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ANURAN POPULATION DECLINES OCCUR ON AN ELEVATIONAL GRADIENT IN THE WESTERN HEMISPHERE

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***Abstract.*—Although the best known cases of enigmatic amphibian population declines come from mountains, the broader relationship between declines and elevation has not been well examined. We analyzed data from the Global Amphibian Assessment (GAA) and minimum and maximum elevation range data to study the association between elevation and population status for 1,918 anuran species in the Western Hemisphere (i.e., North, Central, and South America and adjacent islands). Multifactorial analysis with generalized additive models indicated that enigmatic declines increase consistently with elevation, even after accounting for geographic range area, spatial autocorrelation, and species phylogenetic relationships. Although the GAA data are coarse, we found a continuous increase in the percentage of species experiencing enigmatic declines with increasing elevation, starting at sea-level, suggesting that declines in mountains may simply be the upper end of a continuum. Establishing the existence of a strong elevational gradient in population declines will help focus amphibian decline research on factors that could possibly produce such a pattern, such as the role of temperature in disease dynamics.**

Key Words.—amphibian declines; *Batrachochytrium dendrobatidis;* elevation; mountains; temperature

INTRODUCTION

A striking and unexplained feature of enigmatic global amphibian declines is their apparent concentration in mountains (Muths and Hero 2010). Enigmatic declines are population declines due to factors other than habitat destruction or human exploitation. In Australia, population declines have been observed in the mountains along the eastern edge of the country (Hero and Morrison 2004). In the Americas, declines have been reported from the Sierra Nevada (Bradford 1991) and the Rocky Mountains (Carey 1993) of the United States, the mountains of Mexico (Lips et al. 2004), the mountains of Central America (Pounds and Crump 1994; Lips et al. 2006), and the Andes of South America (Young et al. 2001; Ron et al. 2003). In Europe, declines have been observed in the mountains of Spain (Bosch et al. 2003) and in Africa there have been declines in the mountains of Tanzania (Channing et al. 2006). On a global scale rapidly declining anurans with chytrid fungal disease are more prevalent at high elevations (Bielby et al. 2008), and enigmatic declines have been particularly sharp among topical montane amphibians in Latin America (Stuart et al. 2004).

Some of most detailed study of the relationship between the elevation and amphibian declines comes from Pounds et al. (2006) who analyzed declines of 100 species of harlequin frogs (*Atelopus* sp.) in Central and South America. They found harlequin frogs had declined more at mid-elevations (1,000−2,000 m) than at lower or higher elevations. However, Lips et al. (2008) reanalyzed their data and found greater declines at high elevations. Pounds et al. (2006) also found that for Western Hemisphere amphibians that the percentage of species "endangered or threatened" (IUCN red listing categories of critically endangered, endangered, or vulnerable) peaks in mid-elevations. They did not, however, analyze Western Hemisphere declines by elevation. Despite the striking nature of the montane decline pattern, to date no one has

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evaluated whether enigmatic amphibian declines in general occur on an elevational gradient with increasing declines with increasing elevation.

We used data from the Global Amphibian Assessment (IUCN, Conservation International, and NatureServe. 2007. Global Amphibian Assessment database. Available from http://www.globalamphibians.org [Accessed 2 February 2007]) to analyze the relationship between elevation and population declines of anurans in the Western Hemisphere (i.e., North, Central, and South America and adjacent islands). Data for the Global Amphibian Assessment (GAA) were compiled by 33 regional coordinators from published and unpublished sources and then reviewed by over 500 experts in over 60 countries (Stuart et al. 2004). Although there are data limitations based on the extent of existing knowledge, conservative estimates of species ranges, and missing species due to the high rate of new species discovery, the GAA is the best large scale data source available on the status of amphibians (Stuart et al. 2004). Because of species and country differences in the extent of monitoring and knowledge of population status, GAA data are best suited for broad taxonomic and geographic analyses (e.g., Stuart et al. 2004; Bielby et al. 2008; Cooper et al. 2008; Sodhi et al. 2008) rather than species or country specific analyses.

We focused on declines defined in the GAA as "enigmatic," rather than declines that are the result of habitat destruction or human exploitation because we were interested in contributing to understanding declines not caused by obvious human factors. The GAA defines enigmatic declining species as ones whose IUCN red-listing threat category has increased since 1980 and for which habitat loss or overexploitation is not a main cause of decline (Stuart et al. 2004). Red-list threat categories are based on information on population size, trends, and fluctuations, range size, fragmentation and loss, and threats to the species (IUCN 2012). We limited our analysis to anurans because declines are better understood for this group than for salamanders or caecilians.

Materials and Methods

We obtained minimum and maximum elevation range data for Western Hemisphere anurans from Pounds et al. (2006). We used population status information and family level taxonomy on these species from the GAA database (IUCN, Conservational International, and NatureServe. 2007. *op. cit*.). All species categorized as "Data Deficient" in the GAA were excluded from the analysis. From the GAA digital range maps, using ArcGIS (ESRI, Redlands, California, USA) we extracted geographic range area and the longitude and latitude of the geographic range centroid for each species. Combining elevation data from Pounds et al. (2006) and status and other information from the GAA produced a dataset of 1,918 Western Hemisphere anurans (see Appendix 1 and 2 for the taxonomic and country distribution of these species).

We used a multifactorial generalized additive model (GAM) to evaluate the importance of elevation range midpoint on whether or not a species had experienced enigmatic declines, while controlling for covariates. The goal of the multifactorial analysis was to determine if there was an elevational gradient in declines once we controlled for the covariates of geographic range area, location, and phylogenetic relationship. We therefore built a single GAM model with elevation and all covariates, rather than employing a model selection approach. A GAM is similar to logistic regression, but relaxes the assumption that the relationships between the dependent variable (when transformed to a logit scale) and predictor variables are linear (Hastie and Tibshirani 1991). The resulting relationships between dependent variable (enigmatic declines) and the predictor variables can be plotted allowing us to evaluate the existence of an elevational gradient in declines. All analyses were conducted using S-Plus 6.2 (Insightful Corp., Seattle, Washington, USA). Whether a variable significantly contributed to the overall model was tested using a likelihood ratio test (Hosmer and Lemeshow 1989).

We included geographic range area, because range area affects species vulnerability to a variety of threats (Rabinowitz et al. 1986; Hero et al. 2005), and because in our data high elevation species on average have smaller geographic range areas than lowland species. Geographic range area was skewed and was therefore log transformed for the multifactorial analysis.

Statistical models that use spatial data are complicated by the fact that species distributions and associated habitat and status data are often spatially autocorrelated (Legendre 1993), violating the assumption of independence of error terms inherent in most statistical tests (Augustin et al. 1996). Correct inference from spatially autocorrelated data is possible by including a spatial location covariate as a predictor variable (Hobert et al. 1997; Davidson and Knapp 2007). We followed this approach by including in our model a spatial covariate constructed in S-Plus from the longitude and latitude for the geographic range centroid for each species. The spatial covariate was constructed with the S-plus GAM function and uses latitude and longitude jointly to explain the likelihood of enigmatic declines (Davidson and Knapp 2007).

Felsenstein (1985) pointed out that in analysis of multiple species data, each species is not truly an independent data point because species are related to each other phylogenetically. Statistical analyses that assume independence can produce downward biased variance estimates and therefore can lead to false conclusions of statistical significance. We addressed this by incorporating an explicit phylogenetic covariate into the generalized additive model. We used taxonomic family (e.g., Ranidae, Bufonidae) from the GAA as our categorical phylogenetic covariate (see Appendix 1 for a list of the families).

To complement the main multifactorial analysis we used a univariate sliding window analysis to calculate the percentage of species experiencing enigmatic decline by 500-meter elevational bands. The sliding window analysis served as an alternative way to illustrate and analyze elevational patterns of enigmatic declines.

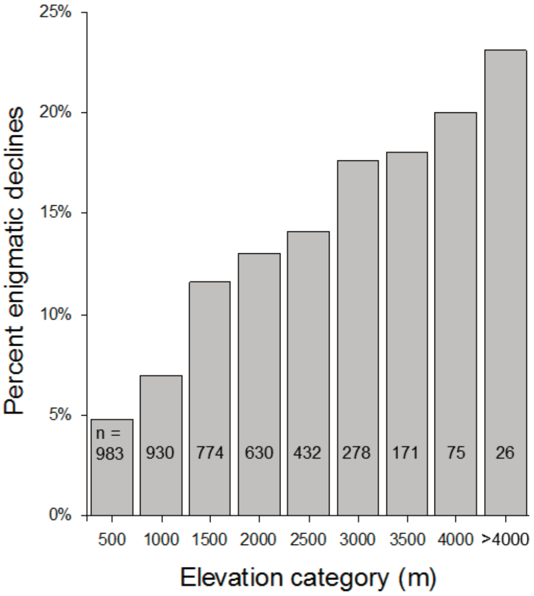

Figure 1. Sliding window analysis of the percentage of anurans experiencing enigmatic declines by elevational band for 1,918 Western Hemisphere anurans. Each elevational category includes all species with all or part of their geographic range occurring within a 500 m band with the elevation category as the upper bound. Thus the 1,500 m elevational category includes all species with all or part of their geographic range occurring above 1,000 m and up to and including 1,500 m. The numbers within the bars are the total number of species in each category. Species may occur in more than one elevational band.

RESULTS

In the Western Hemisphere, the sliding window analysis indicated the percentage of anurans experiencing enigmatic declines increased monotonically with elevation, with a low of 4.8% for species found up to 500 m, consistently increasing to 23.1% for species occurring above 4,000 m (Fig. 1).

In the GAM model, elevation was a significant predictor of whether a species had experienced enigmatic declines (Table 1), even with the inclusion of covariates for geographic range area, spatial location, and taxonomic family. Like the sliding window analysis, the Western Hemisphere GAM model indicated a continuous increase in the chance of experiencing enigmatic declines with increasing elevation (Fig. 2a), when controlling for geographic range area, taxonomic family, and spatial location. The spatial location variable, constructed from latitude and longitude, had the strongest explanatory power (Table 1), consistent with the non-random spatial distribution of declines. For geographic range areas greater than 100 km^2 the chance of enigmatic declines decreases with increasing range area. However, we found that for range areas less than 100 km^2, the relationship between range area and declines was reversed: decreasing range area was associated with a decreasing chance of enigmatic declines (Fig. 2b). Taxonomic family was a very strong variable in the GAM model (Table 1), indicating that there is a strong phylogenetic signal in enigmatic declines.

TABLE 1. Analysis of deviance table for the generalized additive model for 1,918 Western Hemisphere anurans. The dependent variable is whether or not a species has experienced enigmatic declines. The independent variables are a species' elevational range midpoint and three covariates: geographic range area, spatial location, and taxonomic family. The spatial location variable is constructed from the longitude and latitude of the centroid of a species' geographic range.

	Model		Test		
Model Test	Deviance	df	Deviance	df	P
Null Model	1221	1917			
Full Model	743	1856			
Full Model less:					
Spatial Location	915	1897	172	40	< 0.0001
Taxonomic Family	898	1869	155	13	< 0.0001
Geographic Range Data	759	1860	16	4	0.002
Elevational Range Midpoint	789	1860	45	3	< 0.0001

[a] Test deviance = (deviance of full model less one variable) – (deviance of full model).

[b] Test df = (df of full model less one variable) – (df of full model).

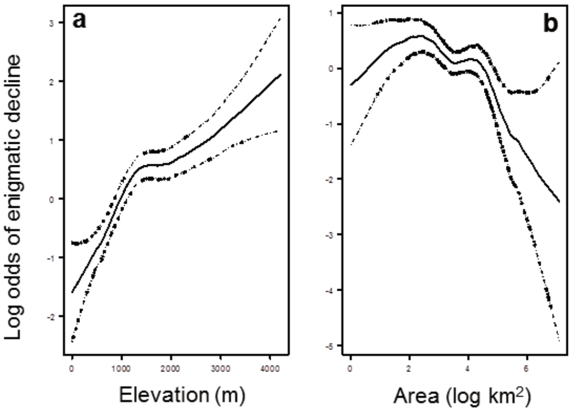

FIGURE 2. Response curves generated from the generalized additive model for Western Hemisphere anurans (n = 1,918). For each plot, the y-axis indicates the log odds of a species experiencing enigmatic declines as a function of the predictor variable (x-axis) after the influence of other variables have been accounted for. The solid line indicates the log odds and the two dashed lines indicate the approximate 95% confidence interval. (a) Predictor variable is elevation, which is the midpoint of a species' elevational range. (b) Predictor variable is geographic range area for a species.

DISCUSSION

Our results demonstrate that in the Western Hemisphere the frequency of enigmatic declines of anurans increased consistently and sharply with elevation. Not only were the chances of enigmatic declines greater at higher elevations, consistent with the well observed pattern of declines concentrated in mountains, but in the Western Hemisphere, according to both the univariate sliding window analysis and the multifactorial GAM model, the chance of enigmatic declines increased with elevation even at low and mid-elevations. This suggests that the greater incidence of enigmatic declines in mountains is just the upper end of a continuum rather than a unique phenomenon in mountains. The GAM model shows that declines increased with elevation, even when controlling for geographic range area, spatial location, and phylogenetic relationships. The strength of the spatial location and phylogenetic family variables in the GAM model indicates that declines were spatially non-random and that there was a strong phylogenetic signal in declines. We present and discuss four hypotheses for the increasing frequency of enigmatic declines with increasing elevation: (1) changes in temperature with elevation enhance the potential for amphibian disease; (2) the high rates of climate change in mountains over time can alter disease dynamics; (3) enhanced deposition of pesticides in montane environments increases the chances of amphibian population declines; and (4) elevational gradients in ultraviolet radiation produce an elevational gradient in amphibian declines.

The elevational gradient in declines may be due to cooler temperatures and greater moisture with increased elevation and their effects on disease dynamics of the chytrid fungus *Batrachochytrium dendrobatidis* (Bd). Bd has been associated with amphibian declines around the globe (Bosch et al. 2003; Hero et al. 2006; Lips et al. 2006; Rachowicz et al. 2006). Laboratory physiology studies of Bd and temperature support the possibility of an elevation and temperature gradient in declines: Bd has been shown to favor cooler temperatures (Longcore et al. 1999; Johnson et al. 2003) and has an optimal activity range in the laboratory between 17° C and 25° C (Piotrowski et al. 2004). Although Bd zoospores are inactive below 4° C, they survive freezing and become active again following an increase in temperature. Conversely, in the laboratory Bd does not grow above 28° C (Longcore et al. 1999; Piotrowski et al. 2004) and high temperatures reduce the lethal effects of chytridiomycosis (the disease caused by Bd) (Woodhams et al. 2003). Bd is also very sensitive to low moisture and cannot survive desiccation (Johnson et al. 2003). A number of field studies confirm that temperature and moisture affect Bd prevalence. For example, a survey of Bd in Stony Creek Frogs (*Litoria lesueuri* complex) in eastern Australia found that Bd infection was widespread across a 2,315 km latitudinal gradient; however, the prevalence and intensity of Bd infections were significantly greater at sites with high rainfall and cool temperatures (Kriger et al. 2007).

Although the effects of elevational temperature gradients on Bd are a plausible explanation for an elevation gradient in declines, field studies of Bd prevalence and intensity on elevational gradients have found mixed results. For example, in tropical Queensland, Woodhams and Alford (2005) found Bd infections were widespread (6−8 years post declines), but had higher prevalence at high elevations. Piovia-Scott et al. (2011) found that in early summer the probability of infection of metamorphosed Cascades Frogs (*Rana* [=*Lithobates*] *cascadae*) in northern California increased with elevation. However, by late summer infection differences by elevation had abated. Although there was an elevational gradient for probability of infection, site maximum summer temperature was not a significant predictor of probability of infection. In contrast, Kriger and Hero (2008) found no consistent evidence that high-elevation frogs in subtropical southeast Queensland were more likely to be infected than were their lowland conspecifics (20 years post declines). Furthermore, frogs from lower elevations carried fungal infections as intense as their high-elevation counterparts, suggesting that Bd infection and elevational temperature gradients alone are not capable of explaining the elevational patterns of amphibian population declines. Similarly, Knapp et al. (2011) studied Bd infection intensity, population size, and population persistence of Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) along an elevational/temperature gradient in the Sierra Nevada mountains of California. They used resurveys of sites with known populations, a translocation experiment, and detailed tracking of lake water temperatures and Bd infection across seasons. Although populations were larger at higher elevations, they found no relationship between elevation on Bd infection intensity and population persistence, and no relationship between temperature and Bd infection intensity.

While average temperatures may not drive infection, the seasonal timing of temperature changes, and therefore the timing and duration of infection may be significantly different in mountains than in lowlands. Sodhi et al. (2008) found that negative changes in amphibian IUCN red list status were associated with climatic seasonality. Complex relationships between the timing of metamorphosis and Bd thermal optima may render montane amphibian populations more susceptible to Bd induced mortality than their lowland counterparts. For example, in Queensland, Bd infections persist longer into summer in upland as compared to lowland areas (Kriger and Hero 2008).

In addition to differences in climate (temperature and precipitation) with elevation facilitating amphibian disease, climate change over time could also contribute to the concentration of declines in mountains. For example, climate change may create conditions in mountains that are more favorable for disease than in lowlands. This could come about if changes in climate have been greater in mountains than in lowlands, as some research suggests (Beniston et al. 1997), or even if lowlands and mountains have experienced similar changes, but climate change has shifted montane conditions more in line with optimal temperatures for Bd growth or host susceptibility. In their "climate-linked epidemic" hypothesis for amphibian declines, Pounds et al. (2006) argue that climate change, by increasing night time temperatures previously below optimal for Bd, and lowering daytime temperatures, has shifted temperatures to be more favorable for Bd epidemic outbreaks. However, in their analysis of harlequin frogs in Central and South America they predict the shift in temperatures would favor declines at mid-elevation sites.

There are several difficulties in assessing the possible effect of temperature changes on disease dynamics. Temperatures measured by weather station thermometers may not translate into temperatures experienced by amphibians which can actively thermoregulate by choosing microclimates (Richards-Zawacki 2010). Climate change may, however, alter the availability of suitable microhabitats if it exceeds a critical physiological threshold. Furthermore it is unclear what constitutes optimal temperatures for Bd epidemics because an optimum needs to take into account optimal temperatures for Bd transmission, amphibian susceptibility to infection, Bd virulence, and the ability of an amphibian to fight off an initial infection. These conditions may be species specific, and may be quite different in the laboratory than under natural conditions.

In addition to the effects of abiotic factors on disease, the elevational gradient in amphibian declines may be related to the possible role of contaminants as a contributing factor in amphibian population declines (Sparling et al. 2001; Davidson 2004; Davidson and Knapp 2007; Rohr and Palmer 2013). While the release of environmental contaminants such as pesticides is concentrated at low elevations, contaminants may undergo atmospheric transport and deposition in mountains, resulting in some cases in increasing concentrations with increasing elevations (Blais et al. 1998; Grimalt et al. 2001; Ribes et al. 2003). Daytime heating and upslope winds result in the transport of contaminated air masses into mountains. Colder temperatures in mountains than in adjacent lowlands can result in greater precipitation scavenging at higher altitudes, which in turn, can lead to greater deposition of pesticides in mountains than in lowlands (Lei and Wania 2004; Daly and Wania 2005). In addition, colder temperatures at higher elevations can slow the degradation rate of contaminants, and in areas with heavy snowfall these contaminants may be released into lakes and streams during seasonal snowmelt (Daly and Wania 2004) often when amphibians are breeding.

Hageman et al. (2006) showed that pesticide concentrations in seasonal snowpack, collected from several high elevation sites in North America, were most influenced by proximity to agricultural sources (Hageman et al. 2006). In Costa Rica, Daly et al. (2007) found that precipitation scavenging in tropical montane forests was responsible for higher current-use pesticide concentrations in the soil at high elevations than in lowlands. These studies suggest that amphibians living in mountains that are bordered by agricultural areas may be particularly vulnerable to pesticide exposures. This is consistent with many of the best known amphibian population declines which are from mountains bordered by and downwind from intensive agriculture: the Sierra Nevada in California, the mountains of Central America, the mountains on the east coast of Australia, and the South American Andes. On a smaller spatial scale, amphibian population declines in California are strongly associated with upwind agricultural land use and upwind pesticide use, both within the Sierra Nevada for a single species (Davidson and Knapp 2007), and across the state for multiple species (Davidson et al. 2002; Davidson 2004). However, these studies assumed that pesticide exposure would decline with distance from the source, which has not been supported by several recent studies (Bradford et al. 2011; Davidson et al. 2012). More studies are needed to understand the biological consequences of pesticide exposure on amphibians, and to determine the differences in exposures across elevational gradients.

The sensitivity of early life history stages of amphibians to ultraviolet radiation (UV) damage has long been recognized (Higgins and Sheard 1926). Over the past three decades, substantial ozone depletion has occurred in the lower stratosphere. This has resulted in increased exposure to UV radiation on a global basis. Because UV exposure increases with elevation, UV radiation could potentially explain both the timing of global amphibian declines and an elevational gradient of declines.

In temperate regions, UV exposure is likely to be much more severe for amphibians at higher elevations for several reasons. First, incident UV exposure increases approximately 24% per 1,000 m of elevation for the shorter wavelength 300 nm UV, and 11% and 9% per 1,000 m for 320 and 370 nm UV, respectively (Blumthaler et al. 1997). Second, although changes in vegetation across elevations vary greatly with exposure and microclimates, there is a general decrease in terrestrial vegetation with increasing elevation as first trees, and eventually even shrubs, herbaceous plants, and grasses decline and give way to regions dominated by snow, ice, and rock at the highest elevations. Declines in vegetation, particularly when crossing tree line, reduce the potential for shaded habitats in amphibian breeding habitats. While vegetation may not differ as strongly with elevation in lower elevation montane habitats, vegetation may be reduced by steeper slopes in montane vs. lowland regions due to landslides, avalanches, or loss of soil and nutrients due to more vigorous runoff and erosion. Third, Dissolved organic carbon (DOC) in water is the major regulator of underwater UV radiation because it preferentially absorbs the shorter more damaging wavelengths (Kirk 1994). In temperate and boreal regions, terrestrial vegetation decreases at higher elevations leading to decreases in DOC concentration in water (Rose et al. 2009). For example, DOC concentrations across elevation gradients can vary from close to 2,000 µM in lowland areas down to less than 40 µM in alpine lakes (Morris et al. 1995). In high DOC subalpine habitats, damaging UV radiation may be absorbed in the top few centimeters of the water column, while in low DOC alpine habitats, damaging UV radiation may penetrate to depths of over 10 meters (Morris et al. 1995; Williamson et al. 1996). Low DOC at higher elevations potentially makes amphibians in montane and alpine habitats more susceptible to UV damage. In addition to absorbing UV radiation, dissolved organic carbon can also reduce the toxicity of contaminants such as heavy metals and pesticides (Williamson et al. 1999). Thus DOC can serve as a “buffer” against a variety of environmental stressors and interact with some of the agents outlined in the other hypotheses discussed here.

While the UV hypothesis for an elevational gradient in amphibian declines is plausible for temperate regions, it does not work well for the tropics where canopy cover even at fairly high elevations both shades amphibians from direct UV exposure and likely contributes to higher DOC concentrations. Furthermore, while amphibians may receive higher UV exposure in mountains, at least in temperate regions, the role of UV radiation in amphibian population declines is unclear. While numerous studies support the hypothesis that UV can damage the early life history stages of amphibians (Blaustein et al. 2001), recent work suggests that a combination of the absorption of UV by DOC in the water in which the amphibians spawn (Adams et al. 2001; Palen et al. 2002), and the behavioral responses of amphibians during spawning (Palen et al. 2005) may mitigate much of this potential damage.

There are two caveats that should be kept in mind in interpreting our results. The first is that although our analysis includes almost two thousand species from across the Americas, from Canada to Chile, the results are largely driven by tropical species which account for 89% of the total, and 96% of the enigmatic decline species. Here we define tropical species as those having their range centroid between the Tropics of Cancer and Capricorn. Our finding of an elevational gradient in enigmatic declines is unchanged if we restrict the analysis to only tropical species (see Appendices 3, 4, and 5). Temperate species also show the same elevational gradient of enigmatic declines in a sliding window analysis (Appendix 6), but there are not enough temperate enigmatic decline species to do a comparable multifactorial analysis. A second caveat is that our finding of increasing enigmatic declines with increasing elevation is a species-level pattern. At the population level, the mechanisms driving declines and therefore the patterns of decline may be different. For example, site data for a number of declining species in California show the opposite elevational pattern, with the species having higher occupancy of historic sites at higher elevations than at lower elevations (Davidson et al. 2002).

None of the four hypotheses alone appears to fully explain the elevation gradient in declines. Nonetheless, our analysis clearly demonstrates a strong elevational gradient in enigmatic declines in the Western Hemisphere and highlights that high elevation species may be at greatest risk of declines. Although we lack a satisfactory explanation for this pattern, recognition of an elevational gradient in declines should stimulate research on factors such as temperature or seasonality that change with elevation. High elevation species may be further challenged by climate change which is expected to lead to greater temperature changes at high elevations; and therefore, high elevation species may be most in need of actions to mitigate the impacts of climate change (Rohr and Raffel 2010; Shoo et al. 2011; Rohr and Palmer 2013).

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Kerry Kriger is the Founder and Executive Director of SAVE THE FROGS!, a California-based nonprofit dedicated to amphibian conservation. He conceived and coordinates Save The Frogs Day, the world's largest day of amphibian education, and he teaches students worldwide about amphibians through live presentations and free online SAVE THE FROGS! Academy classes. Dr. Kriger holds a Ph.D. in Environmental Science from Griffith University in Gold Coast, Australia, and a Bachelor of Science degree in Mechanical Engineering from the University of Virginia in Charlottesville, Virginia. (Photographed by unknown photographer).

Appendix 1. Family, genus, and species count by genus for 1,918 Western Hemisphere anurans included in the analysis of enigmatic declines.

Family	Genus	Species (N)
Hylidae	*Hylomantis*	5
	Hyloscirtus	23
	Hypsiboas	51
	Isthmohyla	11
	Itapotihyla	1
	Lysapsus	3
	Megastomatohyla	4
	Myersiohyla	1
	Nyctimatntis	1
	Osteocephalus	15
	Osteopilus	8
	Pachymedusa	1
	Phasmahyla	2
	Phynomedusa	3
	Phyllodytes	5
	Phyllomedusa	21
	Plectrohyla	35
	Pseudacris	3
	Pseudis	6
	Ptychohyla	11
	Scarthyla	1
	Scinax	69
	Smilisca	8
	Sphaenorhynchus	8
	Tepuihyla	2
	Tlalocohyla	4
	Trachycephalus	9
	Triprion	2
	Xenohyla	1
Leptodactylidae	*Adelophryne*	4
	Adenomera	8
	Alsodes	6
	Atelognathus	6
	Atopophrynus	1
	Barycholos	2
	Batrachophrynus	2
	Batrachyla	4
	Caudiververa	1
	Ceratophrys	6
	Chacophrys	1
	Craugastor	93
	Crossodactylodes	2
	Crossodactylus	3
	Cycloramphus	6
	Edalorhina	1
	Eleutherodactylus	471
	Euparkerella	4
	Eupsophus	8
	Flectonotus	5
	Gastrotheca	37
Leptodactylidae (cont.)	*Geobatrachus*	1
	Hemiphractus	6
	Holoaden	1
	Hydrolaetare	2
	Hylodes	7
	Hylorina	1
	Insuetophrynus	1
	Ischnocnema	2
	Lepidobatrachus	3
	Leptodactylus	57
	Limnomedusa	1
	Lithodytes	1
	Macrogenioglottus	1
	Megaelosia	1
	Odontophrynus	8
	Phrynopus	23
	Phyllonastes	3
	Physalaemus	32
	Phyzelaphryne	1
	Pleurodema	12
	Proceratophrys	11
	Pseudopaludicola	8
	Rupirana	1
	Scythrophrys	1
	Somuncuria	1
	Stefania	10
	Telmatobius	42
	Telmatobufo	3
	Thorpa	4
	Vanzolinius	1
	Zachaenus	1
Microhylidae	*Arcovomer*	1
	Chiasmocleis	12
	Ctenophryne	1
	Dasypops	1
	Dermatonotus	1
	Elachistocleis	4
	Gastrophryne	4
	Hamptophryne	1
	Hypopachus	2
	Myersiella	1
	Nelsonophryne	2
	Otophryne	3
	Relictivomer	1
	Stereocyclops	2
	Stynapturanus	3
	Syncope	3
Pipidae	*Pipa*	5
Ranidae	*Rana*	42
Rhinodermatidae	*Rhinoderma*	2
	Rhinophrynus	1
Scaphiopodidae	*Scaphiopus*	1
	Spea	2
	TOTAL	1,918

Appendix 2. Number of species by country for all 1,918 species included in analysis of enigmatic declines in the Western Hemisphere. Totals by country sum to greater than 1,918 because many species occur in more than one country.

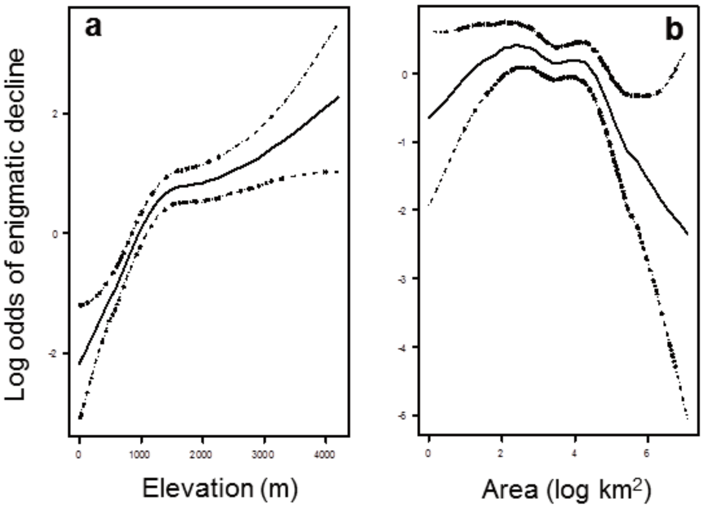
Country	Species (N)	Country	Species (N)
Anguilla	2	Guyana	122
Antigua and Barbuda	3	Haiti	52
Argentina	150	Honduras	92
Bahamas	2	Jamaica	24
Barbados	2	Martinique	6
Belize	32	Mexico	189
Bolivia	236	Montserrat	3
Brazil	556	Netherlands Antilles	2
British Virgin Islands	6	Nicaragua	66
Canada	14	Panama	151
Cayman Islands	2	Paraguay	85
Chile	39	Peru	328
Columbia	577	Puerto Rico	21
Costa Rica	129	Saint Kitts and Nevis	3
Cuba	58	Saint Lucia	4
Dominica	4	Saint Vincent & Grenadines	4
Dominican Republic	37	Suriname	97
Ecuador	375	Trinidad and Tobago	36
El Salvador	31	Turks and Caicos Islands	1
French Guiana	98	United States of America	59
Grenada	4	United States Virgin Islands	8
Guadeloupe	7	Uruguay	47
Guatemala	92	Venezuala	218

Appendix 3. Analysis of deviance table for the generalized additive model for 1,702 tropical Western Hemisphere anurans. Tropical is defined as a species having the centroid of its geographic range between the Tropics of Cancer and Capricorn. The model dependent variable is whether or not a species has experienced enigmatic declines. The independent variables are a species' elevational range midpoint and three covariates: geographic range area, spatial location, and taxonomic family. The spatial location variable is constructed from the longitude and latitude of the centroid of a species' geographic range.

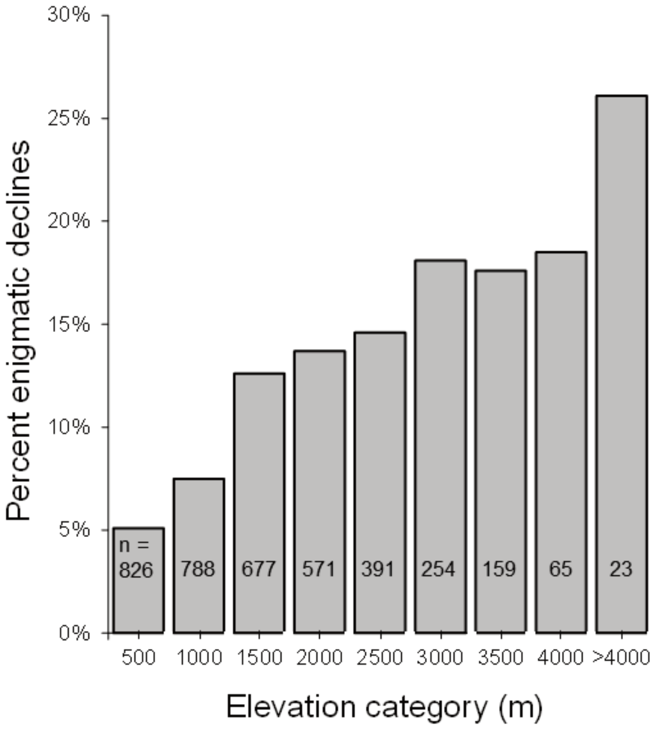
	Model		Test		
Model Test	Deviance	df	Deviance	df	P
Null Model	1145	1701			
Full Model	690	1645			
Full Model less:					
Spatial Location	852	1684	162	39	< 0.0001
Taxonomic Family	838	1656	148	10	< 0.0001
Geographic Range Data	706	1649	16	4	0.002
Elevational Range Midpoint	731	1648	41	3	< 0.0001

[a] Test deviance = (deviance of full model less one variable) – (deviance of full model).
[b] Test df = (df of full model less one variable) – (df of full model).

Appendix 4. Sliding window analysis of the percentage of anurans experiencing enigmatic declines by elevational band (a) and area (b) for 1,702 tropical Western Hemisphere anurans. Each elevational category includes all species with all or part of their geographic range occurring within a 500 m band with the elevation category as the upper bound. Thus the 1,500 m elevational category includes all species with all or part of their geographic range occurring above 1,000 m and up to and including 1,500 m. The numbers within the bars are the total number of species in each category. Species may occur in more than one elevational band.



Appendix 5. Response curves generated from the generalized additive model for tropical Western Hemisphere anurans (n = 1,702). For each plot, the y-axis indicates the log odds of a species experiencing enigmatic declines as a function of the predictor variable (x-axis) after the influence of other variables have been accounted for. The solid line indicates the log odds and the two dashed lines indicate the approximate 95% confidence interval. (a) Predictor variable is elevation, which is the midpoint of a species' elevational range. (b) Predictor variable is geographic range area for a species.



Appendix 6. Sliding window analysis of the percentage of anurans experiencing enigmatic declines by elevational band for 216 temperate Western Hemisphere anurans. Temperate is defined as a species having the centroid of its geographic range north of the tropic of Cancer or south of the Tropic of Capricorn. Each elevational category includes all species with all or part of their geographic range occurring within a 500 m band with the elevation category as the upper bound. Thus, the 1,500 m elevational category includes all species with all or part of their geographic range occurring above 1,000 m and up to and including 1,500 m. The numbers within the bars are the number of species in each category. Species may occur in more than one elevational band.