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BIASES IN THE PROTECTION OF PERIPHERAL ANURAN POPULATIONS IN THE UNITED STATES

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***Abstract.*—Many governments maintain lists of species of conservation concern (SCC), and jurisdictions at the peripheries of species' ranges can help prevent declines of species that are common range-wide by protecting peripheral populations. However, patterns in the sizes of jurisdictions may bias where common species are likely to be protected at their periphery. We used simulations of hypothetical species ranges to determine whether the geographic pattern in sizes of U.S. states has the potential to bias the proportion of anurans listed as species of concern at the state level. Then, we investigated whether the bias found in the simulations was evident as a bias in state listing decisions. The distribution of states resulted in a pattern of more peripheral occurrences (< 10% of a species' range occurring within a state) predicted in the eastern states than central or western states when range size was small to medium and more in the central states than eastern or western states when range size was large. Despite this pattern, species were more likely to be both listed as SCC and peripheral in the western states, and this is not sufficiently explained by higher risk of extinction in the west (estimated as the percentage of state species listed as federally threatened or endangered). Thus, despite being predicted to have fewer peripheral occurrences because of their large size, western states list a higher proportion of peripheral species than central and eastern states. Similar patterns in the sizes of political units elsewhere could bias our global preparedness to detect shifting ranges of both anurans and other species and to respond to those shifts in the face of climate change.**

Key Words.—frogs; listing decisions; marginal populations; peripheral populations; policy; state endangered species lists; threatened species; United States of America

INTRODUCTION

The first step in managing populations of species is to identify which species are at risk of extinction, after which the species identified as being at risk are afforded management priority or legal protection. Listing species of concern (often including "threatened" and "endangered" categories) is therefore an important part of conservation and is practiced by many local, national, and international groups and governments. Local lists of species of concern might seem redundant with federal or global lists at first glance, and have been criticized because they often direct conservation efforts toward peripheral populations of species that are stable range-wide (Bunnell et al. 2004). This criticism is important because being on the periphery of a species' range is one of the most common reasons for listing a species at the local level (Hayes 1991; Bunnell et al. 2004; Leppig and White 2006; Wells et al. 2010). However, local lists serve an important role in protecting populations at the edge of a species' range, where declines are likely to begin (Brown et al. 1995) and where important sources of genetic variability are found (Lesica and Allendorf 1995). Protecting peripheral populations can be particularly critical when adjacent political units do not provide necessary protections for the core of a species' range (Abbitt et al. 2000). In protecting peripheral populations, local lists help to keep common species common by addressing decline where it usually starts, at the edge of a species' range, before declines become significant range-wide (e.g., Channell and Lomolino 2000).

The likelihood of any species being protected at the periphery of its range might depend on the sizes of geopolitical units in that species' range. Any given species' distribution in an area with small geopolitical units may be more likely to have its edge protected in several units because it occurs peripherally there (Fig. 1).

FIGURE 1. Two hypothetical circular species ranges of equal size plotted in the U.S. Red indicates parts of the ranges that might be listed as peripheral populations in each state.

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Conversely, a species distributed in an area dominated by large geopolitical units may be less likely to occur peripherally in individual jurisdictions, and thus less likely to be conserved at its edge.

In the U.S., there is a pattern in the sizes of the states that allows us to test the effects of varying sizes of geo-political units on listing decisions. The pattern of east-to-west expansion of the U.S. resulted in a pattern of state sizes among the contiguous 48 states, where state size tends to increase from east to west. Does this pattern of state sizes result in a bias in the conservation of species at the peripheries of their ranges? We approached this question in four parts: Do state sizes increase from east to west? Is the frequency at which species occur peripherally in states related to the pattern of state sizes? Does the longitudinal pattern of peripheral occurrences in the U.S. match predictions based on simulations? Does the pattern of peripheral occurrences result in a bias in the listing of species by states?

We addressed these four questions by compiling data on the distribution of the 93 anuran (frog and toad) species native to the 48 contiguous states. We chose anurans as a case study because they are widespread, occupy a wide range of habitat types, and many are of conservation concern (Lannoo 2005). We compared anuran distribution with the patterns of listing by states to determine whether there is a geographic bias in the state listing of peripheral populations.

MATERIALS AND METHODS

Data on species distributions were taken from Lannoo (2005). We extracted two variables from the distribution of each species in each state. The first variable was the percentage of the species' global distribution included within each state. This variable was generally based on county maps, where a single occurrence in a county was marked by shading the entire county, and thus undoubtedly overestimated species ranges. Minor civil divisions, a unit of the U.S. Census Bureau, were used as mapping units instead of counties in several western states with large counties so that map resolution was approximately constant (see Lannoo 2005 for detailed explanation of mapping methods). When the global distribution was not contained in the U.S., maps in Stebbins (2003) and Conant and Collins (1998) were first consulted (51 species). When a species' entire range was not shown in the figures contained therein, the range map generated from the IUCN Global Amphibian Assessment was used to estimate global range on a world map (22 species; http://www.iucnredlist.org/ amphibians).

The second variable recorded was an indicator variable designating whether a state was at the edge of the species' distribution. To qualify as an edge, the state had to include an exterior edge of the species' global distribution; interior edges (i.e., unoccupied areas completely surrounded by occupied areas) were not included in this definition. In addition, edges formed only by the coast were not included. To be considered a "peripheral" occurrence in a state, the state had to contain ≤ 10% of the species' global range and the state had to include an exterior edge of the species' distribution (following Bunnell et al. 2004). These criteria do not account for the proportion of the state that is occupied by the species; however, including such a criterion would generate artificial patterns in peripheral occurrences because small states would, by definition, have more conservative criteria for the area in a state that a species would be required to occupy. Furthermore, the resolution at which these distributions were mapped would prohibit the mapping of small range areas in small states.

We excluded four species that only occur in the contiguous U.S. due to anthropogenic introduction (*Eleutherodactylus coqui*, *E. planirostris*, *Osteopilus septentrionalis*, and *Xenopus laevis*). We also excluded the Bullfrog (*Lithobates catesbeianus* [=*Rana catesbeiana*]) because of uncertainty about the boundary between its native and introduced ranges (Casper and Hendricks 2005). We excluded the introduced parts of the ranges of seven species that have both native and introduced ranges in the contiguous U.S. (*Acris crepitans*, *Lithobates* [=*Rana*] *berlandieri*, *L. clamitans*, *L. pipiens*, *Pseudacris regilla*, *Rana draytonii*, and *Rhinella marina* [=*Bufo marinus*]). We did not include species from Alaska, Hawaii, and U.S. territories in the analysis. After these exclusions, we conducted the analysis on 93 anuran species.

We surveyed the wildlife management agencies of all 48 contiguous states for their current lists of species of conservation concern. State lists generally included three categories. The terms "Endangered Species" and "Threatened Species" have legal meanings for the protection of species. A third category of variable terminology, often called "Species of Concern," "Monitor Species," or "Rare Species," identifies a species as a research and management priority without providing legal protection. The legal implications of these lists vary among states (Olson 2007), but universally indicate a closer level of monitoring or management, or both, than that of unlisted species, and thus provide a meaningful if imperfect index of a state's ability to detect and act on range contractions. We considered a species on any one of the three kinds of lists as "listed" for the purposes of these analyses (following Wells et al. 2010). Although the third category of listing does not offer legal protection, it provides for focused research, monitoring, and management of a species, which are key to conservation, especially in detecting declines. We did

not include "Candidate" or "Data Deficient" listings or other categories of impending evaluation. One state, North Dakota, does not maintain a state list of species of conservation concern.

We conducted all analyses using simple or multiple linear regressions with longitude as the independent variable. Because we collected data from every state (i.e., we did not draw samples from a population), inferential statistics are not applicable (Gill 2001). To facilitate the interpretation of the patterns we observe, we provide *P*-values and regression coefficients based on standard parametric tests, but because these assume that the samples were independent and were drawn randomly from a larger population, *P*-values and regression coefficients should only be taken as an approximate indication of strength of the relationships.

We first tested whether there was a geographic pattern in state sizes among the contiguous states using a simple linear regression of state land area on state longitude (at the geographic center of each state). Second, we used simulated species ranges to test whether the current distribution of state sizes predicts a geographic pattern in the occurrence of peripheral species, regardless of species biology or actual distributions. These simulated distributions were designed specifically to generate predictions of where the distribution of state sizes in the U.S. would lead to increased occurrences of periphery for hypothetical randomly distributed taxa. We conducted three groups of simulations corresponding to typically small, medium, and large range sizes. Simulated ranges were defined as circles of the areas 8,703 km^2, 349,707 km^2, and 1,812,108 km^2. These range sizes represent the 5th percentile, median, and 95th percentile anuran range sizes, and correspond to the range sizes of *Lithobates* (=*Rana*) *okaloosae*, *Hyla femoralis*, and *Rana luteiventris*, respectively. However, the implications of these simulations do not depend on the species involved and would apply to any taxon with similar range sizes. We randomly applied each of three simulated ranges to the U.S. one hundred times using ArcGIS (v. 9.2, Esri, Redlands, California, USA). We then tested whether the geographic arrangement of states predicts a pattern in periphery. We performed a linear regression for each range size with the longitude of the center of the simulated range as the independent variable and the number of states qualifying as peripheral with each random application as the dependent variable to explore whether the distribution of state sizes is expected to create patterns in periphery.

Third, we tested whether the observed pattern of anuran distributions results in patterns of periphery similar to those predicted by the simulations. For each state, we calculated the proportion of anurans within its borders that qualified as peripheral. We used the proportion rather than the number of anuran species as our dependent variable to control for the uneven distribution of anuran species richness across the U.S. (Lannoo et al. 2005). We then plotted the proportion of anurans qualifying as peripheral as a function of state longitude. Coastal states could create artificial patterns because edges formed only by the coast were not considered as edge states in our analyses, potentially reducing the number of peripheral occurrences in coastal states. To test whether coastal states were affecting our conclusions, we repeated the same analysis with coastal states excluded.

Finally, we tested whether the observed pattern in periphery translated to a pattern in protection of species at their peripheries. We plotted the proportion of anurans in each state that were both listed by the state and peripheral as a function of state longitude. A geographic trend in the listing of protected peripheral species is not necessarily a bias in listing unless the actual risk of extinction of those species does not correspond with their listing. To test whether a geographic pattern in state listings is explained by risk, we also plotted the proportion of anurans in each state that were on the federal endangered species list as a function of state longitude. True risk of extinction is difficult to estimate for any taxon. We used proportion of species in each state on the federal list of endangered species as an independent assessment of risk to anurans within each state because this is one of very few independent assessments of anuran risk that exist for our entire study region. We included federally listed Endangered, Threatened, and Candidate species, the latter because federal Candidate species are those that have been determined to be warranted for listing but precluded by other priorities. Then, we included the proportion of species in a state on the federal list as a covariate in a multiple linear regression with longitude as an independent variable and the proportion of anurans both state listed and peripheral as the dependent variable. This procedure effectively subtracted out the real range-wide risk of extinction from the analysis, so that if a relationship remained between longitude and proportion of species that were listed and peripheral, this relationship would be interpreted to be in addition to what was accounted for by real risk (i.e., a bias; cf Forester and Machlis 1996).

RESULTS

A linear regression of state land area on state longitude revealed that larger states were found in the western U.S. ($r^2 = 0.53$, $P < 0.001$). Texas was an obvious outlier and was removed from subsequent analyses (Fig. 2). After removing Texas, longitude explained an even greater proportion of variation in land area among states ($r^2 = 0.76$, $P < 0.001$).

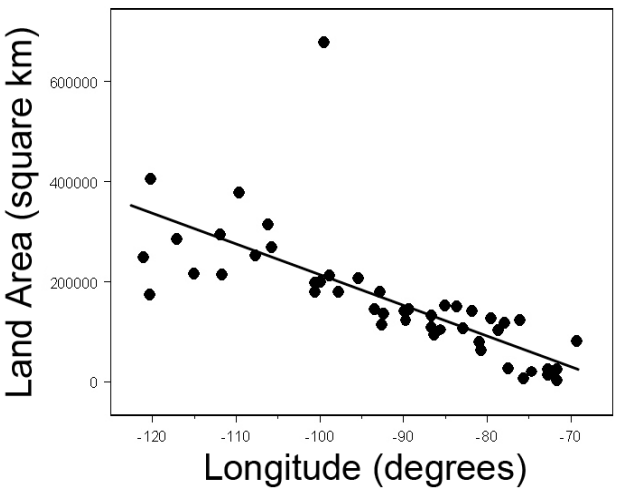

FIGURE 2. State size is correlated with longitude among the 48 contiguous states in the U.S. The outlier is Texas, which was excluded from the calculation of the best-fit line shown and from subsequent analyses.

Randomly applying ranges of three species to the U.S. revealed predictions of periphery that varied according to range size (Fig. 3). Small ranges had more peripheral occurrences in the east than in the west (r^2 = 0.07, P = 0.007). Medium-sized ranges also had more peripheral occurrences in the east (r^2 = 0.22, P < 0.001). In contrast, large ranges qualified as peripheral in more central states than near either coast (r^2 = 0.50, P < 0.001). The quadratic model fit these data better than a model including only a linear term (extra sum of squares F-test, $F_{1,97}$ = 39.15, P < 0.001).

The actual distribution of anuran periphery in the U.S. more closely followed the pattern predicted by the species with large ranges. Anuran periphery (measured as the proportion of species in each state that qualify as peripheral) peaked in the central part of the country and declined toward each coast (Fig. 4; r^2 = 0.59, P < 0.001). The quadratic model fit these data better than a model including only a linear term (extra sum of squares F-test, $F_{1,45}$ = 18.90, P < 0.001). The central peak in periphery was not simply an artifact of coastal states having low periphery because of their position on the coasts, as the pattern remained when coastal states were removed from the analysis (r^2 = 0.53, P < 0.001).

A peak of periphery in the central states did not translate into a peak in listing of peripheral species in the central part of the country. Rather, western states had the highest proportion of all species that qualified as peripheral and were state listed (Fig. 5; r^2 = 0.16, P = 0.006). This pattern corresponded with the pattern in actual risk, as indicated by the proportion of anurans in each state occurring on the federal list of endangered species (Fig. 6; r^2 = 0.49, P < 0.001). However, controlling for actual risk by including the proportion of anurans on the federal list as a covariate in the analysis revealed that longitude still explained a significant portion of the variation in the percent of species that were peripheral and listed (t = -3.04, P = 0.004).

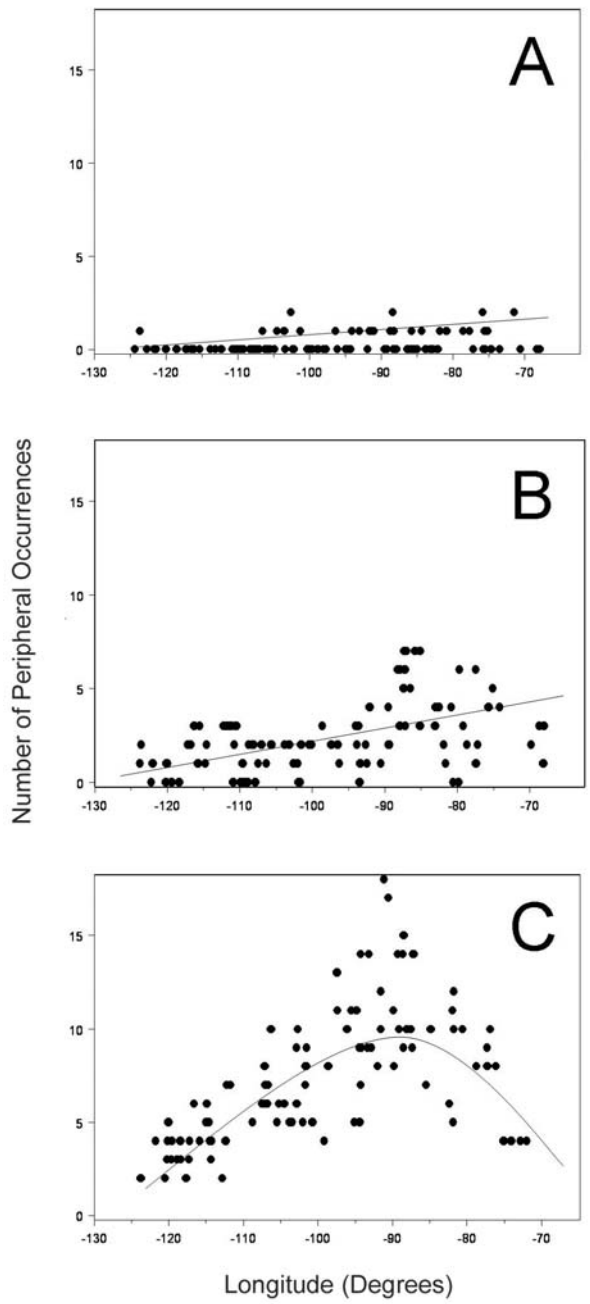

FIGURE 3. Simulations predicted more peripheral occurrences in eastern states for species with small (A) and medium (B) ranges than large (C) ranges.

DISCUSSION

Previous researchers have speculated that the listing of species at their peripheries might obscure relationships between risk variables and species listings (Forester and

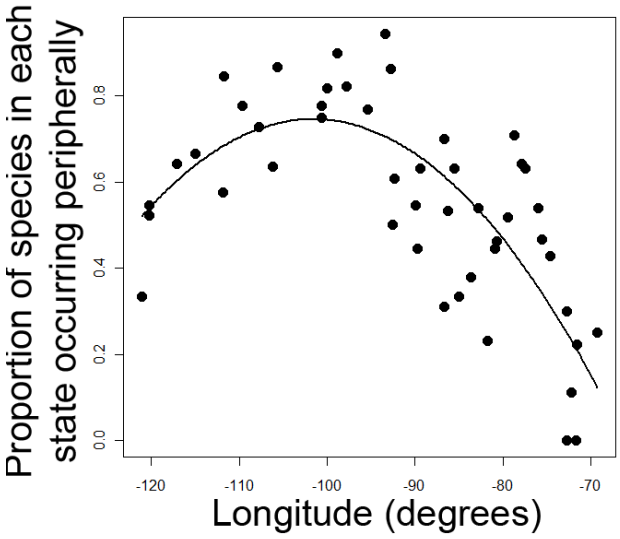

FIGURE 4. Using actual distributions of anurans, more species occurred peripherally in central states than towards either coast.

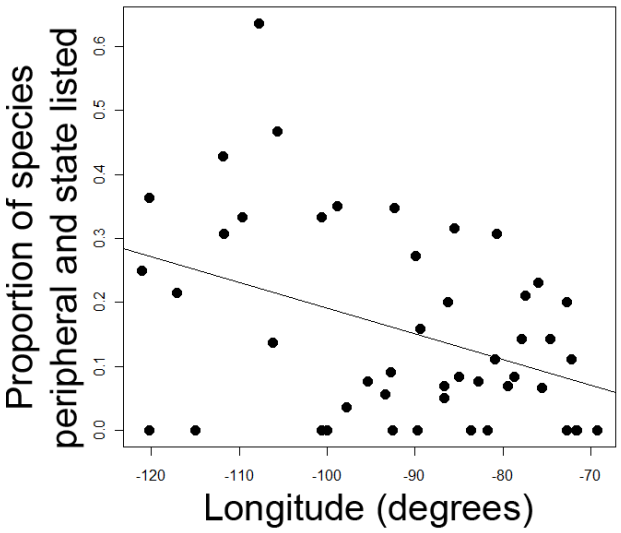

FIGURE 5. The proportion of all anurans present in a state that are both listed by the state and peripheral in the state is highest in the west.

Machlis 1996). In other cases, researchers have altogether ignored state listing decisions because of the complications of peripheral listings dominating state lists (Kirkland and Ostfeld 1999). The present data indicate that this complication, listing peripheral populations on state lists, might also have real consequences for conservation. For randomly distributed species' ranges, the geography of U.S. states creates a bias in where populations will occur peripherally, and that bias varies with range size. We used anuran range sizes to generate these predictions, but the findings could apply to any taxon with similarly sized ranges.

Species are not distributed randomly, however, and anuran species most often occur peripherally in the central U.S. In contrast, protection of peripheral populations is highest in the western U.S. A higher proportion of western species were designated by the U.S. Fish and Wildlife Service as Threatened or Endangered (Fig. 6), apparently justifying a pattern of more peripheral listings in the west.

That anurans are at greater risk in the west might come as a surprise to some, given that human population density is greater in the eastern U.S. (Markham and Steinzor 2006). Kirkland and Ostfeld (1999) found that human population density was not related to mammal risk in the U.S., but noted that the ". . . exclusion of this variable from the models may reflect the fact that the highest human population densities are in smaller states, which have relatively few total mammalian species and therefore few listed taxa." Using proportional losses, rather than absolute losses, revealed that the highest losses of mammals in North America have indeed been in the east (Ceballos and Ehrlich 2002). However, we found that proportion of anurans at risk of being lost was greater in the west. This is consistent with the findings of Bradford (2005) that anurans were at greater risk of extinction in the western states than the eastern states. These trends may be due to the issues associated with hydrology in the western U.S., where hydrologic cycles and riparian zones have been dramatically altered to provide hydropower, irrigate crops, and build cities in deserts (Richter et al. 1997). Although a higher proportion of anurans in the western U.S. were at risk, according to the U.S. Fish and Wildlife Service's list, this measure of real risk was not sufficient to account for the longitudinal pattern of peripheral listings we observed. This means that relative to their frequency, western states are over-listing peripheral populations (even more so than explained by risk), and central states are under-listing peripheral populations.

It is curious that central states had a higher proportion of anurans qualify as peripheral given that eastern states are predicted to have more peripheral species based on simulations of both small- and medium-ranged species. There are at least two possible explanations for this unpredicted result. First, there might be a high turnover of species in the central part of the country if species tend to be either "eastern" or "western" in distribution but not both. This explanation seems to fit with a qualitative assessment of the range maps, but quantitative analysis would lend credence to the hypothesis. Second, the simulations performed here assume that species' range sizes do not vary systematically across the continent. States do get larger across the U.S. from east to west; however, if species' ranges get larger in the same direction at an even greater rate, then western states might actually be smaller than eastern states relative to the range sizes of the species in those areas.

The value of protecting peripheral populations has been

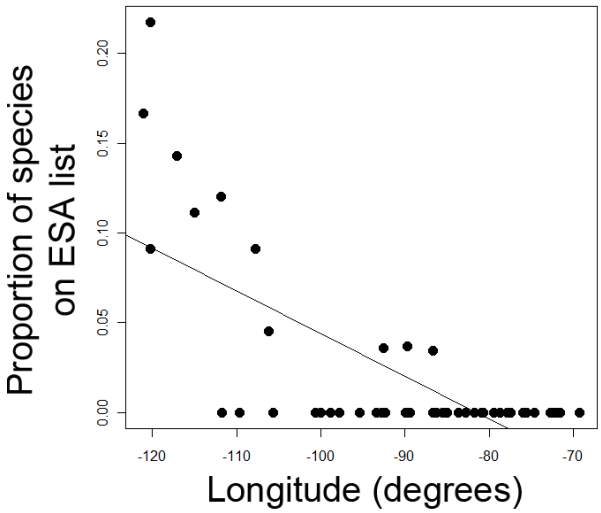

FIGURE 6. The proportion of anurans in a state on the federal endangered species (ESA) list peaked in the west, indicating that actual risk to anurans was highest in the west.

a matter of much debate (e.g., Furlow and Armijo-Prewitt 1995; Lesica and Allendorf 1995; Samways 2003; Garner et al. 2004). Protecting peripheral populations has a variety of potential benefits, including maintaining unique adaptations (Scudder 1989; Lesica and Allendorf 1995; Hampe and Petit 2005) and retarding the loss of species by stopping range contractions where they start (Furlow 1995; Nathan et al. 1996; but see Lomolino and Channell 1995). Protecting peripheral species also has costs, including the direct costs associated with managing any species, and potential diversion of funds away from species in need of range-wide conservation (Bunnell et al. 2004). Regardless of the costs and benefits of protecting peripheral populations, our data indicate an imbalance in the protection of peripheral populations of anurans in the United States. As species' ranges shift or contract due to climate change, habitat loss, and other factors, western states are relatively well prepared to recognize these shifts through monitoring and to respond to these shifts with management action. Central states are relatively poorly prepared, especially when taking into account the high number of species that occur peripherally in the central part of the U.S. Eastern states are moderately prepared relative to central and western states: despite their smaller size, eastern states have fewer peripheral occurrences than central states and fewer listings than western states. These findings should not be misconstrued to mean that western states list too many species or central states too few. Rather, we intend to emphasize that the listing of peripheral populations of species is not constant across longitudes in the United States.

The causes of these regional differences are difficult to determine and may be varied. There are more public lands in the western states, which may have affected how closely state and federal agencies have monitored anuran populations. There are also many other social, historical, and political factors that vary among states. For example there are geographic patterns in political party affiliations that may have ramifications for listing decisions, and the non-game species have been managed for a longer period of time in some states than in others. Addressing these and other potential covariates in the future may help to explain the patterns we document here.

These results emphasize the importance of considering the distribution of geopolitical units in assessing our global preparedness for detecting and addressing shifts in species ranges. Small geopolitical units are more likely to protect some portion of a species' periphery, and large units are less likely. For example, European countries may be more likely to protect the periphery of species ranges than central Asian countries, and Russian federal subjects (geopolitical units comparable to US states) in the west are more likely to protect species peripheries than eastern subjects. These geographic patterns in political sizes should be considered by federal and international organizations assessing and addressing gaps in the protection of species by their constituent units.

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