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The Global Decline of Reptiles, Déjà Vu Amphibians

Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change

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As a group [reptiles] are neither ‘good’ nor ‘bad,’ but iare interesting and unusual, although of minor importance. If they should all disappear, it would not make much difference one way or the other” (Zim and Smith 1953, p. 9). Fortunately, this opinion from the Golden Guide Series does not persist today; most people have come to recognize the value of both reptiles and amphibians as an integral part of natural ecosystems and as heralds of environmental quality (Gibbons and Stangel 1999). In recent years, as overall environmental awareness among the public has increased, concerns have come to include interest in the ecological state of reptile and amphibian species themselves and of their habitats. Increased awareness may stem from better education about threats to biodiversity in general, and to reptiles and amphibians in particular, and possibly even from an innate attraction to these taxa (Kellert and Wilson 1993).

From the perspective of many nonscientists, the two vertebrate classes comprising reptiles and amphibians, collectively referred to as the herpetofauna, are interchangeable. For example, the Boy Scout merit badge pamphlet for herpetology was called simply *Reptile Study* from 1926 to 1993 (Conant 1972, Gibbons 1993), and major zoos (e.g., National Zoo in Washington, DC; Zoo Atlanta; and San Diego Zoo) use only the name “reptile” to refer to the facility that houses both amphibians and reptiles. Thus, public attitudes about the need for conservation of reptiles are probably linked to concern about amphibian declines and deformities

(Alford and Richards 1999, Johnson et al. 1999, Sessions et al. 1999), which have been the subject of numerous, well-documented scientific studies.

Because amphibians are distributed worldwide, but herpetologists who document amphibian declines are not, it is difficult to accurately assess what portion of amphibian populations are experiencing significant declines or have already disappeared. Furthermore, the means of determining a species' conservation status is a rigorous and time-intensive process, and therefore counts of “officially” recognized endangered and threatened species are likely to grossly underestimate the actual number of imperiled species (Table 1). The worldwide amphibian decline problem, as it has come to be known, has garnered significant attention not only among scientists but also in the popular media and in political circles.

The reptile problem

Despite the fact that reptiles and amphibians are often considered collectively, reptile declines deserve spotlighting and elucidating in their own right. The differences between the two groups are substantial. Modern amphibians and reptiles are products of independent lineages that have been separate for the past 300 million years (Pough et al. 1998). Many of the differences between the groups are obvious and considerable. For example, the integument of reptiles is covered with scales, whereas amphibians have a highly permeable, glandular skin, a feature often touted as enhancing the environmental sensitivity of amphibians to toxic chemicals in both terrestrial and aquatic situations (Vitt et al. 1990). Additionally, reptile eggs possess a calcareous shell, whereas amphibian eggs are enclosed by simple gelatinous membranes, making the eggs more susceptible to uptake of environmental contaminants (but see Pechmann and Wilbur 1994). The differences between amphibians and reptiles are not limited to morphology and reproductive biology; they also include ecological and behavioral traits. Most amphibians rarely travel more than a few hundred meters over the course of their lives (Semlitsch and Ryan 1998); many reptiles may move several kilometers both terrestrially and aquatically and have home ranges encompassing tens or hundreds of square kilometers (Brown 1993), and individual sea turtles may cover half the globe annually (Ernst and Barbour 1989).

Nonetheless, the similarities between the ectothermic tetrapods—amphibians and reptiles—link them inexorably. Species of both classes occupy similar habitats and are equally vulnerable to habitat degradation. Thus, syntopic species of amphibians and reptiles are

correspondingly defenseless against the global threats of deforestation, draining of wetlands, and pollution from agricultural runoff. Although the amphibian decline problem is a serious threat, reptiles appear to be in even greater danger of extinction worldwide (Table 1).

Population declines can be difficult to detect; hence, long-term studies of natural populations and communities are generally regarded as indispensable for understanding normal population trends and fluctuations (Tinkle 1979). Long-term studies of amphibians and reptiles document temporal variation attributable to natural causes (Cody 1996). For example, Shine (1991) reported dramatic declines in Australia of the common blacksnake (*Pseudechis porphyriacus*), a large frog-eating snake, due to food shortages during extended drought conditions. Only the smaller snakes survived, suggesting that large snakes may be relatively more susceptible to declines caused by food shortages. Gibbons (1990) reported a natural decline for an isolated population of slider turtles (*Trachemys scripta*) on a coastal island. The turtle population had no juvenile recruitment, presumably because of constant predation on smaller individuals by alligators (*Alligator mississippiensis*) that had become established on the island; only large adult turtles survived. Natural fluctuations and local extinctions are common in both reptiles and amphibians (Pechmann et al. 1991, Blaustein et al. 1994c) and generally are no cause for alarm. However, not all declines are natural.

In this article, we consider the vulnerability of reptiles within the context of the factors known or suspected to be associated with amphibian declines, using the six categories of concern established by Partners in Amphibian and Reptile Conservation (PARC; Gibbons and Stangel 1999): habitat loss and degradation, introduced invasive species, environmental pollution, disease and parasitism, unsustainable use, and global climate change. An additional category comprises unexplained declines for both reptiles and amphibians, wherein the disappearance of populations or a decline in numbers is a certainty but the cause is unknown. Of course, decline of a species may often be a cumulative effect of more than one of the potential causes, as proposed for the documented declines of the Milos viper (*Microvipera schweizeri*) of Greece (Nilson et al. 1999) and the asp viper (*Vipera aspis*) of the Swiss Jura mountains (Moser et al. 1984, Jaggi and Baur 1999).

Our account is not exhaustive; rather, we provide documented examples of reptile populations in peril and decline. The aggregate of examples of amphibians and reptiles indicates

that the world's herpetofauna face stressors from both known and unknown origins that, without remediation, can only lead to continuing declines, extirpations, and extinctions.

Distinguishing natural declines from anthropogenic ones

Amphibian declines are indisputably real and disquieting on a global scale. Yet providing unequivocal supporting documentation for the decline of any particular population or species can be an onerous task, and some expectations of scientific rigor may be unable to be met (Pechmann et al. 1991). One persistent uncertainty regarding amphibian declines is whether a decline is simply within the natural range of variability for a population or is instead a consequence of anthropogenic causes that could portend an unrecoverable situation.

One difficulty in demonstrating whether observed trends in estimated population sizes constitute normal fluctuations or “unnatural” declines is that most field studies of amphibians or reptiles have not had the duration or consistency to make such determinations convincingly (Pechmann and Wilbur 1994). “Snapshots” (i.e., short-term monitoring) of population size and structure may demonstrate current status but do not reveal long-term trends in population size or health. For example, Petranka et al. (1993), who used short-term monitoring, and Ash (1997), who did long-term monitoring, came to different conclusions regarding the effects of clearcutting on recovery time of terrestrial salamander populations. To be sure, the strongest support for a decline is a long-term data set that has registered population levels for particular species in particular locations. However, the accumulation of numerous accounts from shorter-term studies of a variety of amphibian species in diverse habitats and geographic regions lends credence to pleas for concern about declines.

Studies of decline among reptiles, like those conducted for amphibians, have not always been carried out as rigorously as scientists would prefer. Nonetheless, the ever-increasing number of perceived declines among reptiles and the documentation of adverse impacts on individuals that presumably can be projected into demographic changes are harbingers of a crisis situation. Our intent is to show the phylogenetic and geographic breadth of perceived problems with many reptiles, on the premise that they foreshadow a more intense and widespread problem.

Habitat loss and degradation

Many scientists consider loss of suitable habitat to be the largest single factor contributing to declines of amphibians (Alford and Richards 1999). For example, some regions of the United States retain less than 20% of the wetland acreage they once had (Leja 1998), and consequent declines in associated amphibian populations have been documented (Lannoo et al. 1994). Numerous semiaquatic reptiles rely on those very same wetlands. In South Carolina, the elimination or alteration of more than 90% of Coastal Plain Carolina bay wetlands (Bennett and Nelson 1991) has reduced essential habitat for black swamp snakes (*Seminatrix pygaea*), eastern green water snakes (*Nerodia floridana*), and chicken turtles (*Deirochelys reticularia*), all of whose distribution patterns are restricted primarily to seasonal wetlands (Buhlmann 1995, Dorcas et al. 1998). Likewise, as bogs disappear in the eastern United States, so too do bog turtles (*Clemmys muhlenbergii*), and as streams and rivers are polluted, dammed, or channelized, riverine map turtles (*Graptemys*) decline (Buhlmann and Gibbons 1997). Even if the jurisdictional wetland itself is protected, in many cases the surrounding terrestrial habitat needed by semiaquatic reptiles for nests, hibernation sites, and other refugia is not (Burke and Gibbons 1995).

Just as habitat alterations may affect terrestrial salamanders (deMaynadier and Hunter 1995), they may also cause declines in terrestrial reptiles. The loss of 97% of the southeastern longleaf pine habitat (Ware et al. 1993), which has contributed to the decline of the flatwoods salamander (*Ambystoma cingulatum*; Means et al. 1996), has also reduced suitable habitat for gopher tortoises (*Gopherus polyphemus*), eastern indigo snakes (*Drymarchon corais*), and eastern diamondback rattlesnakes (*Crotalus adamanteus*; Guyer and Bailey 1993, Stephen H. Bennett, South Carolina Natural Heritage, Columbia, SC, personal communication).

Cultivated pine plantations in southeastern South Africa have been implicated in the endangerment of the rare short-headed legless skink (*Acontias breviceps*) and the disappearance of another lizard (Eastwood's long-tailed seps, *Tetradactylus eastwoodae*; Branch 1998). In the Chiricahua mountains of southeastern Arizona, the elimination of native bunchgrasses by cattle grazing was considered to be the primary cause of a detectable decline in the bunchgrass lizard (*Sceloporus scalaris*), which use bunchgrasses for cover from predators and for protection from harsh winter conditions (Ballinger and Congdon 1996). Habitat loss is the biggest problem in the decline of snakes in Australia (Shine 1991). The link between intact habitat and species

persistence and well-being is a basic tenet of ecology and conservation biology (Meffe and Carroll 1994, Mittermeier et al. 1999) and needs no further discussion.

The mere presence of humans may constitute an insidious form of habitat degradation in some instances, even if the habitat itself remains intact. Based on a 20-year study, a wood turtle (*Clemmys insculpta*) population of more than 130 animals in a forested watershed in New Haven County, Connecticut, has been virtually eliminated since the area became open to the public (Garber and Burger 1995). The possible mechanisms of decline included removal, road kill, handling by recreationists, increased number of predators attracted by food waste, and disturbance by dogs.

Introduced invasive species

Introduced species have been cited as a problem for many amphibians (Stolzenburg 1999). For example, the distribution and abundance of several western US frog species have been severely reduced by non-native fishes and bullfrogs (*Rana catesbeiana*), which were and continue to be introduced to wetland “island” habitats of low- and high-elevation lakes (Fisher and Shaffer 1996). The collapse of endemic reptile faunas on true islands after the introduction of exotic species is similarly well documented and pervasive; non-native rats, cats, and mongooses have extirpated numerous lizard species on many islands (Case and Bolger 1991). The tuatara (*Sphenodon punctatus*), a primitive reptile, historically inhabited the two main islands of New Zealand and at least 40 of the offshore islands (Daugherty et al. 1990). The tuatara became extinct on the main islands in the nineteenth century and on 10 offshore islands within the last few decades, and is experiencing population declines on many of the other islands as a result of introduced mammals, primarily rats. Feral pigs in the Galapagos Islands, first noted by Darwin in 1835, are just one of the non-native species that have caused the near extinction of the Galapagos tortoise (*Geochelone elephantopus*; Thornton 1971). Introduced rats are suspected to have destroyed both the eggs and young of the tortoises, but the initial cause of decline was 18th-century mariners who stopped at the islands and stocked their ships with live tortoises as food for the sailors (Pritchard 1967).

Even the introduction of non-native reptiles can disrupt indigenous reptile communities. For example, Losos et al. (1993) showed that the invasion of Grand Cayman by exotic brown anoles (*Anolis sagrei*) caused behavioral changes and shifts in habitat use by the native species,

Anolis conspersus. Likewise, the introduction of the brown tree snake (*Boiga irregularis*) has been implicated in the extirpation of the gecko (*Nactus pelagicus*) from the islands of Guam and Tinian; the brown tree snake is also considered responsible for dramatic declines in other species of native lizards on 13 of the Marianas Islands (Rodda 1992).

Although island faunas are most susceptible to disruption, the detrimental effects of invasives on native reptiles are not limited to islands. In the continental United States, imported fire ants (*Solenopsis invicta*), introduced in Mobile, Alabama, as early as 1918 (Wilson 1950), have been reported to prey on both eggs (Moulis 1997) and young (Allen et al. 1997) of reptiles. Fire ants are implicated as a primary cause of extirpation of the Texas horned lizard (*Phrynosoma cornutum*) from part of its geographic range (Goin 1992).

Invasive species need not be other animals. Both the desert tortoise (*Gopherus agassizii*) and the gopher tortoise are threatened by the introduction of non-native plant species (Stewart et al. 1993, Lovich 1995) that alter habitat structure, native plant community composition, and even fire frequency. The black legless lizard (*Anniella pulchra nigra*) was considered for federal endangered status, in part because of the negative impact of non-native Hottentot fig plants on the lizards' prey base in disturbed sand-dune habitat (Rutherford and Rorabaugh 1995); nonetheless, an official decision was made not to list the species after viable lizard populations were found in undisturbed habitat with native vegetation (Morey 1998). In Idaho, reptile species richness decreased an average of 5% from 1978 to 1998 at 24 sample sites in the Snake River Birds of Prey Area (John Cossel Jr. and Charles R. Peterson, Idaho State University, Pocatello ID, personal communication). According to Cossel and Peterson, the changes in reptile populations may have been influenced by a decrease in native shrub habitat caused by the prevalence of exotic annual grasses and the effects of wildfires that have burned over 50% of the area since the 1970s.

Environmental pollution

Numerous environmental contaminants—metals, pesticides and herbicides, and radioactive waste, for example—have direct and indirect effects on both amphibians and reptiles (e.g., Hinton and Scott 1990, Hall and Henry 1992). Amphibians have been the subject of numerous ecotoxicological studies, including assessment of the direct effects of contaminants such as fertilizers (Marco et al. 1999) or the more subtle effects of steroid-mimicking

contaminants (Hayes 1997). Reptiles are studied far less than amphibians with respect to the fate and effects of contaminants (Hopkins et al. 1999), but they have received sufficient toxicological study to provide convincing evidence that some individual reptiles are adversely affected by many contaminants (Hall 1980, Fontenot et al. 1994). For example, slider turtles (*Trachemys scripta*) exposed to metal and radioisotope contaminants incur genetic damage (Lamb et al. 1995). The degree to which contaminants cause population-level effects remains largely unknown, both for amphibians and for reptiles.

Contaminant effects in reptiles are known mainly from turtles and crocodilians. Many turtles and crocodilians, because they have environmental sex determination and large eggs that can incorporate high levels of environmental pollutants, are especially sensitive to endocrine-disrupting chemicals (Guillette and Crain 1996). At some contaminated sites, turtles accumulate PCBs (polychlorinated biphenyls), dieldrin, and other contaminants in tissues and eggs (Bishop et al. 1994, Cobb and Wood 1997); sex reversal and abnormal gonads have been found in turtles exposed to PCBs (Bergeron et al. 1994, Guillette et al. 1995). Male American alligators (*Alligator mississippiensis*) inhabiting Lake Apopka, a chemically contaminated lake in Florida, had significantly reduced plasma testosterone levels and permanent gonadal alterations (Guillette et al. 1994).

Even nonlethal effects of endocrine disrupters on reptiles may result in demographic shifts whose consequences for populations are presumably detrimental. Population-level effects might also occur through changes to patterns of individual energy allocation. For example, in coal-ash polluted wetlands, water snakes (*Nerodia fasciata*) with high body burdens of metal contaminants exhibit elevated metabolic rates, which may result in less energy being devoted to reproduction, growth, and storage (Hopkins et al. 1999).

Disease and parasitism

Parasites and disease have been documented or suspected as causes for declines in some amphibian species (Daszak et al. 1999). In some cases, sublethal environmental stressors may suppress immune systems (Carey 1993) and allow disease agents to kill weakened animals (Alford and Richards 1999). Recently, however, a spreading “extinction wave” of chytrid fungus is thought to be causing the decline of anurans in Central America and Australia (Berger et al. 1998, Lips 1999); moreover, researchers believe that the fungus is killing otherwise healthy

animals (Daszak et al. 1999). An iridovirus may be the primary cause of the periodic population crashes in the Sonora tiger salamander, *Ambystoma tigrinum stebbinsi* (Jancovich et al. 1997). Some amphibian biologists now believe that disease may rival habitat destruction as the largest single cause of the decline of amphibians.

Among reptiles, the widespread upper respiratory tract disease, a contagious respiratory ailment caused by the bacterium *Mycoplasma agassizii*, is a potential cause of population declines in desert tortoises in the US Southwest and gopher tortoises in the Southeast (Jacobson 1993, Smith et al. 1998). Shell diseases have been implicated in the decline of turtles (e.g., shell lesions on sliders, Lovich et al. 1996; cutaneous dyskeratosis affecting the shell and thickened forelimb scutes of desert tortoises, Jacobson 1994; and emaciation and lesions of the plastron of federally listed flattened musk turtles, *Sternotherus depressus*, Dodd 1988). Individuals in many green sea turtle populations are severely affected by viral fibropapillomas, resulting in growths that can impair vision, locomotion, and feeding ability (Herbst 1994). As is often the case in amphibians, diseases that are debilitating to wild populations of reptiles are most likely secondary expressions in individuals with impaired resistance caused by one or more primary environmental stressors, such as habitat degradation, invasive species, or pollution.

Unsustainable use

Human use of animals, including reptiles and amphibians, is an integral part of many cultures. Harvesting must be biologically sustainable, however, if populations and species are to persist (Pough et al. 1998). Overcollection for food, the pet trade, and biological supply houses has been suggested as having had an impact on some amphibian populations (Dodd 1997). In the United States, noteworthy examples for amphibians occurred in the late 1800s to early 1900s, when commercial collectors harvested for the frog legs market. Hundreds of thousands of red-legged frogs (*Rana aurora draytonii*) were collected from wetlands in California (Jennings and Hayes 1985), and over 20 million leopard frogs (*Rana pipiens*) were taken annually in northwestern Iowa (Lannoo et al. 1994). Midwestern wetlands today harbor fewer frogs, although it is difficult to apportion the relative losses among the causes of wetland habitat destruction and degradation, introduction of predators, and previous commercial impacts (Lannoo et al. 1994). In India, the frog-leg trade has resulted in severe population declines of the

Indian bullfrog (*Rana tigrina*) and the green pond frog (*Rana hexadactyla*); an estimated 70 million frogs are exported illegally each year (Oza 1990).

Human use of a species is sustainable if it can be continued indefinitely without adverse effects on population survival (Ross 1998). Much of the use of reptiles is clearly unsustainable. Commercial impacts on reptiles have been more pervasive and severe than on amphibians (e.g., see Williams 1999). The severity of the turtle crisis on a global scale was emphasized by Rhodin (1999), who reported that of the approximately 293 taxa (mainly species, but including some subspecies) of freshwater turtles, tortoises, and sea turtles known to be extant over the last few centuries, 3% (9 taxa) are already extinct in the wild. An additional 4% (12 taxa) are critically endangered, 11% (32 taxa) are endangered, and 21% (61 taxa) are vulnerable.

The crisis is particularly acute for Asian freshwater turtles and tortoises, which are harvested as a local food source. Moreover, the international trade in turtles—which are eaten, sold as pets, or used in traditional Chinese medicinal remedies—is both extensive and unregulated (Sharma 1999). A recent report indicated that most turtle species in Vietnam and southern China are endangered and that turtles can no longer be found in the wild in Vietnam (Kiestler and Juvik 1997). China is the biggest consumer of turtles in the food trade. Because the trade in turtles is not regulated, few records have been kept, but existing records indicate that the trade in live turtles to China is thousands of tons per year (Mockenhaupt 1999). The commercial trade in freshwater turtles exceeds any possible sustainable levels, and extinction of some species in the wild can be expected within the next decade.

Most species of sea turtles continue to decline in all warm oceans of the world. The leatherback sea turtle (*Dermochelys coriacea*) was recently reported to be “on the road to extinction and further population declines can be expected” unless appropriate measures are taken to reduce mortality rates in adults, hatchlings, and eggs (Spotila et al. 1996). The estimated worldwide population of leatherbacks nesting on beaches in 1980 was 115,000, compared with just 34,500 in 1995. Exploitation of leatherbacks in the Atlantic Ocean, through illegal harvesting of both adults and eggs, is considered to be a major contributor to the decline of the species (Spotila et al. 1996). Likewise, for Kemp's Ridley sea turtle (*Lepidochelys kempii*), harvests of nesting females and their eggs on the largest known nesting site contributed to declines from 42,000 nesting females in 1947 to only a few hundred by 1975 (Hildebrand 1982).

Among North American turtles, the diamondback terrapin (*Malaclemys terrapin*), a small, estuarine turtle species with a geographic range from Cape Cod to Texas, declined severely following heavy exploitation as a gourmet food item from the late 1800s to the early 1900s (Carr 1952). With forced reductions in harvesting, many populations were able to recover, but the terrapin now faces significant new threats, including highway mortality (Wood and Herlands 1997) and drowning in commercial and recreational crab traps (Bishop 1983, Roosenburg 1991). Renewed commercial harvest of the diamondback terrapin has also been documented (Garber 1988).

Commercial turtle trappers for the restaurant trade stepped up harvests of one of the largest freshwater turtles in the world, the alligator snapper (*Macrolemys temminckii*), from the 1960s through the 1980s (Roman et al. 1999). Consequently, as evidence from survey efforts suggests, the species has been drastically reduced in numbers in some of the southeastern US rivers it once inhabited (Moler 1992, Jensen 1998).

The enormous and once common populations of the arrau (*Podocnemis expansa*), a communally nesting turtle of the Orinoco and Amazon Rivers in South America, are now greatly reduced in size because of human consumption of eggs and nesting females (Pritchard and Trebbau 1984), an overexploitation problem identified almost two centuries ago (Humboldt 1814, from Pritchard and Trebbau 1984). Declines from similar causes have befallen the terecay (*Podocnemis unifilis*) in tropical lowlands of South America (Thorbjarnarson et al. 1993) and the river terrapin (*Batagur baska*) in India (Bhupathy 1997).

Overharvesting for food is a problem not just for turtles but also for lizards, having contributed to declines in green iguanas (*Iguana iguana*) and spiny-tailed iguanas (*Ctenosaura similis*) in tropical America (Fitch et al. 1982).

The pet trade appears especially hazardous for some turtle species. In 1994, population declines were reported in box turtles (*Terrapene carolina*) in 16 states, ranging from Massachusetts to Florida and Oklahoma to Wisconsin (Lieberman 1994). Documentation of box turtle declines—including records showing that, since 1995, 29,896 box turtles had been collected for the pet trade and shipped from Louisiana—resulted in unanimous passage of Act 81 by the Louisiana Senate and House of Representatives in 1999; the act prohibits the commercial harvest of the state's native box turtle populations. Overcollection for export is a serious factor in much of the box turtle decline and may exacerbate the effects of habitat loss (Lieberman 1994).

Habitat destruction and illegal collecting for the pet trade are the primary threats to bog turtles (*Clemmys muhlenbergii*); Copeyon 1997). The number of northern populations has been reduced by 50%, with most of the decline occurring over the last 20 years. Of the 191 remaining bog turtle habitats known in 1996, 33 were classified as in good condition, 67 as fair, and 76 as poor; the status of 15 was unknown.

Overcollecting is also a problem for some snake species. The ocellated mountain viper (*Vipera wagneri*) in eastern Turkey has been sought by the pet trade and removed from the wild in large numbers, posing “a serious threat to survival of the species” (Nilson et al. 1990). Populations of several boa and python species have declined because of harvesting of wild snakes for their skins (Pough et al. 1998). Rapid declines of large-bodied snakes, which tend to have a suite of life-history traits that make them more susceptible to population declines than smaller species (e.g., Dodd 1993), have been documented throughout the world in recent years (e.g., Shine and Fitzgerald 1996). For example, females of the increasingly rare timber rattlesnake (*Crotalus horridus*), which may exceed a meter in length and typically take 9 years to reach maturity, produce fewer than a dozen young every 3 years (Brown 1993). Large-bodied species such as rattlesnakes (*Crotalus*) have long generation times, a life-history trait that, when combined with habitat loss, human persecution, and intensive overcollection (e.g., “rattlesnake roundups”; Brown 1993), has led to dramatic declines of some species and made approximately one-third of rattlesnake species vulnerable to extinction (Greene 1997). High harvest rates of snakes with low reproductive frequencies, such as the filesnake (*Acrochordus arafurae*) in Australia, would almost certainly be unsustainable (Shine et al. 1995).

These examples demonstrate that sustainable use of some long-lived reptile species is problematic. Because longevity in reptiles is associated with delayed sexual maturity, high adult survivorship, and low fecundity (Pough et al. 1998), populations of long-lived species cannot remain stable (or grow) when adults and older juveniles are harvested at high rates (Congdon et al. 1993, 1994). This is not to say, however, that all such long-lived species should be commercially off-limits. The key to sustainability is having species- and population-specific management plans and tightly controlled use (Ross 1998).

For example, three decades ago, several species of crocodylians were on the verge of extinction because of a combination of threats, including habitat destruction (Ross 1998) and unsustainable harvest of adults for the leather trade (Brazaitis 1989). After years of total

protection, several species have recovered; a few are farmed or ranches commercially (King 1989). In some crocodile species, adult females are protected and only small numbers of eggs, small juveniles, and larger males are removed from the wild (King 1989). In contrast, 7–8% of all alligators more than 1.2 m in length are harvested annually in some Florida populations (David et al. 1996). In addition, a 50% annual harvest rate of alligator eggs or hatchlings is allowed because removal at these life stages does not reduce recruitment into adult-size classes (Rice et al. 1999). Closely monitored alligator populations, and presumably populations of other long-lived species of reptiles, can sustain the legal, regulated harvest of some proportion of eggs, hatchlings, or adults with negligible effects.

Global climate change

Few ecologists will dispute the link between increases in greenhouse gases and global temperature. However, whether the current rate of climate change reflects natural variation or has an anthropogenic cause is hotly debated. For the purposes of this article, we accept the argument that the earth is undergoing unprecedented rapid climatic change (Schneider and Root 1998) that includes alterations in climate variables such as temperature and rainfall patterns, storm severity, and storm frequency. If one accepts that human-induced climate change is occurring (e.g., Vinnikov et al. 1999), then the consequences for herpetofaunal diversity can be addressed.

The obvious effects of climate change on biodiversity are mediated through changes in habitat. For example, global warming may further diminish prairie wetland habitat in the United States (Poiani and Johnson 1991). Future wetland acreage in the United States may be greatly reduced under a variety of climate circulation models (Halpin 1997), and aquatic and semiaquatic species will suffer declines as habitat disappears. Although many habitats are expected to undergo dramatic change (e.g., Guertin et al. 1997, Still et al. 1999), predictions of species habitat shifts in response to global warming cannot be based solely on analyses of climate–space changes, because species distributions are also a function of dispersal ability and biotic interactions (Davis et al. 1998). Existing nature reserves will be inadequate to preserve current biodiversity, because an already fragmented landscape will impede the ability of species to respond to climate-induced habitat changes (Halpin 1997). Because of their limited dispersal abilities, reptiles and amphibians are especially vulnerable to rapid habitat changes and may

suffer many more extinctions than birds as a result of a rapid rate of climate change (Schneider and Root 1998).

In discussions of observed amphibian declines, little mention has been made of climate change (Dodd 1997), with two notable exceptions. First, the famed golden toad (*Bufo periglenes*) extinction in Costa Rica may have been caused, at least in part, by global warming effects on montane dry-season mist frequencies (Pounds et al. 1999). Fauna in tropical montane cloud forests may be particularly susceptible to rapid climate shifts that may change patterns of cloud formation and thereby the availability of water (Still et al. 1999). Second, Blaustein et al. (1994a) have suggested that ultraviolet B (UVB) radiation has adverse effects on some amphibians, including reduced hatching success and decreased survival to metamorphosis. However, an increase in the level of UVB caused by depletion of the ozone layer probably does not pose an immediate threat to reptile eggs, which are seldom exposed to UVB radiation.

As with the amphibian studies, few researchers have directly assessed effects of climate change on reptiles. It is nonetheless reasonable to expect that climate changes could result in conditions that eliminate or severely restrict species with limited distributions (Schneider and Root 1998), as has been suggested for some Australian lizards (Brereton et al. 1995) and crotaline snakes of North America and the neotropics (Greene and Campbell 1993). Additional effects of warming on some reptiles, based on empirical evidence with freshwater turtles, include enhanced juvenile growth rates, earlier ages at maturity, and shifts in functional sex ratios (Frazer et al. 1993). Global warming may have the greatest impact on those reptiles (crocodilians and some turtles) that have temperature-dependent sex determination (Janzen 1994), whereby the sex ratio of the hatchlings is determined by nest temperatures during incubation. Unless shifts occur in the pivotal temperatures at which sex is determined, or female nest-site choices (i.e., shade versus sun) evolve to keep pace with rising temperatures, altered sex ratios could affect population demographics and persistence.

Enigmatic declines

Finally, in addition to the many cases of declines that have some reasonably understood causes, some amphibian populations have declined, and even gone extinct, without any discernible causes. One well-known example is the gastric brooding frog (*Rheobatrachus silus*) of Australia. Shortly after the discovery of its unusual system of parental care, in which the

young develop in the safety of the mother's stomach (Tyler and Carter 1981), the gastric brooding frog ceased to be found in nature. Disjunct populations of the green salamander (*Aneides aeneus*) in the southern Appalachians have apparently declined, but without similar declines in other portions of its range (Jeff Corser, USGS-BRD, Twin Creeks Resource Center, GSMNP, Gatlinburg, TN, personal communication).

Similar cases exist for reptiles. For example, no living specimen of the Round Island burrowing boa (*Bolyeria multocarinata*) in the Indian Ocean has been seen since 1975 (Bullock 1986); the species may have become extinct in recent decades (Greene 1997). Although all species of reptiles native to North America in precolonial times persist in some regions, the current ranges of many are but a remnant of the much larger areas formerly occupied. Natural populations of indigo snakes have not been found in some regions of their historic range in more than 40 years (Mount 1975, Conant and Collins 1998), and the species is “declining in abundance and distribution throughout its U.S. geographic range” (Hallam et al. 1998). Likewise, sightings of the southern hognose snake (*Heterodon simus*) have not been reported from either Alabama or Mississippi in more than 18 years (Tuberville et al. 2000), even in large protected areas with relatively pristine habitats.

Documenting declines

Regrettably, many amphibian populations and species that are thought to be declining have not been monitored over long periods of time, making short-term changes in population size difficult to evaluate critically. The best long-term studies of amphibian populations that allow for critical evaluation of population trends share a common characteristic: The subjects of these studies occur in high density either spatially (e.g., Jordan's salamander, *Plethodon jordanii*; Hairston 1987) or temporally (e.g., mole salamanders, *Ambystoma talpoideum*; Pechmann et al. 1991; and natterjack toads, *Bufo calamita*; Banks et al. 1994).

Many of the species that have become symbols for the declining amphibian phenomenon are seasonally active anurans that arrive over restricted periods of time at breeding sites where they congregate in greater densities than at any other time of the year. Researchers sit ready to record their arrival and abundance, and if the animals fail to show up when expected, a problem is suspected; if such absences are protracted, then the change is presumably real (Blaustein et al. 1994c). The phenology of these amphibians permits detection of breeding activity; therefore,

determination of whether the absence of breeding adults is a short-term aberration or an indication of a real decline becomes a matter of accumulating the data necessary to demonstrate a statistically significant trend (for discussion, see Blaustein et al. 1994c, Pechmann and Wilbur 1994, Reed and Blaustein 1995).

Among reptiles, declines in sea turtles are perhaps the best documented because, like many amphibians, they engage in an annual reproductive event (in this case, oviposition) with a predictable site and time. A few snake species in colder temperate regions are known to hibernate communally, and numbers can be assessed upon emergence (Parker and Brown 1973). But what of the majority of reptile species that do not congregate to breed or hibernate and do not occur in particularly high densities? For example, the racer (*Coluber constrictor*), a common North American snake, is found in a wide variety of terrestrial habitats. Like most other ectotherms, racers are more active, and therefore more commonly encountered, in the warmer months. However, aside from some regions where communal hibernation occurs (Parker and Brown 1973), determining the abundance of racers is difficult because of their stochastic patterns of activity. Herpetologists would be hard-pressed to describe densities accurately during any season over a wide geographic range. Because racers do not congregate at a breeding site, how could we take a census to know when and if racer populations were declining at a substantial rate on a widespread basis without mounting an intensive, long-term sampling program? The clandestine nature of many reptiles, often combined with comparatively large home ranges, low population densities, and rareness of congregational behavior, makes documenting population trends very difficult. As a result, populations may wither with little notice. Once an unmonitored species or population is recognized as being unexpectedly depauperate or absent, the cause of decline may be unknown and unknowable.

Based on the accumulated evidence that many if not most declines reported for amphibians are indeed real, the proper course for conservation initiatives is to assume the worst for all herpetofauna, and therefore to implement abatement measures while gathering more data. Although the lack of long-term data often may preclude the identification of the cause of a decline, or even in some cases the corroboration of a decline, the absence of that data does not rule out the existence of a correctable problem.

Conclusion and recommendations

The declines of many reptile populations are similar to those experienced by amphibians in terms of taxonomic breadth, geographic scope, and severity. As with amphibians, the causes are known with certainty in some instances, suspected in many, and unknown in others. Some extirpations are local whereas others are more widespread. The difficulty in documenting the scope and source of each reptile (or amphibian) population decline should not be underestimated.

Biologists must be pragmatic in assessing which causes of population declines can be obviated directly. The impact of habitat degradation, introduced invasive species, and unsustainable use can be controlled immediately and proximally through legislation and cultural shifts in environmental attitudes. Minimally, society must place a premium on maintaining habitats of sufficient size and quality not only for imperiled taxa but for herpetofauna in general (Beebee 1992, Semlitsch 1998). For example, protecting the basins of wetlands is pointless if the surrounding terrestrial zone that is fundamentally linked to the wetland is allowed to be destroyed. Second, the release of invasive non-native species that could be harmful to reptile populations must be proscribed. Third, restricting trade in sensitive reptile species for which sustainable removal cannot be demonstrated will require the passage or strengthening and enforcement of legislation. In the case of Asian turtles, legislative remedies could be too little, too late—a stopgap remedy is necessary. The only way to prevent the imminent extinction of a large number of the more than 80 species of turtles native to southern Asia will be to maintain populations in ex situ captive breeding and genetic reserve programs. With changes in cultural attitudes, strengthening of international trade regulations, and increased habitat protection, the reintroduction of these species into the wild may be possible.

Much of today's commercial exploitation of reptiles in the United States and elsewhere requires urgent governmental action to implement internationally accepted and enforced controls. Despite the fact that conservation measures can be implemented effectively through legislation (as happened with legislation for protection of Louisiana box turtles and American alligators), the political pressures against accomplishing such goals cannot be overstated. The lack of support by the World Trade Organization for recommendations to curtail sea turtle exploitation (WTO 1998) brings the problem into perspective on an international scale.

Direct and indirect effects of environmental pollution, disease and parasitism, and global climate change are more difficult to quantify in many instances and will be more difficult to

change in the short term. Nonetheless, we must endeavor to understand these potential factors to ameliorate their impact on natural populations of reptiles and their habitats.

Finally, long-term monitoring of reptile populations is essential and must be aided by the establishment of standard methods and techniques. It is equally important that the academic community, land managers, and conservation organizations recognize that rigorous field programs focusing on the distribution, abundance, status, and trends of populations and species are critical and worthwhile. Herpetofaunal inventories should become a standard part of environmental assessment programs, and the publication of field survey efforts that document potential or suspected declines should be encouraged. When long-term and widespread monitoring becomes the norm, declines are likely to become less equivocal (in terms of protracted declines versus natural fluctuations) and the causes less mysterious.

The disappearance of reptiles from the natural world is genuine and should be a matter of concern not simply because of reptiles' perceived associations with amphibians, but because reptile declines, like those of amphibians, are growing and serious in their own right. Current evidence suggests that amphibian and reptile declines, which are exacerbated by burgeoning human populations, constitute a worldwide crisis.

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Table 1. Conservation status of reptiles and amphibians, according to the US Fish and Wildlife Service (FWS), Convention on International Trade in Endangered Species (CITES), and The World Conservation Union (IUCN)

Taxon	Approximate number of species ^a	FWS ^b		CITES ^c			IUCN ^d		
		Endangered	Threatened	Appendix I	Appendix II	Appendix III	Extinct	Endangered	Vulnerable
Amphibians	4680	17	9	13	68	0	5	49	75
Frogs and toads	4100	9	5	11	66	0	5	38	50
Salamanders	415	8	4	2	2	0	0	11	25
Caecilians	165	0	0	0	0	0	0	0	0
Reptiles	7150	70	18	70	383	19	20	100	153
Turtles	260	33	4	25	49	6	6	38	58
Crocodylians	22	15	3	16	8	0	0	7	3
Tuatara	2	2	0	2	0	0	0	0	1
Lizards	5066	14	8	16	238	0	11	30	66
Snakes	1800	6	3	11	88	13	3	25	25

^aThe approximate number of species for each taxon is from Pough et al. (1998). The numbers in the table reflect worldwide estimates of species only (excluding subspecies and populations) listed by each organization under selected conservation rankings.

^bData from FWS (2000).

^cAppendix I species are threatened with extinction and are, or may be, affected by trade; Appendix II species are not currently threatened but are likely to become so unless trade is restricted; Appendix III species are listed to prevent or restrict exploitation. Data from CITES (2000).

^d“Extinct” refers to complete taxonomic extinction, rather than the IUCN category “extinct in wild”; “endangered” includes those species listed by IUCN as “critically endangered”; “vulnerable” indicates that species are likely to become extinct if current trends continue. Data from IUCN–World Conservation Union (2000).