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Landscape analysis of jaguar (*Panthera onca*) habitat using sighting records in the Sierra de Tamaulipas, Mexico

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Summary

The Sierra de Tamaulipas is a biogeographically isolated mountain system in Northern Mexico, where habitat fragmentation by land-management practices is a possible threat to wildlife conservation. As a case example, we used GIS analyses to evaluate how human activities influence the landscape structure of jaguar (*Panthera onca*) habitat in the region. The study: (1) ranked potential habitat based on associations between environmental attributes (topography, streams and vegetation) and the frequency distribution of jaguar sighting records; (2) classified current land cover from a 1990 Landsat-TM image and mapped the landscape structure of high potential habitat; and (3) compared the degree to which mature natural vegetation is fragmented by different types of owners. Jaguar sites showed significant associations with tropical deciduous and oak forests, and low, west or south-east slopes, between 400 and 900 m. About 52% of the high potential habitat was mapped as mature natural vegetation, which was distributed as two large patches (28% of the land area) and many small forest patches (98% at < 80 ha). The number and size-class distribution of high-potential habitat patches varied little amongst four ownership types, but the dispersed distribution of more subsistence and commercial-based owners across the landscape suggests the need for collaborative participation in a conservation plan. From our study the need to scale up from managing individual land parcels is substantiated and areas that promote regional contiguity of jaguar habitat in the Sierra de Tamaulipas are identified.

Keywords: fragmentation, geographic information systems (GIS), landscape ecology, North America, remote sensing, wildlife conservation

Introduction

The isolated mountains and surrounding plains of north-eastern Mexico are recognized as important areas for regional wildlife conservation (Fig. 1; Alvarez 1963; Ceballos & Navarro 1991; Arita *et al.* 1997). At a maximum elevation of about 1400 m, the Sierra de Tamaulipas forms a 4000 km^2 physiographic discontinuity in a landscape of generally low relief (Instituto Nacional de Estadística, Geografía e Informática [INEGI] 1994). It is disjunct by about 65 km from the more major mountain system of the region, the Sierra Madre Oriental. The region forms a biogeographic transition between the Nearctic and Neotropical biota of the North American continent (Hershkovitz 1958; Alvarez 1963; Ceballos & Navarro 1991). The Sierra de Tamaulipas contains a high diversity of both temperate and tropical species, some of which are biogeographically isolated by the surrounding lowland. Such conditions of natural isolation are

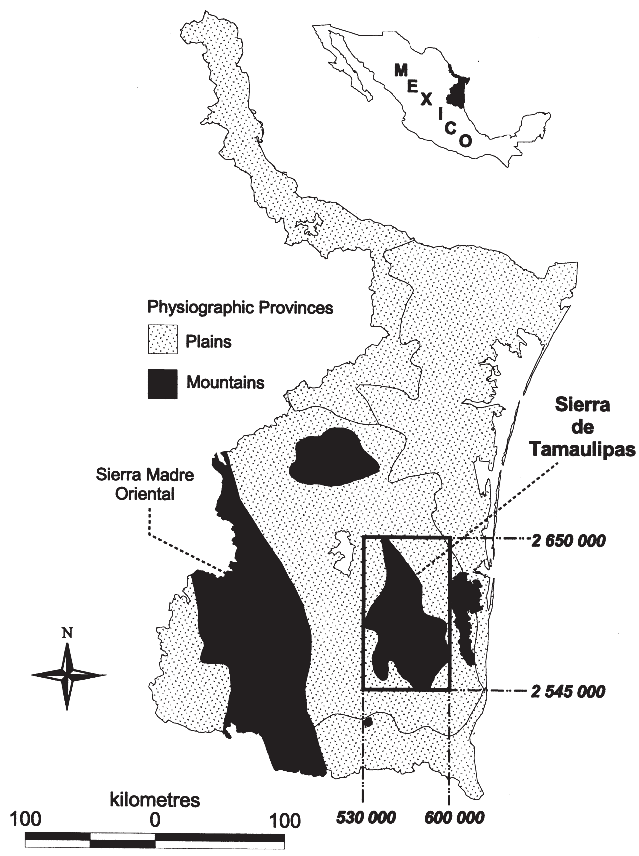

Figure 1 State of Tamaulipas, Mexico, showing the location of the major mountain systems and surrounding plain provinces: Cuahuita Nuevo León plains in the north, Tamaulipan coastal plains to the east, and the Western plains. The study region was approximately 7400 km^2 and is defined by the UTM coordinates and box that surrounds the Sierra de Tamaulipas.

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exacerbated by accelerated rates of land transformation during the last decades, both on the coastal plain surrounding the mountain system and in ecologically sensitive areas such as steep slopes and thin soils on the mountains (Secretaría de Desarrollo Urbano y Ecología [SEDUE] Delegación Tamaulipas 1989). Major land-use activities include cattle grazing on introduced grasslands and in secondary vegetation, and to a much lesser extent, crop production.

In order to mitigate damaging patterns of landscape change, Mexican (1988) and State of Tamaulipas (1992) legislation now require environmental impact assessments. Although federal legislation mandates the development of regional land-use plans, the impacts of forestry and other land-use practices are evaluated on the basis of local, parcel-size impact assessments. The lack of regional ecological assessments and the isolated approach in evaluating individual parcels can promote a process of fragmentation across the Sierra's landscape. Land-cover types may be conserved within a parcel but isolated by the land-management practices on the adjacent parcels. For regional biodiversity conservation, very little is known on the spatial distribution and environmental conditions of biota in the mountain system, their habitat preferences, and the degree to which human activities are contributing to the loss and isolation of important habitats.

The purpose of this study is to evaluate how human influences on land cover in the Sierra de Tamaulipas are related to the distribution of important areas for wildlife conservation. One overall question concerns the degree to which regional distributions of wildlife habitat are disrupted across land parcels by the management practices of different types of owners. The question necessarily relies on a holistic understanding of wildlife habitat conditions, land cover and the regional fragmentation of wildlife habitat, and landowners and their documented influences on these landscape patterns. Wildlife habitat quality is used as a ranked variable in this study to describe land areas which provide resources and conditions suitable for occupancy by more or less individuals (cf. Morrison *et al.* 1992; Hall *et al.* 1997), and fragmentation refers to the break-up, isolation and loss of high-quality habitat (Morrison *et al.* 1992).

As a case example, we examined the spatial distribution of habitat for the jaguar (*Panthera onca*) in the Sierra de Tamaulipas. Jaguar in Mexico and Central America is now reduced to 33% of its original range, and the Sierra Madre Oriental and Sierra de Tamaulipas represent the most north-eastern limit of its range in the North American continent (Swank & Teer 1989). The threatened status of this species in Mexico clearly supports habitat protection (Ceballos & Navarro 1991), but the absence of knowledge about the behaviour and ecology of the jaguar in the Sierra de Tamaulipas complicates the modelling of its habitat.

A few studies developed in Central America (Rabinowitz & Nottingham 1986; Aranda 1990, 1996) and Brazil

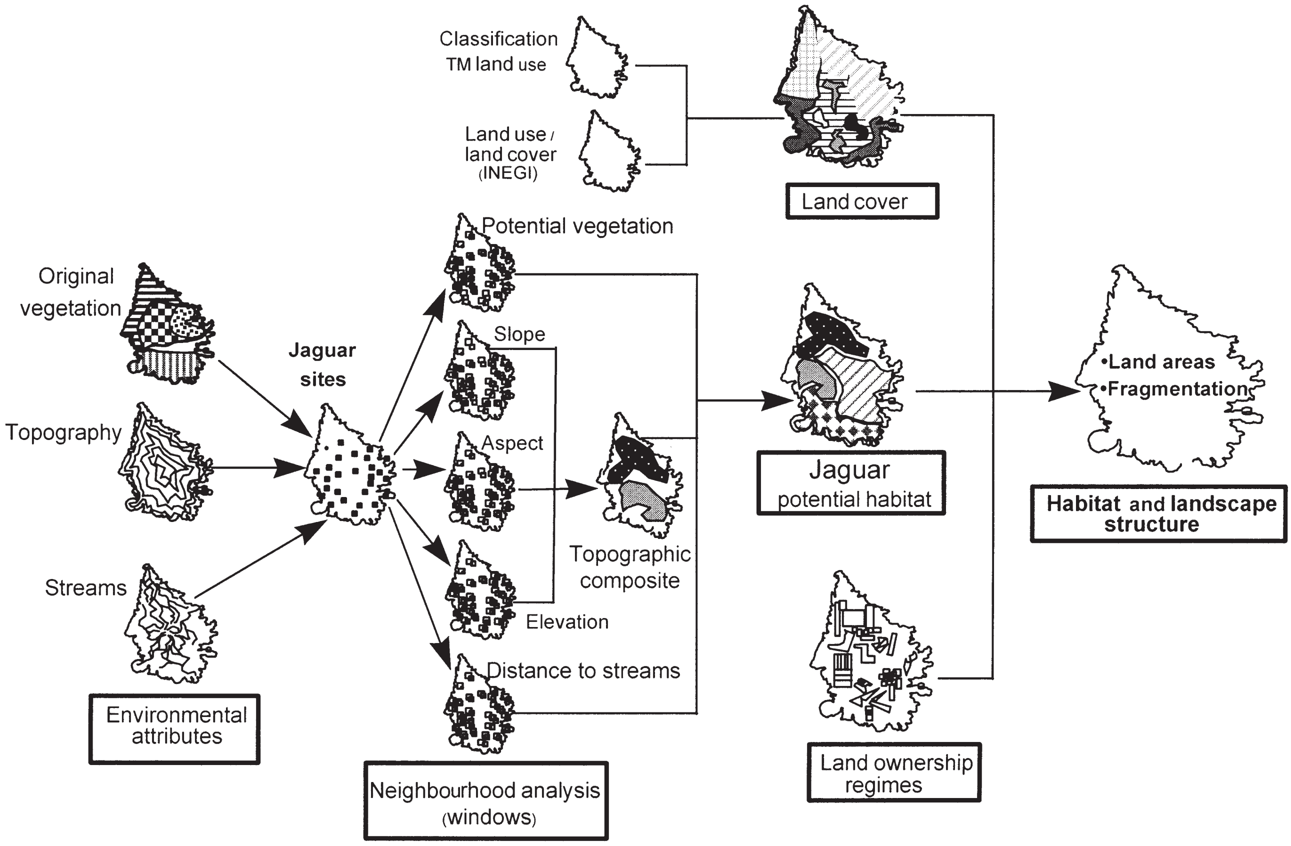

Figure 2 Study approach, using GIS analyses to model potential habitat for the jaguar in the Sierra de Tamaulipas, Mexico.

(Crawshaw & Quigley 1991) provide general ecological attributes for comparison. Ranges are large and reflective of the distribution of jaguar prey. In the subtropical wet forest habitat of Belize, Rabinowitz and Nottingham (1986) determined a home-range of 33.4 km^2 for mature adult male jaguars in comparison with 142.1 ± 25 km^2 for jaguars on a mixture of inundated grassland and woodlands in the Pantanal Brazil (Crawshaw & Quigley 1991). Aranda (1990) estimates a density of one jaguar per 40–60 km^2 in the tropical forest of southern Mexico, and one jaguar per 60–100 km^2 in other regions. These predicted densities show that the ecological conditions of a geographic area influence the relative population sizes (cf. Smallwood & Schonewald 1996, for mammalian carnivores). If one assumes that the predominant tropical deciduous forest conditions of the Sierra de Tamaulipas (Puig 1970) are comparable to ecological conditions in other regions in Mexico (i.e. one jaguar per 80 km^2) and the reported geographic land area of 4000 km^2, then the approximate size of the population would be about 50 animals. Habitat studies show a preference for tree cover (Crawshaw & Quigley 1991), a close association with water (Line & Ricciuti 1985; Sunquist 1987; Swank & Teer 1989), and an avoidance often of high elevations of very disturbed habitat (Quigley & Crawshaw 1992). These findings, while not directly applicable to a new geographic setting, do provide habitat and behavioural attributes that support using jaguar as a representative species for wildlife conservation and allow for regional comparisons of habitat conditions.

The habitat model we develop is based on jaguar sighting records in the Sierra de Tamaulipas and the recognized importance, described above, of topography, streams and natural vegetation (Fig. 2). A geographic information system is used to identify correlations between site localities (neighbourhoods) and a set of environmental attributes, and then relates a hierarchical ranking of habitat quality with current land-cover and ownership structure (e.g. Davis *et al.* 1990; Burrough *et al.* 1996; Heit *et al.* 1996). Coupling an examination of landscape patterns and their quality as jaguar habitat, we aimed to: (1) estimate the jaguar's potential habitat in the Sierra de Tamaulipas based on relationships between environmental attributes and sighting records; (2) classify current land cover from a 1990 Landsat-thematic mapper image and measure the landscape structure of high-potential habitat; and (3) compare the landscape structure of high-potential jaguar habitat amongst different types of landowners.

Methods

Jaguar potential habitat model

A 1 × 1 degree Digital Elevation Model (DEM), purchased from the Instituto Nacional de Estadística Geografía e Informática (Instituto Nacional de Estadística, Geografía e Informática [INEGI] 1994), portrayed topography at a resolution of 3-arc seconds between different elevations in metres. The elevation map was re-sampled to a 50 × 50 m grid-cell resolution and separate data layers for slope and aspect in degrees were calculated using Arc-Info GRID functions. Three stream types (main and secondary perennial and main intermittent) were digitized from the INEGI Land Use and Vegetation chart F142, scale 1:250 000 (Instituto Nacional de Estadística, Geografía e Informática [INEGI] 1985), using Atlas-GIS software and then converted to raster in ARC-INFO with a 50 × 50 m grid-cell resolution. The EUCDISTANCE GRID function calculated separate coverages showing distances from a single stream type and from the three stream types. Puig's (1970) potential vegetation map was digitized to show ecological conditions suitable for the development of indigenous vegetation types: thorn forest, oak forest, pine forest, tropical deciduous-*Bursera* forest, tropical deciduous-*Phoebe* forest, and thorn scrub. These data were mapped on a UTM-14 coordinate system using a Clarke spheroid projection and shown for a rectangular area centred on the Sierra de Tamaulipas that was approximately 7400 km^2 (Fig. 1).

The Secretariat of Urban Development and Ecology (Secretaría de Desarrollo Urbano y Ecología [SEDUE] Delegación Tamaulipas 1991) in the State of Tamaulipas gathered information over a three-year period on sightings from the region's inhabitants, government officials and local taxidermists for six species of wildcats in the Sierra de Tamaulipas: jaguar, puma (*Felis concolor*), jaguaroundi (*Felis yagouarundi*), margay (*Felis wiedi*), ocelot (*Felis pardalis*), and bobcat (*Felis rufus*). From a total of 77 sighting records for the six species, 50 were related to the jaguar. These sightings were based on jaguar kills or tracks (35 records), or locations where jaguar were killed (15). The SEDUE study mapped along the one paved and ten very rough roads in the region, but localities provided by the local residents (33 of 50) were mostly at inaccessible sites. We included the 24 sites located within the present study area. In January 1995, nine more jaguar sightings were mapped on 1:50 000 charts from field interviews in areas not covered by the SEDUE study (Ortega-Huerta 1995). All 33 sighting records were mapped on 1:250 000 charts and digitized as point features (UTM coordinates) into ARC-INFO. We focused the analyses on rectangular polygons (neighbourhoods) around the mapped sites (cf. Agee *et al.* 1989); this is a technique that filters local variability and reduces biases attributable to the positional accuracy of the points (cf. Goodchild 1994, 1996). These sighting records represent an approximate eight-year record for the species (i.e. about five years of sightings by participants in the three-year survey), and were the only information available on jaguar populations in the Sierra de Tamaulipas (Secretaría de Desarrollo Urbano y Ecología [SEDUE] Delegación Tamaulipas 1991).

The ARC-INFO GRID-FOCAL functions computed median (for topographic and stream attributes) or majority (for vegetation and land cover) environmental conditions for different neighbourhoods (windows) in order to explore variations amongst the attributes at scales that ranged from the immediate vicinity of a sighting record (~2 ha) to an estimate of the jaguar's daily range of 90 ha (Rabinowitz & Nottingham 1986; Crawshaw & Quigley 1991). Frequency distributions showed the degree to which environmental conditions in neighbourhoods around the jaguar sites were different from those computed, using similar-sized window samples for the total study area. These were statistically compared by G-tests (Sokal & Rohlf 1981). We considered all variables to be of equal importance to the jaguar, but constructed the model based on those that were statistically different and accordingly helped to distinguish potential habitat from the surrounding landscape.

Habitat maps for statistically different attributes were created by re-coding in ARC-INFO (RECLASS), according to the respective frequency distributions for the jaguar sites: low (1), medium (2), high (3) and very high (4). The potential habitat map was compiled in a step-wise fashion through addition. We re-sampled the compiled map to a grid cell size equal to 100 × 100 m (1 ha); this final resolution showed the distribution of ranked habitat conditions at a scale that was appropriate for regional planning (about 1:250 000; Tobler 1988).

Landscape analyses of jaguar potential habitat

A 1990 Landsat thematic mapper (TM) image was used to differentiate amongst land-cover types in the study region. Ortega-Huerta (1995) compiled three unsupervised classifications in ERDAS 7.5 and IMAGINE 8.0.2 based respectively on reflectances in the visible and near-infrared bands (TM 3, 4 and 5), reflectances in six bands (TM 1, 2, 3, 4, 5 and 7), and on the Transformed Normalized Difference Vegetation Index (TNDVI; Myers 1983; Crippen 1990). Ten 1:50 000 sampling rectangles, 10 × 3.5 km in size, were selected for each scheme by a stratified random approach and field-checked with a Global Positioning System (GPS) in January 1995 (Ortega-Huerta 1995). Finally, a 1:250 000 1970 land cover map for the region (10 cover classes; Instituto Nacional de Estadística, Geografía e Informática [INEGI] 1985) was digitized and overlaid onto the selected TM classified land-cover map in order to identify further the types of original vegetation. The final land-cover map was rectified and projected in a UTM-14 coordinate system that was registered to the habitat model.

The actual land-cover map was first used to identify significant associations between jaguar sighting records and the distribution of human-modified vegetation. We hypothesized that the jaguar records, measuring sighting potential (sensu Agee *et al.* 1989), may be biased by the distribution of their human observers to modified lands and/or the species may show ecological plasticity (Rabinowitz & Nottingham 1986; cf. Smith *et al.* 1997) that is adaptive to conditions established by humans. The same methodological approach (comparing neighbourhood windows) used in creating the ranked potential habitat map was applied to determine the association between the actual land cover and the jaguar sites.

Second, for the landscape analyses, areas of potential habitat ranked as 'high' and 'very high' were merged and used to extract the different land-cover classes. This map was then re-sampled from a 30 × 30 m grid-cell size for the land-cover map to a 100 × 100 m grid-cell size for the habitat model, and

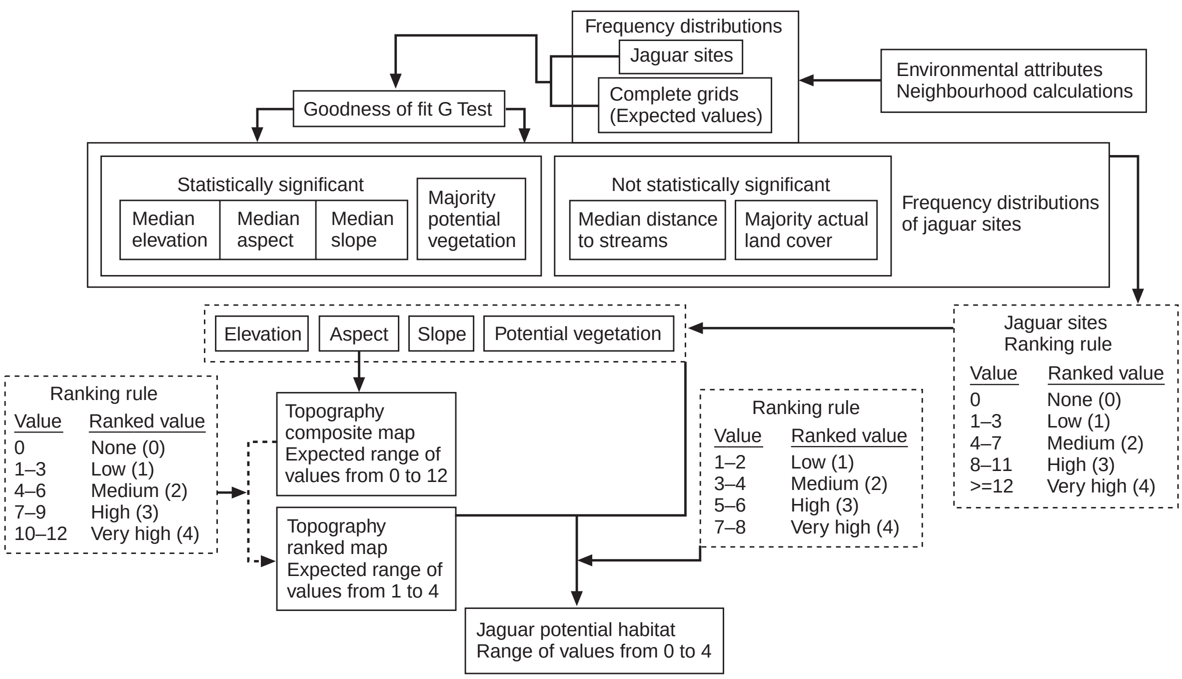

Figure 3 Creation of the potential habitat model based on statistical analyses and summed ranks for selected (statistically different) environmental attributes.

imported into the GRASS 4.1 in a SPARC SunX-Station 20 system for analyses using the r.le. (raster landscape ecological) programmes developed by Baker and Cali (1992). The minimum size of a recognized polygon (land-cover patch) was 1 ha.

Land-ownership structure

Maps of 1994 land parcels, 1:50 000, were provided by the Federal Agrarian Registry for the State of Tamaulipas. Parcels were coded by ownership type and digitized in registration with the actual land-cover and potential-habitat maps. We measured patterns of land cover associated with each land-ownership type and focused on differences between the communal, more subsistence-based owners and private, more commercially-based owners. Actual land cover on areas of 'high' and 'very high' potential habitat was extracted for each respective ownership type and analysed in GRASS 4.1 using the r.le. programmes (Baker & Cali 1992).

Results

Potential habitat model

The potential habitat model was constructed using ranks for those environmental attributes that showed statistically different frequency distributions between the jaguar sites and the whole study area (Fig. 3). All topographic attributes were significantly different for the jaguar sites. Median aspect was most different from the surrounding landscape for the 12 ha neighbourhood window (G = 12.9, $\chi^2_{[0.05]} = 12.6$), and 21% of the jaguar sites occurred on south-east facing (121–180°) and 36% on west-facing (241–300°) slopes. Together, these frequency percentages were 40% higher than those measured for the whole study area. Median slope values were most different for 42 ha neighbourhood windows surrounding the jaguar sites (G = 17.9, $\chi^2_{[0.05]} = 16.9$). Frequency percentages for the first two slope intervals (0–5° and 6–10°) were 48% and 33%, respectively, mostly attributable to the abundance of these slopes across the region. Jaguar sites were distinguished by their relatively higher frequency percentages on medium (11–20°; 15% versus 10% for the study area) and high (26–30°; 3% versus < 1%) slopes. Frequency distributions in 42 ha windows for median elevation were the most significantly different amongst the examined neighbourhoods (G = 52.4, $\chi^2_{[0.05]} = 21.0$). At this resolution, 79% of the jaguar sites occurred at 401–900 m, which was much different from the > 75% of the total study area at elevations < 400 m. Elevations were between 0 and 1300 m. Sighting records for jaguar were most frequent at a mid-elevation range that roughly corresponded with the original distribution of tropical deciduous and oak forest in the Sierra de Tamaulipas (Puig 1970).

Median aspect, slope, and elevation maps were ranked according to their respective frequency distributions, and a summed topographic composite map was re-coded to reflect relative site conditions (Fig. 3). 'Low potential' areas were on steep (> 20°), east-facing (0–120°) slopes, and at low and very high elevations in the Sierra de Tamaulipas. 'Very high potential' areas were on west-facing, low slopes (0–10°), and at elevations between 400 and 500 m.

The frequency distributions of jaguar sites with distances from main perennial, secondary perennial, and main intermittent streams, varied similarly between < 1 to > 40 km. They were combined in the statistical analyses, and were not significantly different from those compiled for the whole landscape (e.g. for the 42 ha window, G = 13.3, $\chi^2_{[0.05]}$ = 21.0). All sites were found at a median distance of less than 20 km and 36% of the sites are proximate to the streams at < 5 km. Stream distances, when ranked, did not improve the designation of potential habitat for jaguar and were not included in the model (Fig. 3).

Majority (i.e. dominant) potential vegetation-type (sensu Puig 1970) frequencies for the jaguar sites were significantly different from those of the total study area, and the same for all examined neighbourhood windows (11–87 ha; G = 26.5, $\chi^2_{[0.05]} = 11.07$). The tropical deciduous forest, *Bursera* and *Phoebe* components, were the dominant vegetation type for 58% of the jaguar sites (10 and 9 sites, respectively), but 24% were dominated by oak forest (8 sites), and 18% were dominated by thorn scrub (3 sites), pine forest (2 sites) and thorn forest (1 site). Especially distinctive were the high percentages of jaguar sites dominated by oak forest and the tropical deciduous *Bursera* and *Phoebe* forest types (24.2, 30.3 and 27.3%, respectively), in contrast to those measured for the total study area (7.6, 14.9 and 25.5%). Land areas of tropical deciduous forest and oak forest were ranked as 'high' potential, and areas of thorn forest, pine forest and thorn scrub as 'low' potential (Fig. 3).

Potential habitat quality was based only on frequency distributions for environmental attributes that showed significant differences for the jaguar sites, which included the ranked topographic composite map and potential vegetation (Fig. 3). Ranks for these two maps were summed and re-coded to show relative differences in quality across the study area. When stream distances, an attribute that did not show significant differences between the jaguar sites and whole study area, were ranked and included in the model, the very high potential areas disappeared and low potential areas were less frequent (Ortega-Huerta 1995). The jaguar siting records showed a more broad distribution relative to streams, reducing the overall resolution of the habitat model.

The potential habitat model, which was influenced by the positional accuracy of the jaguar sites on the 1:250 000 maps and also by the grid-cell resolution of the topographic (30 m^2) and vegetation (50 m^2) data, was re-sampled to present a regional view of habitat conditions at a more coarse, 100 m × 100 m (1 ha) grid-cell resolution (Fig. 4). In the study region, about 46% of the total area (329 km^2) was mapped as 'high' (44%) or 'very high' (2%) potential. Vegetation types as mapped by Puig (1970) determined the boundary of a nearly contiguous region of high quality habitat (Fig. 4). Only 8% of

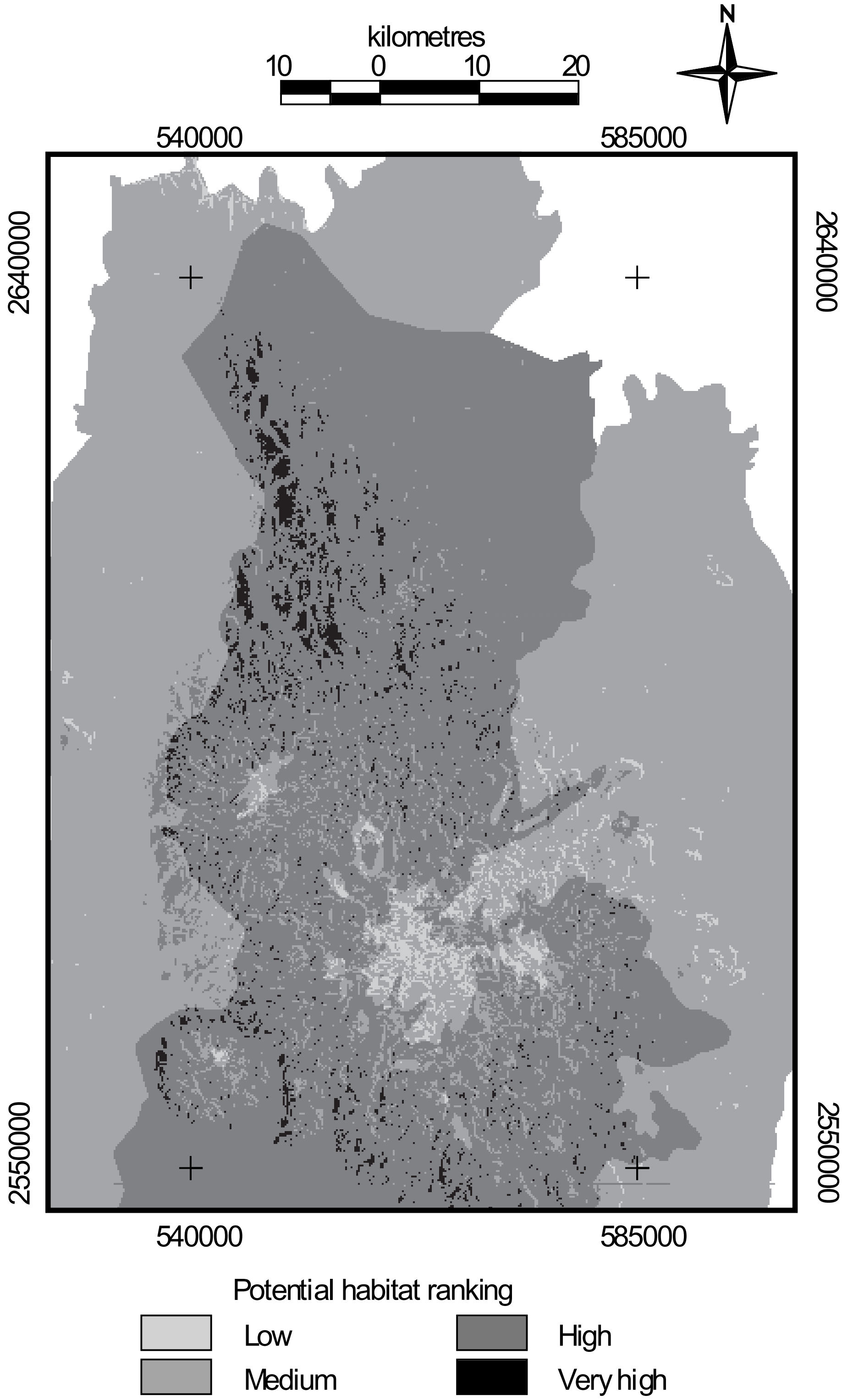

Figure 4 Potential habitat model for the jaguar based on the associations between topography (aspect, slope and elevation), potential vegetation and the jaguar sites. The grid-cell resolution is 100×100 m (1 ha).

the total area covered by deciduous and oak forests was not ranked as 'very high' or 'high' potential. Topographic characteristics distinguished 'very high' potential habitat within these vegetation types, emphasizing the greater value of west-facing, moderate slopes at mid elevations (Fig. 4).

Landscape analysis of jaguar habitat

Amongst the three different unsupervised classifications verified in the field, the TNVDI (8 classes) showed the best relationship with actual land cover. Classes 1 and 2 correlated with secondary vegetation that was dominated by shrubs < 1.5 m in height but ranged in composition from grassland mixed with shrubs to open woodlands. Classes 3 (gallery and canyon settings) and 4 were identified as mature natural vegetation, distinguished into seven types with the INEGI land-cover map (Instituto Nacional de Estadística, Geografía e Informática [INEGI] 1985). Class 6, introduced grassland, also included open areas with a mixture of streams, rocks, grass and shrubs. Class 7 included soil that was open due to cultivation (agriculture on lowlands) or without vegetation cover on cliffs and rocky soils (bare soil on the mountain). Classes 5 and 8 were present in only two of ten field maps, in areas smaller than 3 ha (a pond for cattle in one instance); they were not included in the analyses along with a portion of coverage in the south-west that was under cloud cover. The final classification distinguished the distribution of mature natural vegetation types (submontane scrub, pine-oak forest, oak forest, tropical deciduous forest, mesquite, palm forest, and thorn scrub) as they were related with disturbed (introduced grassland, cultivated/bare) and secondary vegetation.

We hypothesized that the jaguar siting records, all less than eight years old, would show significant relationships with the distribution of current land cover. Jaguar sighting records were most frequent in sites dominated by tropical deciduous forest and secondary vegetation, but the respective frequency of their associations changed with the size of the neighbourhood window (Fig. 5). For instance, in a 11 ha neighbourhood window (121 grid cells), 12 sites had secondary vegetation as the majority vegetation and 11 had tropical deciduous forest, but in the 87 ha window, only eight sites had secondary vegetation and 15 sites had tropical deciduous forest as the majority vegetation. Jaguar sites occurred in secondary vegetation, but most were proximate to tropical deciduous forest vegetation.

The frequency distribution for the jaguar sighting records across the land-cover types was more different with an increase in the neighbourhood window (2, 11, 40 and 87 ha) but not significantly different from that measured for the whole study area ($G = 8.5$ in the 87 ha window; $\chi^2_{[0.05]} = 21.0$; Fig. 3). Jaguar sites occurred across the region in proportion to the region's availability of land-cover types. The designation of habitat based on actual land cover was weakened by the broad occurrence of secondary vegetation (~40% of the total land area) that probably differed in habitat conditions (i.e. secondary from different natural vegetation types) and certainly differed in its proximity to mature natural vegetation. Actual land cover did not improve the designation of high-potential habitat, or suggest a statistically significant association with disturbed or secondary vegetation.

Our landscape analyses focused on the structure of 'high' and 'very high' potential habitat (Fig. 4) within a contiguous area defined by the boundaries of tropical deciduous and oak forest. From a total of 329 025 ha covered by high potential habitat (Fig. 4), only 27 532 ha (8.4%) did not correspond with the distribution of these two vegetation types and only 21 600 ha of low and medium potential habitat occurred within a boundary defined by these two vegetation types. All very high potential areas were included in the analyses (see Fig. 4).

About 52% of the land area modelled as high and very high potential habitat was mapped as mature natural vegetation and 48% was disturbed (6% bare soil, 2% introduced

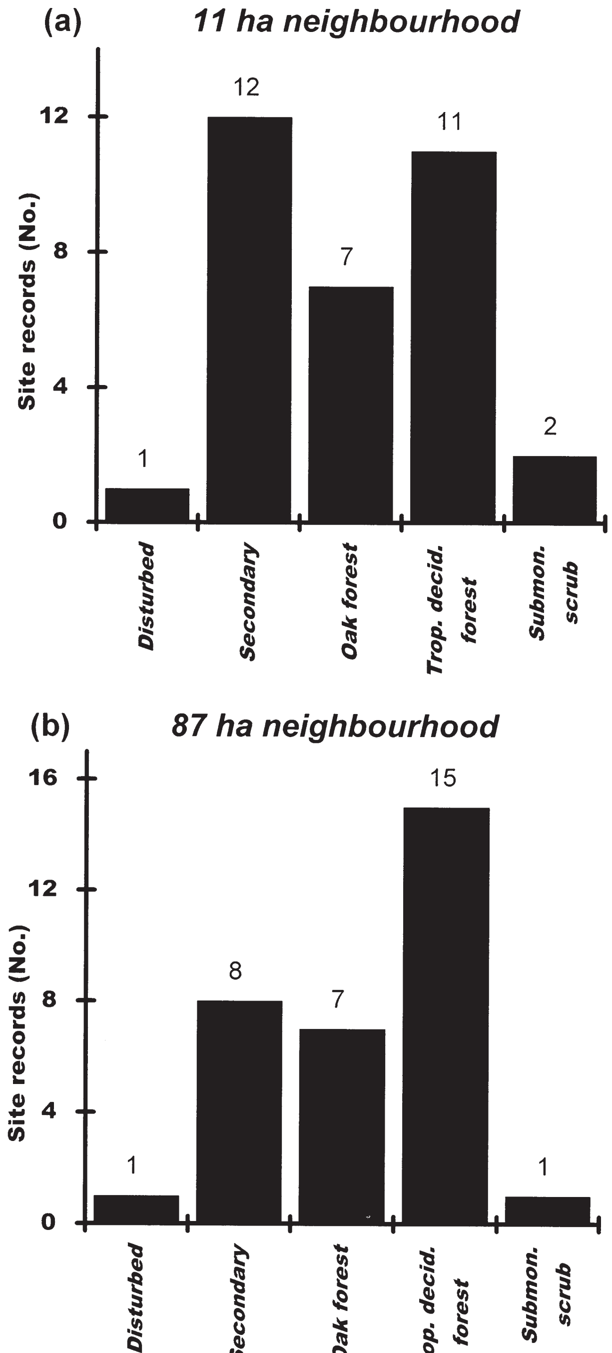

Figure 5 Frequency distribution of jaguar sighting records for the majority land-cover type in: (a) 11 ha (11 × 11 grid cells); and (b) 87 ha (31 × 31 grid cells) neighbourhood windows. One site record is excluded from the 87 ha neighbourhood because it included missing, i.e. cloud covered, data.

grassland, and 40% secondary) (Fig. 6). A total of 4696 original vegetation patches or 1.5 patches per km^2 occurred in the region (Table 1). The landscape included one large contiguous patch of mature natural vegetation in the centre (784 km^2; 24% of the original vegetation), one large patch in the southeast (135 km^2; 4%) portion of the area, and increasingly smaller patches and greater fragmentation away from these two large patches. Whereas 98% of the patches were small

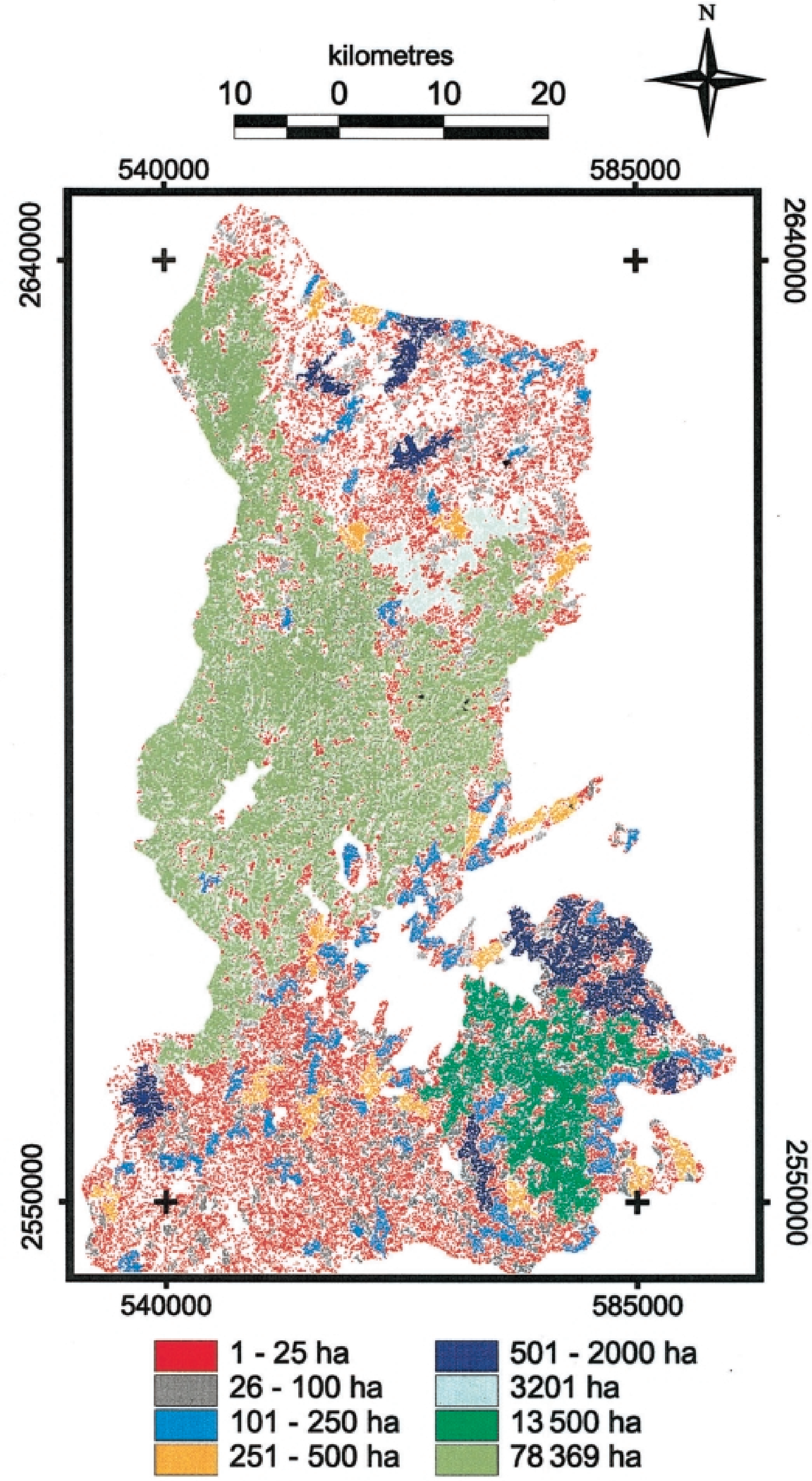

Figure 6 The distribution of original vegetation by patch size classes in a contiguous area of high potential habitat defined by the boundary of tropical deciduous forest in the Sierra de Tamaulipas. The grid-cell resolution is 100 × 100 m (1 ha).

Table 1 Landscape structure of high potential habitat in the Sierra de Tamaulipas, Mexico, for a contiguous land area defined by the boundary of tropical deciduous forest and for the respective land-ownership types in this region. Landowner types were derived from maps of 1994 land parcels, 1:50 000, provided by the Federal Agrarian Registry for the State of Tamaulipas.

	'High' potential habitat (% total)	*'High' potential habitat in mature natural vegetation*			
		% total area	*Patches < 80 ha*		*Patch densities (number/km²)*
			% total patches	*% land area*	
Total	3231 km² (100%)	51.5	98	20	1.5
More subsistence-based owners					
Ejido – campesinos whose production systems use family and community labour (individual and collective parcels)	530 km² (16.4)	52.1	95.9	22.3	4.6
NCP (Nuevo Centro de Población) – new population settlement; legally, an earlier stage of Ejido	294 km² (9.0)	48.1	97	26.1	7
More commercial-based owners					
Colonia – a form of private property – family production and sales	956 km² (29.5)	48.5	97.4	16.9	3.8
Private – individual ownership for commercial production	1396 km² (43.2)	57.5	95.8	9.6	2.9

(< 80 ha), they represented only 20% of the total area. Habitat fragmentation, characterized by the loss and consequent isolation of mature natural vegetation around the large patches was incipient; 97% of the original vegetation patches were between 100 and 1000 m from each other and 85% were between 100 and 500 m. The corridor that ran north–south in the western portion of the largest patch (Fig. 6) was a particular concern for regional conservation because of its spatial relationship with very-high potential habitat (Fig. 4). Further clearing along the corridor will essentially isolate the north-western sector of the largest patch.

Ownership structure of potential habitat

Parcel-map data from the Federal Agrarian Registry, overlaid on the region of high-potential habitat, identified four major types of owners (Table 1). *Ejido* and NCP (*Nuevo Centro de Población*) ownership types are considered more subsistence-based (25% of the high potential area), whereas *Colonia* and Private ownership types are based more on commercial production (73%) (Toledo 1993; La Secretaria de la Reforma Agraria, personal communication January 1993). Because of their low land percentages (~2%), four ownership types classified on the maps ('in litigation', 'unknown owner', federal, and national) were excluded from the landscape analyses.

The percentage of the high potential land area in mature natural vegetation varied little amongst the four landownership types, from 58% for private lands to 48% for the Colonia and NCP (Table 1). Cultivated/bare soils and introduced grassland were under 10% for all ownership types. All of the landowner types contain high-potential habitat for jaguar conservation in the Sierra de Tamaulipas.

Fragmentation, which was measured by the density and size-class abundances of the mature natural vegetation, was only slightly higher for the more subsistence-based owners (Table 1). Ejido had 22% and NCP had 26% of their land in small, < 80 ha patches, in contrast to the more commercial Colonia with 16% and private landowners with 10%. The NCP type also had the highest density of forest patches at about 7 per km². Patch densities for all ownership types, > 2 to 7 per km², were higher than the 1.5 patches per km² calculated for the whole study area. The number of patches was greater for the ownership types because of their dispersed distribution across the Sierra de Tamaulipas. For instance, most of the land area in the largest high-potential patch (784 km²; see Fig. 6) was under private ownership, but Ejido owners were important at locations in the north and south, NCP owners to the north-east and south, and Colonia to the east and north-east (Ortega-Huerta 1995).

Discussion

The Sierra de Tamaulipas is a geographically isolated mountain system positioned along the boundary between the Neotropical and Nearctic zoogeographic regions, which is rich in mammal diversity, rich in endemic species, and a priority area for the conservation of biodiversity in Mexico (Ceballos & Navarro 1991; Arita *et al.* 1997). The purpose of this study was to identify, by example, important areas for the regional conservation of jaguar habitat in the Sierra de Tamaulipas, Mexico, and identify the degree to which they are impacted by human activities. Regional assessments of wildlife habitat in tropical countries remain limited by the effective compilation of spatial data on environmental conditions and an understanding of species behaviour and resource needs. Our approach paralleled habitat studies that develop a hypothesized index of suitability for a single species (e.g. Berry 1986; Boyle & Fendley 1987; Yonzon *et al.* 1991), which is based on sighting records (cf. Agee *et al.* 1989; Christie & Low 1996). Similar to the application of GAP analysis in regional planning (Scott *et al.* 1993; Kiester *et al.* 1996), the study compared the current distribution of high-potential habitat with ownership structure. Traditional methods of agriculture found in Mexico involve certain 'ecological rationality' (sensu Toledo 1993), such that *campesinos* (peasant farmers) base their production systems on achieving long-term stability (Altieri 1991). In contrast, private landowners show systems of land-use more oriented toward market needs. Conservation plans for the jaguar need to be sensitive to the impacts imposed by these different types of owners and their spatial distribution across a priority region.

From interviews with local residents (Ortega-Huerta 1995), it was clear that the jaguar is a rare and elusive species. All of the sighting records originated from jaguar tracks, jaguars that were killed, or jaguar kills. These records, compiled through a government survey (Secretaría de Desarrollo Urbano y Ecología [SEDUE] Delegación Tamaulipas 1991) and field research (Ortega-Huerta 1995), were the only information available for the species in the Sierra de Tamaulipas and one of the best data sets for wildlife in the region. They represent three years of field work and document an approximate 8-year record from the local informants. The sample is limited in size, which would be expected in an elusive animal of a small population size (about 50 animals), and may be biased by accessibility and visibility in the landscape (cf. Christie & Low 1996; Smith *et al.* 1997). Still, they reflect associations with environmental conditions and are comparative with existing behavioural and habitat data from other studies (e.g. Rabinowitz & Nottingham 1986; Aranda 1990, 1996; Quigley & Crawshaw 1992). Our study provides a first regional assessment of habitat conditions for jaguar in the Sierra de Tamaulipas. Conducted at the landscape scale, the study forms a basis for research on local habitat preferences by jaguar (Morrison *et al.* 1992; Hall *et al.* 1997), relationships with wildlife diversity patterns (cf. Simberloff 1998), and impacts attributable to human activities.

Jaguar sighting records occurred distinctively on moderate-steep, west and south-east facing slopes, and at elevations between 400 and 900 m. These findings contrast with related research that predicts jaguar to be isolated to steep slopes, probably in response to hunting pressure and landscape transformation (Quigley & Crawshaw 1992), or at elevations above 1000 m in Mexico (Swank & Teer 1989). Jaguar showed significant associations with the distribution of potential vegetation, occurring most frequently in tropical deciduous and oak forests. On the final habitat map, these two vegetation types correspond most directly with the region mapped as high potential and topographic preferences identify locations of very high potential within this region. The non-significant relationships with stream distances in the study region may be explained by a high density of all stream types in a dissected mountain system.

Statistical associations between the jaguar sites and a composite of topographic attributes and potential vegetation were first compared amongst differently-sized neighbourhoods around the sighting records, and were evenly reflected in the ranking of potential habitat. We did not include weights to emphasize a particular attribute because we did not know from behavioural research how any variable might, in fact, be influencing the numbers and distribution of jaguar. Whereas the inclusion of variables with significantly different frequency distributions for the jaguar improved the resolution of the model (slope, aspect, elevation and potential vegetation), the inclusion of non-significant variables, irrespective of their importance to wildcats (e.g. distance from streams, Swank & Teer 1989; Smallwood & Fitzhugh 1995; Smallwood 1997), weakened the designation of relative habitat quality in the region.

The GIS analyses combined a number of spatial data sets that varied in their resolution and for the sighting data, their positional accuracy (cf. Goodchild 1994). We examined raster (grid-cell) data for topography at a 50 m^2 resolution, streams at a 50 m^2 resolution, potential vegetation at a 30 m^2 resolution, and land cover at a 30 m^2 resolution. These data, in the final habitat map and landscape analyses, were re-sampled at a resolution equal to 10 000 m^2 (1 ha). This process of spatial averaging imposed inaccuracies when local variability is lost through a process of filtering, but at the same time reduced error attributable to the co-registration and the positional accuracy of the data used in the analyses (Goodchild 1994, 1996; Burrough *et al.* 1996; Friesen & Sondheim 1996). We viewed the final resolution of the analyses (10 000 m^2 or 1 ha) appropriate for regional planning at an approximate 1:250 000 scale (Tobler 1988; Davis *et al.* 1990).

Regionally, the Sierra de Tamaulipas can be considered a less impacted and important habitat remnant for jaguar in the northern part of its range. Low-elevation habitats on the coastal plain, where the jaguar had been reported, were too small and isolated near the Sierra de Tamaulipas (cf. Arita *et al.* 1997). Within the mountain system, jaguar showed non-significant associations with current land cover; they occurred mostly in original tropical deciduous forest or near its boundary in modified secondary vegetation. This distribution, while it may reflect the distribution of human observers, identifies a habitat edge that is in conflict with human activities in the area. One would predict that with increased landscape alteration, the jaguar will move up the slopes (e.g. Quigley & Crawshaw 1992), or be threatened by greater hunting pressure along a proportionately greater edge habitat. The model we propose may be used to stratify a sampling design that more rigorously examines density patterns (e.g. Smallwood & Fitzhugh 1995) and explores finer-scale patterns in how the jaguar use resources in the region (i.e. scales of habitat use; Hall *et al.* 1997).

The proportion of high potential habitat in original vegetation was about 50% for the whole region, and also for each of the four ownership types. A low proportion of bare/cultivated soil and high occurrence of secondary vegetation suggest that crop production was a non-significant activity or shifted across locations in the region. The implications of having a cover of 50% mature natural vegetation are significant. Contiguous forest clusters which stretch or 'percolate' across a landscape, occur only if the respective land cover occupies about 60% or more in a random landscape (O'Neill *et al.* 1988). For instance, in the Sierra de Tamaulipas, most of the land area of high potential habitat was in a few very large patches, but most of the patches were small and decreased in size with distance from the large patches. Without some protection from forest clearing, persistence of the region's jaguar population will depend on their adaptation to processes of fragmentation that isolate high-quality habitat (Morrison *et al.* 1992). These processes are predicted to be profound with further loss in the proportion of mature natural vegetation.

In the Sierra de Tamaulipas, the time is critical for protecting land areas under a plan that will ensure habitat contiguity with future land development. The jaguar in the Sierra de Tamaulipas represents an isolated population of a nationally endangered species (Ceballos & Navarro 1991), separate from others in the Sierra Madre Oriental and possibly the coastal plain. The distribution of jaguar reflects relative habitat conditions along a human-impacted edge in an area of predicted importance to regional wildlife conservation (Arita *et al.* 1997). The study identified two large patches of original vegetation, which together were about 919 km^2 in area or equivalent to 28% of the high potential habitat (Fig. 6). Of particular importance is the largest patch in the central portion of the mountain system that connects along a western corridor the very high potential habitat on west-facing slopes (Fig. 4). These large patches represent a core habitat area for jaguar in the Sierra de Tamaulipas. We present them as a proposed region for protected-area management, which may be expanded by corridors to smaller patches (cf. Harris & Atkins 1991).

The designation of these lands for regional protection, however, is complicated by another level of fragmentation in the different types of landowners. All owner-types showed similar land-cover patterns in the region and all occurred in, or adjacent to, suitable habitat. Their dispersed distribution across the landscape complicates the coordination of a regional plan. Local, parcel-scale assessments may guide use by a landowner within a parcel, while also promoting segregation from land-use activities outside of the parcel. Collaboration with a particular landowner type (more subsistence or more commercial) may isolate effectively-managed parcels in the landscape. Our study clearly showed the need to scale up from managing land parcels. A regional plan for wildlife conservation, targeting only the core habitat areas identified in the Sierra de Tamaulipas, would have to involve the collaboration of different owners (individual parcels), and more importantly, different types of owners.

The simultaneous examination of environmental and landowner data compiled by this study provide an important first step toward the establishment of planning priorities for jaguar protection in the Sierra de Tamaulipas, Mexico. Considering the large home range documented for jaguar ($>$ 33 km^2; see Rabinowitz & Nottingham 1986; Aranda 1990; Crawshaw & Quigley 1991), its avoidance of highly disturbed areas (Quigley & Crawshaw 1992) and its function as a top predator dependent on the spatial distribution of suitable prey (Rabinowitz & Nottingham 1986; Sunquist 1987), our model might provide a measure of habitat potential for many species in a landscape where little is known on the spatial patterns of wildlife diversity. Questions concerning the use of jaguar as an 'umbrella species' for biodiversity conservation may be explored through research on relationships with other wildlife populations (Simberloff 1998). For instance, whereas the species that prefer the tropical deciduous and oak forest regions of the Sierra de Tamaulipas would be included in a plan that protects the high-quality habitat for jaguar modelled by our study, those that rely on resources in the thorn scrub, thorn forest and pine, which were mapped as low potential habitat for the jaguar, are not addressed. Regional conservation plans benefit from studies that apply an investigation of wildlife populations toward 'ecosystem management,' as presented by our case study (see Simberloff 1998). An important *next step* will be to apply this assessment of landscape conditions for jaguar toward a better understanding of regional patterns of biodiversity and collaborative plans for conservation amongst landowners in the Sierra de Tamaulipas.

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