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Conservation priorities for carnivores considering protected natural areas and human population density

David Valenzuela-Galván · Hector T. Arita · David W. Macdonald

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Abstract We conducted a prioritization exercise for 47 terrestrial carnivores in North and Central America. We used 2 by 2 degree cells to explore the spatial patterns in overall richness, regionally endemic and threatened species and identified the hotspots (the top 10% of cells in each category). We obtained optimal minimum sets of cells to represent each carnivore either (1) at least once, (2) three times, or (3) in at least 10% of its regional distribution range. Our analysis considered cells with 50% or more of their area protected, and considered human population density (HPD) per grid cell, excluding the top 10% cells with higher HPD. We found low congruence among hotspots, suggesting these should not be used alone in directing conservation strategies. About 7, 18 and 84 grid cells are needed to reach each representation goal, respectively. A much higher number of protected cells are needed to achieve the same goals. Representing 10% of each species' distribution range required optimal sets of 47 additional cells to complement the protected cells. Irreplaceable cells had a similar or higher HPD than average values for all cells. By excluding the top 10% of cells with higher HPD, irreplaceable cells in optimal sets had much lower average HPD, but three species cannot be represented at all. By defining conservation priorities and proposing optimal networks of areas needed to represent all carnivores in the region, actual conservation efforts can be reviewed and revised. Furthermore, if our results are incorporated into a general strategy, limited resources available to conserve carnivores might be directed more efficiently.

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Introduction

Mammalian carnivores are an essential component of natural communities, with many representatives considered flagship, umbrella, keystone and indicator species (Noss et al. 1996; Gittleman et al. 2001). Conservation of carnivores is therefore important to preserve the structure and function of natural communities.

Carnivore conservation is different from "biodiversity" conservation for several social and ecological reasons. One of the primary issues in carnivore conservation is conflict with human interests, a consequence of diet, range and habitat resource requirements of many species, along with the human perception of threats posed to individuals or livelihoods (Sillero-Zubiri et al. 2007). At one extreme are cases of highly resilient species that directly or indirectly threaten humans, versus extremely sensitive species that are highly threatened by human activities (Purvis et al. 2001). Although the perception of threat may be greater than the reality, the conflict results in many carnivores being persecuted (Ginsberg 2001).

In the book "Carnivore Conservation", Gittleman et al. (2001) ask whether carnivore conservation would be better served by prioritizing geographical areas or ecological communities, rather than by the use of a species-by-species (taxonomic) approach. In this study we perform a prioritization exercise for the terrestrial carnivores of the northern part of the American continent. The region examined in this exercise spans 10 countries and includes 14% of the world's land mass (World Atlas 2006), 8% of the world's human population (US Census Bureau 2006) and 23% of the world's 228 terrestrial carnivore species (Wilson and Reeder 1993). Defining broad regional priorities for this area could represent a significant contribution to carnivore conservation and may help to develop local management strategies. Establishing priorities for conservation on a regional scale acts as a coarse filter to help allocate scarce resources (funds, expertise, time; Ginsberg 1999, 2001), guides conservation efforts, provides a framework for productive collaborations between scientists, managers and politicians, and "can act as a cost-effective shortcut for the identification of fine-scale priorities" (Larsen and Rahbek 2003).

Currently we know of no studies aimed at defining regional priorities exclusively for carnivores at a sub-continental level. Furthermore only a few countries, notably the United States and Canada, have carried out exercises to establish conservation strategies for carnivores (Noss et al. 1996; Ferguson and Larivière 2002). Generally research has focused on one species (e.g., jaguar—Sanderson et al. 2002; Medellín et al. 2002) or a small group of species from a global perspective (e.g., Glatston 1994; Nowell and Jackson 1996; Servheen et al. 1998; Sillero-Zubiri et al. 2004). As far as we know, the only study aimed at prioritizing conservation exclusively for all terrestrial carnivores in a region of continental proportions is that of Mills et al. (2001) which was performed for African carnivores.

The aim of this study is to offer a tool to obtain a quick and clear view of the potential difficulties in reaching the goal of conservation for all carnivore species at the sub-continental scale. Carnivores in this work have previously been considered in a few broader studies that have analyzed geographical distribution patterns for mammals and proposed conservation strategies for them as a group (Ceballos and Navarro 1991; Ceballos and Brown 1995; Arita et al. 1997). By building on this previous work we attempt to establish priorities for carnivore conservation in the North and Central American region. Specifically, we attempt to identify areas of relevance for carnivore conservation, evaluate the effectiveness of current conservation efforts (protected areas) in preserving carnivores, and explore how human population density can affect the potential of carnivore conservation throughout this region.

Methods

Database on carnivore species distribution

The study region consisted of the 10 countries in North and Central America from Canada to Panama, excluding the insular countries.

We obtained distribution data for 47 terrestrial carnivore species (Table 1) from the North American mammals Atlas Project (Arita and Rodríguez-Tapia 2004), which compiled maps of the extent of occurrence for mammal species in the region in half-degree (latitude–longitude) grid cells. To identify taxa we followed Wilson and Reeder (1993). We excluded the polar bear (*Ursus maritimus*), whose range it is limited to areas of sea-ice and seldom occur on land (DeMaster and Stirling 1981; Amstrup 2000). Additionally, four insular endemics from the Channel Islands in the United States and Marías and Cozumel Islands were excluded, as the islands are smaller than our scale of resolution, and conservation of these carnivores depends on conservation of their insular habitat.

We assessed carnivore distribution by imposing a grid of $2^{\circ} \times 2^{\circ}$ cells (approximately 200 × 200 km; 1089 cells) on the species distribution maps. This scale was the same used by Mills et al. (2001) in their analysis for Africa; it is a coarse-scale that can be readily connected to defining conservation sites on the ground (Larsen and Rahbek 2003). The presence of each carnivore species in each cell was then recorded using ArcView 3.2 GIS software (ESRI 2000). A species was considered to be present if its distribution map covered all or part of the cell.

We then explored the distribution patterns of richness, regional endemism and vulnerability of carnivore species. We considered a species as a regionally endemic if its entire distribution range was within the studied region, and vulnerable if it was listed by the World Conservation Union (IUCN 2006) as extinct in the wild (EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT) or lower risk/conservation dependent (LR/cd; Table 1).

Protection level and human density of grid cells

We used the 2006 version of the World Database of Protected Areas (WDPA) (UNEP-WCMC 2006) and considered only the map of national conservation areas of IUCN categories I–VI with known boundaries. We excluded protected areas listed as historical, archaeological, cultural, or non-terrestrial sites. We then estimated the percentage of each grid cell that was covered by these protected areas.

To explore representativeness of these protected areas, we calculated the number of times each carnivore species is represented at different thresholds of protection, from 0.05 to 100% of the area of a cell.

CanidaeAlopex lagopusArtic foxCanis latransCoyoteYesCanis lupusGrey wolfCanis rufusRed wolfCR DSpeothos venaticusBush dogVU C2a(i)Urocyon cinereoargenteusGrey foxVulpes vulpesRed foxVulpes veloxSwift foxYesFelidaeHerpailurus yagouarondiJaguarundiLeopardus pardalisOcelotNTLeopardus wiediiMargayYesLynx canadensisCanadian lynxYesPanthera oncaJaguarNTMustelidaeConepatus leuconotusEastern hog-nosed skunkYes
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Vulpes veloxSwift foxYesFelidaeHerpailurus yagouarondiJaguarundiLeopardus pardalisOcelotLeopardus tigrinusLittle spotted catNTLeopardus wiediiMargayLynx canadensisCanadian lynxYesLynx rufusBobcatNTPanthera oncaJaguarNTPuma concolorMountain lionNTMustelidaeConepatus leuconotusEastern hog-nosed skunkYes
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Puma concolor Mountain lion NT Mustelidae Conepatus leuconotus Eastern hog-nosed skunk Yes
Mustelidae Conepatus leuconotus Eastern hog-nosed skunk Yes
Conepatus mesoleucus Western hog-nosed skunk Yes
Conepatus semistriatus Striped hog-nosed skunk
Eira barbara Tayra
Galictis vittata Grater grison
Gulo gulo Wolverine VU A2c
Lontra canadensis Northern river otter Yes
Lontra longicaudis Neotropical river otter
Martes americana American marten Yes
Martes pennanti Fisher Yes
Mephitis macroura Hooded skunk Yes
Mephitis mephitis Striped skunk Yes
Mustela erminea Ermine
Mustela frenata Long-tailed weasel
Mustela nigripes Black footed ferret EW Yes
Mustela nivalis Least weasel
Mustela vison American mink
Spilogale putorius Eastern spotted skunk Yes
Spilogale pygmaea Pygmy spotted skunk Yes
Taxidea taxus Badger Yes
Procyonidae Bassaricyon gabbii Bushy-tailed olingo LR/nt
Bassaricyon lasius Harris' olingo EN D Yes
Bassaricyon pauli Chiriqui olingo EN D Yes
Bassariscus astutus Ringtail Yes
Bassariscus sumichrasti Cacomistle LR/nt Yes

 Table 1
 Terrestrial carnivores present in the region of North America and Central America considered in our study, indicating vulnerable and regional endemic species (see Methods)

Family	Species	Common name	Vulnerability based in IUCN (2006)	Regional endemic
	Nasua narica	White-nosed coati		
	Potos flavus	Kinkajou		
	Procyon cancrivorus	Crab-eating raccoon		
	Procyon lotor	Northern raccoon		
Ursidae	Ursus americanus	Black bear		Yes
	Ursus arctos	Brown bear		

Table 1 continued

We also calculated an average human population density (HPD) for each cell based on HPD (people km^{-2}) data for 2005, adjusted to match United Nations totals, at a grid resolution of 2.5 arc-minute (CIESIN 2005). All spatial analysis were done using ArcView 3.2 GIS software (ESRI 2000).

Geographic distribution of richness, endemic and vulnerable carnivores

For each grid cell the total number of species, number of endemic species and number of vulnerable species were calculated. Maps of species richness, endemism and vulnerability were created based on the cumulative number of carnivore species occurring in each cell. Hotspots were identified from the top 10% of each criterion. We explored their spatial congruence by calculating their spatial overlap as a percentage using the Jaccard coefficient as follows:

Jaccard coefficient: $X/(A + B + X) \times 100$

where *X* is the number of grid cells shared by two criteria and A and B are the number of cells that are selected exclusively by each criterion.

Optimal sets of grid cells for the conservation of terrestrial carnivores, protected natural areas and human population density

Optimal sets could potentially facilitate a more efficient implementation of strategies for carnivore conservation. We performed complementarity analysis to select the optimal sets of cells required for different representation goals (Underhill 1994; Justus and Sarkar 2002) for carnivores. We used CPLEX optimization software (ILOG 2001) to identify a set of optimal solutions for representing each species most efficiently in at least one and three grid cells. We also took into account different area-needs for species by calculating optimal solutions that in cells covering 10% of the species' distribution range. This is a somehow arbitrary target but one that has been used extensively (Ceballos et al. 2005; Rondinini et al. 2006).

We performed this analysis twice, with and without considering existing protected areas. We considered only the cells with 50% or more of their area protected. At this threshold, only 25 species are represented one or three times, and no species is fully represented in at least 10% of its range. We used these 38 cells as a baseline.

Since human population is a major determinant of extinction risk for carnivores (Cardillo et al. 2004), we explored how results are affected when we exclude the 10% of the cells with higher HPD in the region. We also excluded any grid cell with 90% or more of its surface covered by water, to avoid selecting cells where size of potential reserves would be restricted.

Although Harris' olingo (*Bassaricyon lasius*), Chiriqui olingo (*B. pauli*) and the little spotted cat (*Leopardus tigrinus*) were restricted to one or two grid cells each, we included them in the complementarity analysis as those areas would have to be protected in order to conserve all terrestrial carnivore species in the region.

Thus, the optimization procedure involved a total of 47 terrestrial carnivore species and a total of 935 2° by 2° grid cells (or less when additional restrictions are used in the selection of cells).

To identify irreplaceable cells (Balmford 2002; Margules et al. 2002), we set the program to obtain 20 optimal solutions, each consisting of the same number of cells, for each representation goal. To avoid repeated selection of the same solutions, each time one was sought, an additional restriction was added that excluded the previous solution (Rodrigues et al. 2000). The irreplaceability of a cell was measured by the number of sets in which it was included (e.g., a cell selected in all sets was completely irreplaceable). A measure of irreplaceability can be important in determining priorities for action (e.g., which cells should be conserved first) or for interactive building of reserve systems (e.g., irreplaceable areas can form the core of the system; Carwardine et al. 2006).

Results

Protection level and human density of the grid cells

The percentage of protection varied greatly among the 935 grid cells considered (on average 9.70%; SD 17.37), but 303 cells did not overlap at all with protected natural areas and for 143 cells $\leq 1\%$ of the surface was covered by a protected natural area.

The average human population density per grid cell was 17.1 people km⁻² (SD 54.8). The top 10% of cells with higher HPD (93 cells) presented an average density of 151.3 people km⁻² (SD 125.9), ranging from 53.5 to 795.4 people km⁻².

Interestingly, average human density in the 606 cells that do overlap with protected natural areas was 23.7 people km⁻² (SD 64.1). This is higher than the average HPD for whole set of grid cells considered (935), and higher than the HPD for the 303 totally unprotected cells (5.0 people km⁻², SD 27.7).

Geographic distribution of carnivore richness, endemism and vulnerability

Carnivore species richness was concentrated along the Rocky Mountains from southern British Columbia in Canada to Arizona and New Mexico in the United States. In México, species richness is concentrated along the Sierra Madre Occidental and the Sierra Madre Oriental, and particularly in the Oaxaca state. Overall six grid cells, one in the United States and five in México, were the richest in species, with 22 species each (Fig. 1a).

Among the 47 terrestrial carnivore species considered, 21 had their entire range contained within the studied region; this endemism is concentrated in the Rocky Mountains, particularly in the south, but also in northeastern California. Nine cells in the United States



Fig. 1 Top 10% of grid cells most rich in (a) species; (b) regional endemic species and (c) vulnerable species of terrestrial carnivores in the sub-continent region between Alaska and Panama

(Utah, Arizona, New Mexico) were richest in regional endemics, with 12 species each (Fig. 1b), including one of the richest in carnivore species.

Only 11 of the 47 species are listed in the 2006 Red List (IUCN 2006). These more vulnerable species are concentrated in Arizona, western New Mexico, and eastern Texas in the United States, but are primarily found in the Mesoamerican region: one cell, shared by Costa Rica and Panamá, had six vulnerable species; two cells, one in Costa Rica and the other shared by Nicaragua and Costa Rica, had five vulnerable species (Fig. 1c).

The spatial overlap between hotspots was relatively low. Vulnerability and regional endemism overlapped 16.25%, and total richness overlapped 23.18% and 58.97% with vulnerability and regional endemism, respectively.

Optimal grid cells sets and irreplaceable cells

We found that seven cells (0.75% of all 935 cells considered) are needed to represent all 47 terrestrial carnivore species at least once. To represent all species at least three times the number of cells increases up to 18 cells (1.9% of all cells). However in order to represent at least 10% of each species' distribution range, 84 grid cells are needed (nearly 9% of all cells).

The 20 optimal sets of seven grid cells needed to represent each carnivore species at least once were selected from a total of 25 different cells. Of these, three were selected in 19 or all of the sets, one occurring in México (in northeastern Tamaulipas state), and two in Central America (one between Nicaragua and Costa Rica, one between Costa Rica and Panamá). Of the remaining cells, three occurred in western México, three in the southern end of Central America and almost all of the remaining cells were located in Canada (provinces of Alberta, Saskatchewan and Manitoba; Fig. 2a).

The 20 optimal sets of 18 cells needed to represent each carnivore at least three times are drawn from a total of 26 grid cells. Irreplaceability notably increased and 15 cells were selected in 19 or all the sets, located as follows: five in Canada (one in the southwestern corner of Northwest Territories, two in the south of Alberta province and two more in Nunavut Territory); two in the United States (one each in Montana and southern Texas); two in México (northeast Tamaulipas and southern Jalisco) and six in Central America (southern Nicaragua, Costa Rica and Panamá). Most of the remaining grid cells are located in the west and south of Mexico (Nayarit, Jalisco, Michoacán, Guerrero and Oaxaca states; Fig. 2b).

Finally, to represent at least 10% of each species' distribution range in the region, sets of 84 cells were required (selected from a total of 103 cells). About 83 grid cells were selected 19 or 20 times, and only 20 cells were chosen one or two times. Most of the irreplaceable cells are spread across Canada and the United States: 48 in northern Canada and Alaska (United States) corresponding to areas of boreal forests/taiga and tundra (biomes from Olson et al. 2001); 16 in the western United States, in areas of temperate coniferous and desert and xeric shrubland biomes of the Rocky Mountains; seven are located in the Great Plains region of United States, in areas of temperate grasslands, savannas and shrubland biomes; and five more are in the region of the Great Lakes, in temperate broadleaf and mixed forest biomes (Fig. 3).

Only four of the irreplaceable cells are located in México: three in a region shared by Sinaloa, Nayarit, Durango and Zacatecas states (tropical and subtropical dry broadleaf forests, tropical and subtropical coniferous forests, desert and xeric shrublands biomes) and another in the eastern end of the Trans-Mexican volcanic belt, shared by Puebla, Oaxaca and Veracruz states (tropical and subtropical coniferous forests, desert and xeric shrublands, tropical and subtropical dry broadleaf forests, moist broadleaf forest biomes). Finally, three more irreplaceable cells located in Central America were also selected in the previous representation goal, in areas of tropical and subtropical dry and moist broadleaf forest biomes (Fig. 3).

Average HPD were 68.8 (SD 15.5), 44.7 (SD 62.9) and 15.2 (SD 33.9), respectively, for the 3, 15 and 83 irreplaceable cells obtained for each representation goal.



Fig. 2 (a) The 25 2° by 2° grid cells used to obtain 20 optimal sets of seven cells needed to represent all carnivores at least one time; (b) the 26 2° by 2° grid cells used to obtain 20 optimal sets of 18 cells needed to represent all carnivores at least three times. The shade intensity shows the level of irreplaceability of each cells (e.g. in how many of the 20 sets was included) according to the legend code

Protected natural areas and conservation priorities for carnivores

Protected area thresholds notably influenced carnivore representation. When all cells with $\geq 0.05\%$ of its area protected are considered (606 cells), all 47 carnivore species are represented in at least the number of cells equivalent to 10% of its distribution range in the area. However, when the threshold is increased to $\geq 20\%$ of a cell's area protected, only 27 species are represented, and just 39 and 38 species were represented at least once or three times, respectively. These numbers drop rapidly as the percentage of protection threshold is raised, and when the threshold reaches $\geq 50\%$ protected (only 38 grid cells or 4% of the 935 cells considered), only 25 species are represented at least once or three times, and no species is protected to at least 10% of its distribution range.



Fig. 3 The 103 2° by 2° grid cells used to obtain 20 optimal sets of 84 cells needed to represent at least the 10% of each species distribution range in the region. The shade intensity shows the level of irreplaceability of each cells (e.g., in how many of the 20 sets was included) according to the legend code

We use this 50% threshold and seek to represent each of the 22 unrepresented species (mostly of neotropical distribution) at least once or three times each, and to optimally complement its representation to reach at least 10% of its distribution range.

Sets of five cells are needed to represent, at least once, the 22 unrepresented species in cells with half or more of their area protected. The 20 optimal sets where drawn from a total of 17 cells, three of which were recurrently irreplaceable in Central America (one shared by Nicaragua and Costa Rica, one shared by Costa Rica and Panamá, and one in Panamá; Fig. 4a).

To represent the same 22 species three times, a set of 12 cells was needed, drawn from a total of 20 cells. From these, eight were selected 19 or 20 times and the rest were chosen in much fewer sets. The irreplaceable cells are located as follows: one in the Gulf coast region in Texas (US), one in the west of Mexico, shared by Nayarit and Jalisco states, and the remaining six cells in Central America, between southern Nicaragua and southern Panamá (Fig. 4b).

To complement the cells with half or more of their area protected, and to reach representation of at least 10% the distribution range of all species, sets of 47 cells were needed, selected from a total of 71 cells. Thirty-eight of these were irreplaceable, mostly located in areas of boreal forests/taiga (11 spread across the Northwestern Territories and Alberta, Saskatchewan, Manitoba, Ontario and Quebec provinces, Canada) and tundra (three in northern Alaska in United States and three in the northeast of Nunavut Territory, Canada) biomes. Another 13 cells were located in the United States, mostly in areas of temperate coniferous forest in the west, and in temperate broadleaf forest biome in the east (Fig. 5).

Two irreplaceable cells are located in México. One cell is shared by Nayarit and Jalisco states, in areas of tropical and subtropical dry broadleaf forests, and tropical and subtropical coniferous forests, and the other in the eastern end of the Trans-Mexican volcanic belt, shared by Puebla, Oaxaca and Veracruz states, on areas of tropical and subtropical coniferous forests, desert and xeric shrublands and tropical and subtropical dry broadleaf and moist broadleaf forest biomes). The remaining three cells are the same cells previously mentioned as irreplaceable in Central America, in areas of moist broadleaf forests (Fig. 5).



Fig. 4 Distribution of the grid cells needed to represent at least: (a) once (optimal sets of five cells drawn from a total of 17 grid cells); (b) three times (optimal sets of 12 cells drawn from a total of 20 grid cells) the 22 species not represented in the cells with \geq 50% of its area already protected. The shade intensity shows the level of irreplaceability of each cells (e.g., in how many of the 20 sets was included) according to the legend code

Average HPD were 71.8 (SD 19.8), 65.3 (SD 77.9) and 27.2 (SD 42.5), respectively, for the 3, 8 and 38 irreplaceable cells obtained on each of the previous representation goal (to complement the carnivore representation on cells with more than 50% of protection).

Human population density and optimal sets for carnivore conservation

When the 10% of grid cells with higher HPD are excluded from the selection process, we found that three species cannot be represented at all, *L. tigrinus, B. lasius and B. pauli*, restricted in the region to only two or one grid cells in high-human-density areas.



Fig. 5 The 71 2° by 2° grid cells used to obtain 20 optimal sets of 47 cells needed to complement the representation of at least the 10% of each species distribution range in the region departing from the grid cells with \geq 50% of its area already protected (38 cells). The shade intensity shows the level of irreplaceability of each cells (e.g., in how many of the 20 sets was included) according to the legend code

The remaining 44 species can be represented at least once in sets of five grid cells (0.6% of the 842 cells considered in this particular analysis). This number increases to sets of 16 cells (1.9% of all available cells) to represent them at least 3 times. Finally, in order to represent at least 10% of each of the remaining 44 species, sets of 86 grid cells are needed (nearly 10.21% of all eligible cells).

The 20 sets of five grid cells needed to represent the remaining 44 species at least once each are drawn from a total of 23 cells. From these, 4 are selected 19 or 20 times, one located in southeast Panamá, one in Oaxaca State in Mexico, one in south Texas, United States and the other one in the southwestern corner of Alberta province, Canada. The remaining cells were chosen once or twice and almost all are located in the northern extreme of the Nunavut Territory, Canada (Fig. 6a).

The grid cell sets of 16 cells needed to represent all 44 carnivore species at least three times were selected from a total of 24 cells. About 14 were irreplaceable, four located in the Rocky Mountains, five in Canada (southwest of the Northwest Territories and Alberta province, and north of Nunavut Territory) and one in central Montana State (United States). Three more in the Coastal Plain region in an area shared by Texas (United States) and Nuevo Leon (México). In México, one cell is shared by Sinaloa, Nayarit and Durango states, and two more cells are located mostly in Oaxaca state. The last two irreplaceable cells are in the southeastern extreme of Panamá. Almost all the remaining 10 grid cells are located in the Yucatán Península, México (Fig. 6b).

For the final goal of representing at least 10% of the distribution range of each of the 44 species, sets of 86 grid cells were needed. The 20 sets were drawn from a total of 129 grid cells. Irreplaceability is lower than before, with only 62 selected 19 or 20 times, and these cells are distributed differently than the other previously described patterns to achieve representation goals.

Only two cells are located in western United States (one shared by Wyoming and Colorado and one in northwest New México), four in British Columbia province, Canada. Eight cells are located in a region shared by Manitoba and Ontario Provinces (Canada) and



Fig. 6 When the 10% of grid cells with higher human population density are excluded, three species can not be represented at all, and the remaining 44 species can be represented: (**a**) At least one time with five cells, 20 optimal sets where drawn from a total of 23 2° by 2° grid cells; (**b**) At least three times (or totally if its distribution range is less than three cells) with 16 cells, 20 optimal sets where drawn from a total of 24 2° by 2° grid cells. The shade intensity shows the level of irreplaceability of each cells (e.g., in how many of the 20 sets was included) according to the legend code

North Dakota and Minnesota states (United States) corresponding to temperate grasslands, savannas and shrublands and temperate broadleaf and mixed forest biomes. Five cells are in the Coastal Plain region in areas of temperate grasslands, savannas and shrublands biome of Missouri, Illinois, Oklahoma and Texas states (United States), and one cell shared by Texas state (US) and Nuevo León state (México). In México the same irreplaceable cells as in the previous result are selected, and one more cell in the southeast of Panamá is included in all the sets. The rest of the irreplaceable cells (39) are located in areas of boreal forests/taiga and tundra biome in Canada and Alaska (United States; Fig. 7).

As expected, when the top 10% of grid cells with higher HPD are not considered, average HPD in the irreplaceable cells found in this portion of our study were the lowest:



Fig. 7 The 129 2° by 2° grid cells used to built up 20 optimal sets of 86 cells needed to represent at least the 10% of each species distribution range for the 44 species that can be represented when the 10% of grid cells with higher human population density are excluded. The shade intensity shows the level of irreplaceability of each cells (e.g., in how many of the 20 sets was included) according to the legend code

29.4 (SD 17.3), 17.0 (SD 15.6) and 5.0 (SD 9.8), respectively, for the 4, 14 and 62 irreplaceable cells obtained for each of the previous representation goals.

Species representation within optimal sets

We choose one optimal set example for each representation goal to explore how each species is represented. In the optimal sets needed to represent all species at least one or three times, nearly two thirds of the species are represented more than the minimum specified number of times. This figure drops to 45% when the target is at least 10% of each species' distribution range, and drops even further, to 20%, when the grid cells with higher human population density are excluded.

Interestingly there are five species (Alopex lagopus, Canis rufus, Gulo gulo, Mustela *nigripes* and *Vulpes velox*) that consistently were represented to just the minimum specified extent in all exercises, implying that most of their distribution ranges are in areas of relatively low richness or in transitional zone where several species reach their southern or northern limits. Also, for some species that were represented only one or three times when that was the minimum number of times specified, more than 10% of their distribution range was represented in the optimal set of 84 grid cells (e.g., Conepatus leuconotus, Lynx canadensis, Martes pennanti, Speothos venaticus and Spilogale pygmaea), a consequence of the higher number of grid cells required to represent the 10% of the distribution range of species with a bigger extent of occurrence. Finally, several other species are consistently represented more often than the minimum representation goal. In the case of species with relatively small distribution ranges (e.g., Bassaricyon gabbii, Conepatus semistriatus, Eira barbara, Galictis vittata or Lontra longicaudis) this indicates that their distributions overlap substantially with species with wider distribution in the region. Certain species (e.g., Canis latrans, C. lupus or Bassariscus sumichrasti), overlap a few cells with the distribution range of several species with more restricted ranges, and hence the cells needed to represent these restricted species also represent the wide ranging species.

Discussion

Establishing regional conservation priorities for carnivores considering existing protected areas and human population density

Our results highlight areas of particular interest for the conservation of carnivores. The Rocky Mountains in the United States and the northern part of the Sierra Madre Occidental in México contained the highest number of species and regional endemics. The junction of Puebla, Veracruz and Oaxaca states in México was a second area rich in carnivore species, whilst vulnerable species tended to occur in México and Central America (Fig. 1a–c). These results provide a coarse-scale initial framework for focusing conservation efforts in this region.

Hotspots of richness or endemic and/or threatened species are often used to set conservation priorities. For example, endemic or restricted-range species have high conservation priority for the countries or regions involved, yet is only a useful criterion within an adequate legal framework is in place (Grill et al. 2002). In our study, we noticed relatively low congruence among hotspots, which agrees with other studies for carnivores and for other taxonomic groups and at different scales (Mills et al. 2001; Bonn et al. 2002; Ceballos and Ehrlich 2006; Grenyer et al. 2006). Because of low spatial overlap among these criteria, they should be considered together in guiding conservation efforts.

Prioritizing areas using our optimal set approach provides a framework for concentrating efforts to conserve species in a relatively small number of cells. A minimum of seven cells was needed to represent all species at least once. A more realistic option, which could reduce extinction risks by representing all species in at least three sites, is achievable with sets of 18 cells, which capture 33 species more than three times. However, in order to achieve the representation of at least 10% of each species' distribution range in the region, nearly 9% of all considered cells are needed, a similar figure to that provided by Ceballos et al. (2005) who found that nearly 11% of the Earth's land surface was needed in order to protect at least 10% of all terrestrial mammal geographic ranges.

As expected, irreplaceability increases as the representation goal becomes more complex (the percentage of irreplaceable cells rises from 43%, when the representation goal is all carnivores at least once, to 99% when the representation specifies that at least 10% of the distribution range of each species is encompassed). Nonetheless, for every representation goal there is certain flexibility as represented by the 20 different sets obtained for each goal.

A challenging outcome of our study was that the majority of the irreplaceable cells needed for each representation goal were found in areas with higher HPD than the average. In other words, efficient carnivore conservation has to occur in areas of relatively high human density. A similar result was reported by Rondinini et al. (2005), who found that more than half of the irreplaceable area needed to protect African amphibians and mammals coincided with high human population density. But, we consider that such an outcome was less surprising for Africa, where human population pressure is expected to be higher than in the region we have studied. As has been stated by others (Araújo et al. 2002; Luck et al. 2004), and as we have shown, it is still possible to identify sets of cells where conservation strategies for carnivores or other groups could be implemented efficiently, in areas of relatively low human population density.

Our study illustrates that there are areas where conservation strategies must be implemented alongside high human populations. This will require new strategies (Brandon et al. 2005; Ceballos et al. 2005; Rondinini et al. 2005; Araújo and Rahbek 2007). Among carnivores, larger animals have a greater potential for conflict in fragmented habitats (Woodroffe 2000; Mills et al. 2001; Crooks 2002; Ogada et al. 2003; Treves and Karanth 2003; Berger 2006), and also, larger animals face energetic constraints that force them to feed on large vertebrate prey (Carbone et al. 1999). They are, therefore, more likely to come into conflict with humans and consequently be threatened or go extinct (Gingsberg 2001).

Furthermore, like other studies in the region but at different geographic scales (Parks and Harcourt 2002; Vázquez and Gaston 2006) we noticed that on average, the grid cells that overlap with protected natural areas, were characterized by much higher human population density than were the cells with no protection. This raises the fear that smaller reserves will suffer more intense human population pressure (Harcourt et al. 2001; Parks and Harcourt 2002).

Interestingly, when partly protected grid cells are considered (without further consideration of how much of the cell is protected or of the sizes of protected areas within) these 606 protected grid cells represent at least 10% of the distribution range for all the 47 species considered. However, considering the sizes of home ranges needed by most of the medium sized or large carnivores we considered in our study (18 species have average body mass higher than 5 kg), it would not be safe to assume that the grid cells offering low percentage of protection are actually protecting these species.

For instance, Wilting et al. (2006) considered that only reserves bigger than 350 km², and those adjacent to others, could sustain stable populations (>50 individuals) of clouded leopard (*Neofelis nebulosa*) in South-East Asian rainforests. Linnell et al. (2001) concluded, based on the home range values they estimated for resident Eurasian Lynx (*Lynx lynx*) individuals in Scandinavian forests (>300 km²) that very few of the protected areas could protect populations of this felid. Brashares et al. (2001) found that for 41 species of large mammals (including eight carnivore species), reserve size was closely and positively correlated with extinction rates (particularly for carnivores) within natural reserves in West Africa, and hence they suggest that reserve size should be increased if possible.

Woodroffe and Ginsberg (1998) have estimated critical reserve sizes (CRS; an area for which a 50% probability of population persistence is determined through logistic regressions) for several carnivore species: grey wolf (766 km²), jaguar (69 km²), black bear (36 km²) or brown bear (3981 km²). Each of the 2° by 2° grid cells we used may be a candidate area where a reserve, or reserves, sufficient for the CRS of wide-ranging carnivores could be established.

The number of species with at least 10% of its distribution range represented within the protected grid cells drops quickly as the protection threshold increased. For example, when only the 200 grid cells with 15% or more of its area protected are considered, seven species fail to meet the criteria that at least 10% of their distribution range will be represented. In comparison, 84 grid cells were needed to achieve this goal for all the 47 species, and if the 38 cells with 50% or more of protection are considered as a starting point, 47 additional cells are needed to achieve the same goal. Clearly, terrestrial carnivores are insufficiently and inefficiently represented in the existing protected natural areas.

The distributions of the species we used were based on historical extent of occurrence maps. It is known that the distribution range of several species in Canada, United States and México, has decreased by more than 20%, and 15 more species have suffered a reduction of less than 13% in their historical ranges (Laliberte and Ripple 2004). It is clearly desirable that new distribution maps are produced.

Conservation planning

Systematic conservation planning (Margules and Pressey 2000) can be achieved efficiently through complementarity analysis using heuristic methods or optimization procedures (Pressey 1994; Underhill 1994; Justus and Sarkar 2002; Margules et al. 2002; Rodrigues and Gaston 2002; Moore et al. 2003). However, when possible, optimization procedures are favored over heuristic methods (Pressey et al. 1996, 1997; Csuti et al. 1997; Rodrigues and Gaston 2002; Moore et al. 2003).

By using optimization procedures we were able to provide several sets of areas that if protected could contribute to the conservation of terrestrial carnivores in the region, representing them at least once, or several times. Several optimal sets were identified and explored to determine the feasibility of conserving the grid cells selected.

The complementarity analysis we present could be refined by adding other variables such as vegetative cover, estimation of actual land costs or connectivity with other reserves (Balmford et al. 2000; Briers 2002). Further refinement would be possible if species specific information were available, such as species density or abundance, the fraction of its population inside each planning unit, life history details or likelihood of persistence (Ferguson and Larivière 2002; Gaston et al. 2002; Margules et al. 2002; Bonn and Gaston 2005; Mace et al. 2007).

Conservation strategies

When prioritizing entities, for example species or areas, it is necessary to identify factors that affect the results. These may be many and varied, such as: the scale of analysis (political or geographical); scope (taxonomic or biotic); concept of species to be used (phylogenetic or biological); objective of the priority setting (more species to be protected or an increase in long term viability of species) and achievability (political and financial considerations).

The scale at which priority analysis is conducted is an important consideration when planning conservation strategies. Larger carnivores tend to occupy large home ranges, so protected areas should be big enough to protect these requirements. The size of grids used in our analysis did not restrict the establishment of appropriate sized reserves in the optimal cells. However, studies at a finer spatial resolution are required to design properly where and how a reserve should be established. These studies may also highlight additional benefits of particular conservation activities. For example, some species such as the bush dog (*Spheotos venaticus*) and the little spotted cat would be best conserved in South America (where they are most commonly distributed). However, they are part of the Mesoamerican carnivore biota and by focusing efforts on conserving all carnivore species in this region they can be protected at no extra cost. Any prioritization must also be flexible and subjected to constant modification and upgrading (Mace and Collar 2002).

Carnivore conservation efforts throughout the world strongly suggest further research is needed to obtain baseline information of the status of the species, including their prey, range and habitat requirements (Weber and Rabinowitz 1996). In fact <15% of carnivore species have been the subject of serious scientific studies (Ginsberg 2001) and many of these are not of conservation concern.

Priority setting exercises tell us, at best, what to conserve first, not how to conserve it. In contrast, operational strategies might be considered a much finer filter. However, operational strategies do not tell us how to allocate scarce resources at a regional level. Both

regional priority setting and operational planning approaches, adapted to local political, ecological and social needs are required to achieve conservation (Ginsberg 1999). Priority setting is essential for providing a framework for conservation to be monitored and revised, and stimulates further debate and studies at finer scales.

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