from top). /Photos by Geoff Hammerson.

Third from top: Tennessee cave salamander (*Gyrinophilus palleucus*). *Vulnerable*. United States. Known from only a few dozen caves in Tennessee, Alabama, and Georgia, it lives its entire life underground. /Photo by Jim Godwin.

Bottom: *Gymnopsis multiplicata* (a caecilian). *Least Concern*. Honduras, Nicaragua, Costa Rica, and Panama. Only 168 species of caecilians are known to science—89 of them in the New World—but additional research will surely unearth many more. /Photo by Piotr Naskrecki.

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Facing page: *Hyla rufitela* (a tree frog). Least Concern. Nicaragua, Costa Rica, Panama. / Photo by Piotr Naskrecki.

This page: *Leptodactylus troglodytes* (a namow-toed frog). Least Concern. Brazil. / Photo by Paula Cabral Eterovick.

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Top: *Scinax elaeochroa* (a tree frog). *Least Concern*. Nicaragua, Costa Rica, Panama, Colombia. /Photo by Piotr Naskrecki.

Bottom: *Red-eyed leaf frog* (*Agalychnis callidryas*). *Least Concern*. Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and Colombia. /Photo by Piotr Naskrecki.

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Above: *Hyla ebraccata* (a tree frog). Least Concern. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Ecuador, and Colombia. / Photo by Piotr Naskrecki.

Left: Spring salamander (*Gyrinophilus porphyriticus*). Least Concern. Canada and United States. / Photo by Geoff Hammerson.



APPENDIX 2. DATA COLLECTION METHODS

INTRODUCTION

The Global Amphibian Assessment (GAA) is a joint project of the Species Survival Commission (SSC) of IUCN—The World Conservation Union, the Center for Applied Biodiversity Science of Conservation International, and NatureServe. The goal of the GAA is to stimulate concerted and well-targeted activities to halt the current wave of amphibian extinctions, through the development of an information baseline on amphibian status and conservation needs.

DATA MANAGEMENT

To collect and manage the data, we developed a Microsoft Access database modeled on the standards and protocols of the IUCN Species Information Service. The GAA database contains fields for the following information for each species.

SYSTEMATICS. Order, family, genus, species, taxonomic authority, commonly used synonyms, English and other common names (if any), and taxonomic notes (if needed to clarify taxonomic issues). We used *Amphibian Species of the World* (<http://research.amnh.org/herpetology/amphibia/index.html>) as our default taxonomy, departing only in a few well-justified circumstances. We analyzed all species we were aware of that were described formally in the scientific literature before June 2004.

GENERAL INFORMATION. Textual narratives describing the geographic range, population status, habitat and ecology (including both breeding and non-breeding habitats and breeding strategy), threats, and conservation measures (in particular noting occurrence in protected areas).

DISTRIBUTION MAP. An ArcView-compatible digital distribution map of the extent of occurrence (see www.redlist.org/info/categories_criteria2001.html#definitions for a definition). The maps are in the form of polygons that join known locations, and can consist of more than one polygon when there are known discontinuities in suitable habitat. Metadata attached to polygons indicate status including presence (extant or extirpated) and origin (native, introduced, re-introduced).

NATIONAL DISTRIBUTION. A list of countries where the species occurs, noting whether the species is native and extant, extirpated, introduced, or re-introduced.

HABITAT. A list of habitats where the species occurs, selected from a standard, hierarchical list of 82 possible habitats (as defined in the IUCN Habitat Authority File, www.redlist.org/info/major_habitats.html).

MAJOR THREATS. A list of threats that act to decrease population size for the species, selected from a standard, hierarchical list of 176 threats (as defined in the IUCN Threat Authority File, www.redlist.org/info/major_threats.html).

RED LIST ASSESSMENT. Based on the information above, IUCN Red List category, IUCN Red List criteria, rationale for the assessment, current population trend, names of assessors, date of assessment, and any notes related to Red Listing.

BIBLIOGRAPHY. A list of important references.

To the extent possible, we filled out all of these fields for each species. However, some species are too poorly known to be able to draw a range map, for example, or to complete other portions of the database. In addition, many species, especially in the tropics, actually are complexes of multiple, undescribed species. We treat these cases as single species pending resolution of their taxonomic status.

DATA COMPILATION

We compiled the data in three phases—initial data collection, data review, and data quality control and consistency check.

PHASE 1. INITIAL DATA COLLECTION

We carried out the initial data collection regionally, appointing a coordinator responsible for initially collecting and entering data for all species for their region into the GAA database. We defined regions based primarily on political and secondarily on biogeographic boundaries. A few countries with small numbers of endemic species (e.g., El Salvador, Nicaragua, and Uruguay) did not have coordinators. We added data for species in these countries during the data review stage. The regions and coordinators for the New World are as follows.



Above: *Centrolene prosoblepon* (a glass frog). Least Concern. Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador. / Photo by Forrest Brem.

Region	Coordinator
Argentina (Patagonia)	Carmen Úbeda
Argentina (north of Patagonia)	Esteban Lavilla
Chile	Alberto Veloso
Paraguay	Lucy Aquino, and Norm Scott
Bolivia	Claudia Cortez
Brazil (Atlantic Forest, Cerrado, Caatinga)	Débora Silvano
Brazil (Amazonia)	Claudia Azevedo-Ramos
Peru	Javier Icochea, Lily Rodríguez, and Ariadne Angulo
Ecuador	Luis Coloma and Santiago Ron
Colombia	Wilmar Bolívar and Fernando Castro
Venezuela	Enrique La Marca
The Guianas	Robert Reynolds
Panama	Frank Solís
Costa Rica	Bruce Young
Honduras	Gustavo Cruz
Guatemala	Bruce Young
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Caribbean Islands	Blair Hedges
United States and Canada	Geoffrey Hammerson

The data for species in the United States and Canada were modified from NatureServe's central databases (see www.natureserve.org/explorer).

PHASE 2. DATA REVIEW

We subjected the data gathered in Phase 1 to extensive peer review by numerous specialists (see Appendix 1 for a list) using two methods—correspondence (for United States and Canada species) and expert workshop (all other species). The expert workshops gathered together herpetologists in regional settings to review, correct, and add to the information compiled in Phase 2. Participants received a printed copy of the data in advance and provided comments during the workshop as we worked through each species. Details of the workshops for New World species are as follows.

Region/Taxonomic Group	Location	Dates
Costa Rica	San Ramon, Costa Rica	17-18 August 2002
Mesoamerica (Mexico through Panama)	La Selva, Costa Rica	11-15 November 2002
Tropical South America East of the Andes	Belo Horizonte, Brazil	31 March – 4 April 2003
Tropical Andes	Tandayapa, Ecuador	18-22 August 2003
Chile	Concepción, Chile	3-4 October 2003
Argentina and Uruguay	Puerto Madryn, Argentina	12-14 October 2003
Caecilians	London, UK	23-25 February 2004
Caribbean	Santo Domingo, Dominican Republic	19-21 March 2004

PHASE 3. DATA QUALITY CONTROL AND CONSISTENCY CHECK

Once the reviews were completed for all species, we checked to ensure consistency of the data entered and especially the application of the Red List criteria. Although we attended the workshops, aiding in consistency, this final consistency check was necessary to standardize data collected over a nearly three-year period. The final database is searchable on the Internet at www.globalamphibians.org.

Species Excluded from the Analysis

We excluded the following named species from the analysis because of uncertainty over the country of origin of the type specimens. In no case can any of these names be attributed to a currently known population of amphibians.

Order	Family	Scientific Name
Anura	Bufonidae	<i>Bufo intermedius</i>
Anura	Bufonidae	<i>Bufo simus</i>
Anura	Dendrobatidae	<i>Epipedobates labialis</i>
Anura	Hylidae	<i>Hyla auraria</i>
Anura	Hylidae	<i>Hyla hypselops</i>
Anura	Hylidae	<i>Hyla molitor</i>
Anura	Hylidae	<i>Hyla quadrilineata</i>
Anura	Hylidae	<i>Hyla surinamensis</i>
Anura	Hylidae	<i>Phyllomedusa megacephala</i>
Anura	Hylidae	<i>Sphaenorhynchus platycephalus</i>
Gymnophiona	Caeciliidae	<i>Caecilia mertensi</i>

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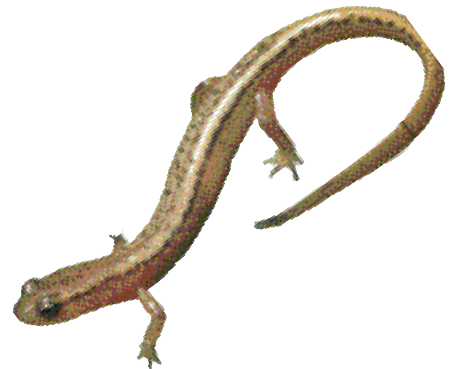
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Above: Northern two-lined salamander (*Eurycea bislineata*). *Least Concern.*
Canada and United States. / Photo by Geoff Hammerson.

Right: Red-eyed leaf frog (*Agalychnis callidryas*). *Least Concern.*
Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and
Colombia. / Photo by Piotr Naskrecki.





This publication is a contribution from the Red List Consortium.

