Asymmetric cross-border protection of peripheral transboundary species

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Abstract
International political boundaries challenge species conservation because they can hinder coordinated management. Peripheral transboundary species, those with a large portion of their range in one country and a small, peripheral portion in an adjacent country, may be particularly vulnerable to mismatches in management because peripheral populations are likely in greater conservation need than core populations. However, no systematic assessment of peripheral transboundary species or their status across borders has been attempted. We show that numerous species in three vertebrate taxa qualify as peripheral transboundary species in North America, and that these species are often protected differently across US–Canadian and US–Mexican borders. Asymmetries in cross-border protection may threaten populations through disruption of connectivity between periphery and core regions and are especially relevant given expected impacts of climate change and the US–Mexico border wall. Our results highlight the need for greater international collaboration in management and planning decisions for transboundary species.

Keywords
climate change, conservation planning, international border, protection status, range, transboundary, vertebrates
INTRODUCTION

Transboundary conservation efforts are growing because of recognition that maintaining intact and connected ecosystems requires large-scale planning and management approaches that cross political boundaries (Lopez-Hoffman, Varady, Flessa, & Balvanera, 2010; Rands et al., 2010). Recent expansion of transboundary protected areas and multicountry conservation planning initiatives and programs attest to this trend (Rüter et al., 2014; Vasilijević et al., 2015). Nevertheless, political boundaries continue to impede conservation because of a lack of coordinated action, and the topic of transboundary conservation of biodiversity remains relatively unstudied (Dallimer & Strange, 2015; Kark et al., 2015). At the species level, transboundary migratory fauna have received some attention through international agreements (e.g., Migratory Bird Treaty), as have specific species or groups of species in a transboundary context (e.g., Agreement on the Conservation of Gorillas and their Habitats), and the need for international coordination in species management is a key component of a wide variety of international legal instruments (Trouwborst et al., 2017). Despite these agreements, however, many species continue to be managed separately between adjacent countries (McPherson & Boyer, 2016; Selier, Slowtow, Blackmore, & Trouwborst, 2016) and interested parties in neighboring countries often do not take advantage of the potential benefits of greater international collaboration in species management and protection (Trouwborst et al., 2017).

Peripheral transboundary species (PTS)—those with a large portion of their range in one country (hereafter “core range”), and a small, peripheral portion in an adjacent country (hereafter “peripheral range”; Figure 1)—present an especially vexing transboundary conservation challenge. Range size is a key determinant of extinction risk (Purvis, Gittleman, Cowlishaw, & Mace, 2000), and vulnerability of PTS is likely to vary markedly on either side of a given border, with populations in the small peripheral range normally being in greater jeopardy because of their smaller range size. A mismatch in conservation standing may result in different research, management or protection strategies across the shared border at both national and regional levels (e.g., states/provinces straddling international boundaries), potentially threatening persistence of more sensitive peripheral populations (Proctor, McLellan, Strobeck, & Barclay, 2005). In addition to their high conservation importance (Channell & Lomolino, 2000; Provan & Maggs, 2011), these peripheral populations of PTS may also perform important ecosystem services (Lopez-Hoffman et al., 2010) and occupy habitat refugia that buffer against environmental degradation and diversity loss in the core range. This point is especially relevant in light of ongoing shifts in species distributions that accompany contemporary environmental variation, such as climate change. These shifts may cause previously peripheral populations to act as fronts of range expansion or persistence, as the climate warms (Gibson, Van Der Marel, & Starzomski, 2009; Rehm, Olivas, Stroud, & Feeley, 2015), thereby increasing their value to the species. Accordingly, greater international collaboration in managing PTS may be needed. However, to date no systematic assessment of PTS and their conservation status across borders has been attempted.

Here, we present results of an analysis focused on three major taxa in North America, where international borders extending through a range of ecosystems offer numerous contrasts in species protection by jurisdiction. North America is also of special interest because the proposed US–Mexico border wall could create an impermeable dispersal barrier for many PTS, leading to disjunct north–south population segments and increased conservation concern for peripheral populations. We determined PTS numbers and whether these species experience asymmetric protection across international borders. We also assessed potential bias toward greater protection of the peripheral range segment, because these smaller peripheral segments are likely of greater conservation concern, and toward the poleward (northern) range segments, given likely impacts of climate change. Our analysis demonstrates the ubiquity of transboundary asymmetry in conservation status of species, and argues for greater cross-border collaboration in research and management of PTS.

METHODS

PTS identification

We overlaid range maps for North American mammals, birds, and herpetofauna on maps of country boundaries for the United States (US), Canada (CA), and Mexico (MX), and calculated the total area of each species’ range that fell within each country. We excluded portions of the range that fell outside of North America or the countries of the specific comparison being made (either US–CA or US–MX) as well as species without terrestrial ranges or border crossings. We identified species that had >75% of their range in one of the paired countries and <25% in the other (for both the US–CA and US–MX comparisons; Figure 1), and defined those species as PTS. We included migratory species in the analysis, recognizing them as special cases where the same individual may be using both segments of the range but still be affected by asymmetric protection. We excluded species with disjunct range segments across an international border (e.g., US–CA), where those range segments did not occur in border states/provinces (only 22 species were excluded through this process). We calculated the proportion of the total number of species shared between country pairs that qualified as a PTS by taxa. We repeated the above analysis using 15% and 85% as the range...
segment thresholds to define PTS, but found qualitatively similar results and therefore only present the analysis using the 25% and 75% thresholds.

2.2 Geographic patterns of PTS

For each PTS, we identified the country with the peripheral versus core range segment. We also examined the spatial pattern of transboundary crossing of PTS by identifying areas where range maps overlapped the international border. Any state/province (for US–CA) or state–state (for US–MX) border pair that had a portion of the range of a species on both sides of the border was categorized as a transboundary crossing. To examine geographic variability in transboundary crossings for PTS, we determined the proportion of total border crossing that occurred between any two border states/provinces for US–CA and US–MX.

2.3 Conservation status assessment

We determined the legal conservation status of each PTS in each country at the federal level. We considered three categories of status: Endangered, Threatened, and Special Concern. We determined conservation status using the Endangered Species Act (US), Species at Risk Act (CA), and species listed by the Secretaria de Medio Ambiente y Recursos Naturales—2010 (MX). The US ESA does not have an official Special Concern category, but we included this category for Canada and Mexico because it is a legally defined protected status in both countries. However, as this step may have biased our analysis toward finding lesser protection of transboundary species in the US, we also performed an analysis that only considered Endangered and Threatened status for all three countries (Figure S1). We excluded subspecies listings from subspecies without ranges in border states/provinces or that were restricted to islands.
We further examined legal protected status at the state/province level for the US and CA (state-level listings do not exist for MX), for border states/provinces only. We only considered species listings if there were legal mechanisms for regulation present in state/provincial law as documented in their constitutions.

Once conservation status was determined, we calculated proportion of peripheral and core range segments that were protected as a percentage of total number of PTS, and determined if there was differential protection of PTS across the border of country pairs at federal and state/province levels. We also determined if there was differential protection between US states bordering MX and Mexican federal listings. Greater protection was defined as either a higher conservation listing in one country (e.g., Endangered in the US vs. Threatened in Canada), or as conservation listing in one country and no listing in the other (>94% of cases of differential protection fell into this latter category). Finally, for those PTS with differential protection, we calculated whether greater protection occurred in peripheral or more poleward (northerly) range segments.

3 | RESULTS

We identified 327 PTS for US–CA and 565 PTS for US–MX across the three taxa assessed, representing 57% and 61%, respectively, of all transboundary species assessed (i.e., species that had range limits crossing the border between the country pairs). This total also represents 17% and 20%, respectively, of all species assessed, including species that are not transboundary (Figure 2A). PTS were more ubiquitous for mammals and birds than herpetofauna (Figure 2A). Peripheral range segments of PTS were less commonly located in the US, and hence core range segments more commonly located in the US, compared to the sister country (14% and 27% of peripheral range segments located in US for US–CA and US–MX comparisons, respectively). Examination of border crossing of PTS revealed hotspots of crossings for birds and mammals between western US states and CA provinces and eastern states and Ontario (Figure S2), and little geographic variability for US–MX (Figure S3).

A substantial proportion of PTS have different conservation status at the federal level across the shared border of each country pair, representing 22% of all PTS for US–CA and US–MX (Figure 2B; Table S1). In most cases (97% and 94% for US–CA and US–MX, respectively), species are protected on only one side of the border. In contrast, almost no PTS have similar levels of federal protection on both sides of the border (1% and 2% for US–CA and US–MX, respectively). Including PTS that have contrasting conservation status at the state/province level for US–CA, and state/federal for US–MX, these patterns are even more pronounced, representing 32% and 29% of all PTS for US–CA and US–MX (Figure 2B). Considering Endangered and Threatened status categories in the comparison, a lower, but still substantial, proportion of PTS are differentially protected, and patterns across taxa are consistent with the analysis including Special Concern categories (Figure S1).

Peripheral range segments were protected at a higher rate than core range segments as a percentage of the total number of PTS (22% vs. 2% for US–CA and 18% vs. 9% for US–MX). In addition, when PTS were asymmetrically protected across the border, peripheral populations typically had stronger protection (Figure 3A). For PTS shared between US–CA, northern range segments (including both core and peripheral segments) were protected at a higher rate than southern range segments as a percentage of the total number of PTS (19% to 5% for north vs. south segments, respectively), but this was not the case for US–MX (5% to 25% for north vs. south segments, respectively). Moreover, when PTS were differentially protected across the border, the northern range segment usually was more strongly protected for US–CA but the reverse was true for US–MX (Figure 3B). When including state listings in the analysis, this pattern is similar but less pronounced (Figure 3B).

4 | DISCUSSION

Our research reveals a substantial number of PTS in North America that are asymmetrically protected across the shared international border at both federal and local levels, with the peripheral range segment more likely to have greater protection status than the core segment. Such mismatches in conservation status across international borders could threaten the persistence of populations in one of the paired countries. As populations of species decline or become more fragmented toward the periphery of the range, protection of the species or its habitat on only one side of the border may reduce overall connectivity across the international boundary and thereby increase extinction risk for peripheral populations. For example, along the US–CA border, Canada lynx (*Lynx canadensis*) have their southern peripheral range segment located in the US. Due to small and fragmented populations at the southern range edge, lynx are listed as threatened in the US, with associated restrictions on harvest or take, whereas they are legally harvested in Canada, even in areas immediately adjacent to the shared border with US populations (e.g., southern British Columbia, western Ontario). Continued harvesting and habitat loss along the international border could limit trans-national population connectivity for lynx, as has been found for other transboundary species (Proctor et al., 2005). Likewise, along the US–MX border, the American black bear (*Ursus americanus*) is listed as endangered in Mexico but still harvested in several border states in the US. This
FIGURE 2  Differential protection of peripheral transboundary species (PTS) in North America. (a) Proportion of species assessed in three taxa that are considered to be PTS for US-CA and US-MX. Orange bars indicate proportion of species that have less than 25% of their range in one of the paired countries, and greater than 75% in the other. Proportions were calculated by dividing the number of PTS in each category by the total number of transboundary and nontransboundary species in the country pair. (b) Proportion of PTS in each taxon that have the same conservation status on both sides of the border (blue), different conservation status on both sides of the border at the federal level (red) and different conservation status on both sides of the border at the federal or state/province level (green). The remainder of PTS did not have conservation status on either side of the border.

disparity in management strategies could reduce bear dispersal into Mexico, thereby decreasing chances for long-term persistence. Given that conservation status often reflects degree of attention paid to species and habitat conservation efforts within a given country, our results regarding asymmetric protection suggest that many PTS in North America face transboundary challenges akin to those we outline above. Even though we did not assess aquatic species, we note similar concerns about asymmetric management of fishes across international borders (Shackell, Frank, Nye, & den Heyer, 2016). Although peripheral populations may be most at risk from asymmetric protection, the reverse situation also is possible, where a more threatened core population benefits from potential rescue from a less protected but currently healthier peripheral population (Buschalski et al., 2015).

Though the plight of PTS demands increased attention, not all PTS will benefit equally from increased international coordination in research or management activities. Rather, we suggest that certain characteristics of PTS may determine when and where differential protection across the border is important. First, wide-ranging PTS (i.e., having large territories or dispersal movements), or migratory species, where individuals often cross international borders during movements may experience direct mortality when crossing from a protected to lesser-protected range segment (Lambertucci et al., 2014; Selier, Page, Vanak, & Slotow, 2014). Wide-ranging PTS may also have heightened potential for peripheral populations to retain connectivity requirements with core populations. Many PTS (mammals and birds: ~25%) with asymmetric protection in our analysis are large-bodied and move or disperse long distances, given established relationships between body mass and territory size or dispersal distance (Jetz, Carbone, Fulford, & Brown, 2004). Second, differential protection may be particularly relevant for PTS manifesting metapopulation dynamics along the range periphery (Holt & Keitt, 2000), where shared conservation actions along the border will benefit metapopulation persistence and population connectivity.
(a) The proportion of differentially protected PTS at the federal level (red) or at the federal plus state/province level (green) where the peripheral range segment has the greatest protection. The numbers next to each bar indicate the total number of differentially protected PTS in each category. Note the bias toward protection of peripheral ranges for both federal and federal/state analyses. (b) The proportion of differentially protected PTS at the federal level (red) or at the federal plus state/province level (green) where the northern range segment has the greatest protection. Total numbers of differentially protected PTS are the same as in (a). Note the general bias toward greater protection of northern ranges for US-CA and southern ranges for US-MX, which is lessened somewhat by considering state/province listings.

Although sufficient data are lacking for estimating numbers of PTS falling into this category, we note that habitat and population structure commonly become more fragmented toward range peripheries (Gaston, 2009), with metapopulation dynamics of extinction and colonization likely influencing range limits (Holt & Keitt, 2000; Kubisch, Holt, Poethke, & Fronhofer, 2014). Third, PTS that are candidates for reintroduction or augmentation in the peripheral part of the range will benefit from healthy core populations immediately across the border, given that donor individuals can be drawn from adjacent source populations with similar habitat (Parlato & Armstrong, 2013; Stamps & Swaisgood, 2007). However, if core populations are not protected or well managed in areas adjacent to the border, they may not support the loss of donor individuals. At least 41% and 13% (for US–CA and US–MX, respectively) of asymmetrically protected PTS mammals in our analysis have been considered as candidates for reintroduction.

Our analysis did not address the fact that conservation listing within a country (e.g., Endangered) does not always equate with levels of protection granted to that species, or that there may be differences in effectiveness of protection measures among the three countries. Nevertheless, listing a species at a national level represents a significant first step indicating need for protection, research, and government attention, and all three countries had very similar listing criteria. Thus, our work should be considered in broad terms as underscoring the ubiquitous nature of the challenges associated with peripheral transboundary species, with future research needed to identify species that are likely to be most responsive to harmonized conservation efforts or strategies across borders.

We note that some of the most effective management actions toward PTS could occur at a more local level within border states or provinces, through collaborations between managers, parks, and other local actors (e.g., NGOs). For
example, researchers and managers in Washington and British Columbia have begun collaborative research projects on both sides of the border on Canada lynx ecology and conservation, aimed at understanding population ecology and connectivity in the transboundary region. This work, which was facilitated by a transboundary working group (Wildlinks) as well as the National Science Foundation, may also be able to inform policy decisions, through ongoing interactions with agency staff on both sides of the border that develop management plans for lynx and outreach to stakeholders (fur trappers) on the Canadian side of the border. Although transboundary collaborative action can be challenging to implement, particularly when national priorities for a particular species differ across borders (Selier et al., 2016) as is the case for many PTS, these types of local transboundary collaborative activities have proven effective for species protection, even along borders affected by conflict (Plumptre, Kuirakwinja, Treves, Owuonji, & Rainer, 2007). Transboundary protected area complexes may be particularly important in encouraging local collaborative action around PTS in border regions, as these cross-border protected areas can facilitate management of biodiversity (Opermanis, MacSharry, Aunins, & Sipkova, 2012; Plumptre et al., 2007; McPherson & Boyer, 2016). For PTS in North America, we note that 61% and 70% of asymmetrically protected PTS (for US–CA and US–MX, respectively) have ranges that overlap at least one transboundary protected area complex in border regions, with approximately half of those with ranges overlapping more than two such complexes (Supporting Information S1), suggesting that collaborations between transboundary protected areas in research and protection of PTS may be a crucial component of long-term management. Furthermore, although many protected areas near borders may not be physically connected across borders as with transboundary protected areas, they may be close enough to enhance dispersal or connectivity (Opermanis et al., 2012), or to play a role in cross-border collaborative management of PTS. Given that protected areas tend to be clustered near borders both globally (Baldi, Texeira, Martin, Grau, & Jobbagy, 2017), and for the three countries in this study (Supplementary Information S2), this situation may apply to many PTS in North America and other continents.

At a regional scale, our results reveal that the US is a hotspot of core range segments for PTS in North America. Increased consideration of transboundary status in US research and conservation planning therefore seems a reasonable next step, and will be most important for regions (e.g., Pacific Northwest) that are overall and taxa-specific hotspots of border crossings. Ongoing debate about border infrastructure in North America is also germane to our analysis. Increasing border development is a global threat that may threaten movement or dispersal, cause direct morality, or fragment populations (Lasky, Jetz, & Keitt, 2011; Linnell et al., 2016). Such problems associated with border development could exacerbate connectivity problems that arise as a result of different protection strategies across the border. For example, the proposed US–MX border fence could disrupt transboundary movement corridors for a variety of species, even including some birds (Flesch et al., 2010), and warrants a more comprehensive analysis, including environmental costs.

Climate change is likely to add complexity to the issue of transboundary conservation of species, as shifting ranges across international borders exacerbate already difficult governance challenges (Lim, 2016; Pecl et al., 2017; Ruter, Vos, van Eupen, & Ruhmof, 2014). In particular, as species shift poleward (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011) and the relative importance of poleward peripheral populations increases, greater protection for more northerly range segments of PTS in North America may be merited, along with more coordinated planning or management of core range segments south of the border that may supply dispersing individuals for range expansion. In accord with these conservation objectives, we found that northern ranges of PTS shared between US–CA were protected at a higher rate than southern ranges. However, the southern ranges were protected at a higher rate for PTS shared between US–MX. Although local protections partially offset the marked difference in federal rates of protection of north versus south range segments for US–MX, northern segments were still protected at lower rates. This second result highlights the need for greater consideration of status of poleward peripheral populations along this border in the context of expected climate change. Indeed, increased protection of expanding populations on the poleward side of an international border, through establishment of new protected areas or other mechanisms, may be a key piece of global climate change adaptation (Hannah, 2010). Yet, for PTS with a southern periphery that will become increasingly stressed by climate change, maintaining connection with northern core populations across the border could enhance long-term persistence (Anderson et al., 2009), suggesting that an exclusive focus on poleward peripheral segments of PTS may be too restrictive.

Although our work focused on North America, issues associated with cross-border management of PTS or other transboundary species are highly relevant to other regions of the globe, and the methods we detail here should be widely applicable. Species range maps are continually being improved, and most countries have species-specific red lists, at least for some taxa, that would enable a comparison of cross-border mismatches in country-level management of transboundary species (e.g., Selier et al., 2016). In the context of climate change, we suggest such comparisons may be most interesting for countries that share borders along an extensive east-west line.

Lack of policy congruence across international boundaries is widely recognized as an impediment to the conservation
of natural resources (Abbitt, Scott, & Wilcove, 2000; Dallimer & Strange, 2015). Nevertheless, our analysis is the first to systematically quantify the extent to which international borders act as obstacles to the conservation of PTS, whose fate is acutely sensitive to this issue. Not all PTS will benefit from transboundary research and management, and decisions to engage in such activities are made more difficult when funding is already lacking for national priorities. However, transboundary efforts can also yield benefits that national efforts would not, for example by pooling resources and expertise, upscaling planning and management activities, increasing accuracy of population monitoring, diversifying avenues of funding, and encouraging cooperation across international partners (Bischof, Brøseth, & Gimenez, 2016; Gervasi et al., 2016; Kark et al., 2015; Vasilijević et al., 2015). The growth of transnational committees or organizations that work across borders (e.g., Landscape Conservation Cooperatives, Tri lateral Committee for Wildlife and Ecosystem Conservation and Management) and transboundary protected areas or ecological networks (Kati et al., 2014; Rüter et al., 2014) may also help to facilitate more collaboration in conservation of PTS, while recent work highlighting governance criteria of successful transboundary conservation should help increase effectiveness of cross-border efforts (Lim, 2016). Such activities in North America could also be supported by, or situated within, existing regional international agreements designed to promote transboundary cooperation in conservation of resources, such as the 1993 North American Agreement on Environmental Cooperation and 1940 Convention on Nature Protection and Wildlife Preservation in the Western Hemisphere, as well as agreements related to migratory species (Migratory Bird Act and 1936 Treaty for the Protection of Migratory Birds and Game Mammals between Mexico and the US). However, even when international agreements or transboundary protected area networks exist to facilitate transboundary conservation, differing national-level priorities for conservation remains a key challenge (Kati et al., 2014; Selier et al., 2016). Given the scope of the asymmetric protection problem revealed by our analysis, it will be necessary for federal and state/provincial governments to give greater consideration to transboundary status of species, and the potential needs of peripheral populations in neighboring countries, when making research, planning and management decisions. This shift is not happening, or at best is occurring only informally for the three countries we examined, no doubt because deliberations regarding research funding and landscape-scale conservation planning are strongly influenced by their local or national protected status. Yet, as we argue here, more coordinated transboundary action could increase the likelihood of persistence of PTS across the entirety of their range, maintain their ecosystem functions on both sides of the border, and provide for a more robust response to the dangers posed by range loss and climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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