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Abstract—The Madrean Archipelago, or Sky Island, region of the southwestern United States and northern Mexico is recognized for its great biological diversity and natural beauty. This conference brought together scientists, managers, and other interested parties to share their knowledge about the region and to identify needs and possible solutions for existing and emerging problems. It provided a forum to update the state-of-knowledge acquired since the first conference in 1994. The proceedings contains over 100 articles and additional abstracts from the plenary sessions and from concurrent sessions covering biogeography, ecosystem monitoring, science-based management, cultural resources/history, invasive species, hydrology and biodiversity, conservation planning, ecology, fire, conservation practice, and global climatic change. Abstracts in Spanish are included. The summary of an open forum at the end of the conference provides additional thoughts about current and future needs for the Madrean Archipelago.

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Connecting Mountain Islands and Desert Seas:

Biodiversity and Management of the Madrean Archipelago II

and

5th Conference on Research and Resource Management in the Southwestern Deserts

May 11-15, 2004
Tucson, Arizona

Compilers:

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Brooke S. Gebow
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Preface

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The Madrean Archipelago, or Sky Island region, of the Southwestern United States and Northern Mexico lies between the Sierra Madre Occidental and the Rocky Mountain Biogeographical Regions. The mountains, deserts, and grasslands of the region are known for their unique biodiversity and natural beauty. In 1994, Leonard DeBano and his associates organized the first conference to determine the state-of-knowledge and to focus management and scientific efforts on sustaining the Madrean Archipelago's ecosystems. The first conference was successful; however, research and management options are not static, and the 2004 conference has provided an opportunity to disseminate new information. The future health of the region was a concern in 1994, and concerns have grown as we enter the 21st century in spite of progress since the first conference. The 2004 conference combines two separate efforts (the "5th Conference on Research and Resource Management in the Southwestern Deserts" and "Biodiversity and Management of the Madrean Archipelago II") for ecosystems that are adjacent and often interconnected physically and philosophically and are under similar pressures from natural forces and human activities.

The Sky Island and Southwestern desert regions are the dubious beneficiary of too much love. More than 300,000 people have moved into the Sky Island region during the past 10 years. Rooftops have replaced open landscapes in some of our most remote valleys and hillsides. New and recent inhabitants view our public lands as their personal playgrounds, and the land often suffers because of overuse and public ignorance. However, people need to see themselves as an integral part of the ecosystem and attempt to understand the complexities in order to truly value biodiversity. Outreach to the general public should be an important component of our efforts. Humans are not the only problem; nature has not been kind to the region in recent years. Extended drought, wildfires, insects, diseases, non-native invasive species, and climate change are impacting, either alone or in combination, all of our major ecosystems from the low-elevation deserts to the mixed conifer and spruce-fir forests on the mountain tops. How can we protect the land while still availing ourselves of its numerous natural and esthetic resources? What must be done to make our ecosystems healthier and more sustainable?

In spite of these alarming changes, there is much hope for the Madrean Archipelago's future. The Forest Service, National Park Service, and other governmental agencies are working with private conservation groups to protect the region. Collaboration among groups will multiply the ability to protect and improve the land and its resources. Private organizations can mobilize their memberships and financial resources for conservation projects. Private land owners, such as members of the Malpai Borderlands Group and the Sonoita Valley Planning Partnership, have joined forces with State and Federal agencies, universities, and non-governmental organizations to protect their own lands with innovative strategies and successful models. An increasingly collaborative approach is needed as we attempt to tackle the region's problems and provide for the future.

Managers need science and particularly current science to accomplish their missions as stewards of the lands. Maintaining the viability of ecosystems and the connectivity among landforms requires sharing science and creative management among all groups.

Science cannot be truly useful if conducted in a vacuum. The 2004 conference, with more than 350 participants and almost 160 oral and poster presentations, was designed to increase communications and collaboration to achieve a common purpose and direction for the Madrean Archipelago and Southwestern deserts. Conferences such as this one provide a forum for the interchange of information, ideas, and views. The full articles and additional abstracts in these proceedings document the diverse research and management activities in the region. Each manuscript (except the abstracts listed at the end of the book) was reviewed for technical merit by at least two peers. Although this increased the time it took to publish the proceedings, it increased the quality of the content. The publication will also be available at **http://www.fs.fed.us/rm/main/pubs/electronic/rmrs_proc.html.**

Clear evidence of the spirit of cooperation and collaboration to achieve a common goal for the Madrean Archipelago is apparent by the members of the conference organizing committee and the diverse mix of agencies and private organizations that they represent:

- **Gerald Gottfried, Co-chair, USDA Forest Service, Rocky Mountain Research Station**
- **David Hodges, Co-chair, Sky Island Alliance**
- **Dale Turner, Program Chair, The Nature Conservancy**
- **Acasia Berry, Logistics Chair, Sky Island Alliance**
- **Brooke Gebow, Program Editor, University of Arizona, School of Natural Resources**
- **Alejandro Castellanos, Universidad de Sonora, Hermosillo**
- **Nina Chambers, Sonoran Institute**
- **Doug Duncan, U.S. Fish and Wildlife Service**
- **Peter Ffolliott, University of Arizona, School of Natural Resources**
- **Bill Halvorson, U.S. Geological Survey, Sonoran Desert Research Station**
- **Andy Hubbard, USDI National Park Service, Southern Desert Network**
- **Sue Kozacek, USDA Forest Service, Coronado National Forest**
- **Larry Laing, USDI National Park Service, Southern Arizona Office**
- **Dean Martens, USDA Agricultural Research Service, Southwest Watershed Research Center**
- **Joan Scott, Arizona Game and Fish Department**
- **Frank Toupal, USDA Natural Resources Conservation Service**
- **Tom Van Devender, Arizona-Sonora Desert Museum.**

Among this group of dedicated individuals we recognize the truly exceptional efforts of the committee chairs: Dale Turner, Acasia Berry, and Brooke Gebow (now with The Nature Conservancy) whose contributions to the success of the conference were far more than can be adequately described. We also acknowledge the assistance of Peter Ffolliott who was influential in the 1994 conference and who aided us with his active participation and insights and Tom Van Devender who accepted numerous extra duties. The activities of Nina Chambers and Andy Hubbard who organized the special ecosystem monitoring program are appreciated.

Three field trips to the deserts and mountains of the southern Arizona put the finishing touches on the conference, and we thank the leaders for organizing and leading the tours. The efforts of the session moderators, numerous student volunteers, art show coordinators, and the team that translated abstracts into Spanish are greatly appreciated. The conference would not have been successful without their efforts. The Rocky Mountain Research Station, Sonoran Institute, International Arid Lands Consortium of Tucson, the School of Natural Resources, University of Arizona, and the Sky Island Alliance provided additional support for the conference. We would like to thank Connie Lemos of the Rocky Mountain Research Station for her expert preparation of these proceedings for publication and Lillie Thomas of RMRS for her editorial assistance.

The comments in this Preface are partially developed from the opening remarks of Alison Hill, Assistant Director for Research, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO; David Hodges, Executive Director, Sky Island Alliance, Tucson; Jeanine Derby, Forest Supervisor, Coronado National Forest, Tucson; and Dale Turner, Conservation Planner, The Nature Conservancy, Tucson.

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Peter B. Stacey and Zach Perry. Coping with fragmented habitats on mountain islands: dispersal and metapopulation structure in the Mexican spotted owl.

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Caren S. Goldberg, Kimberleigh J. Field, and Michael J. Sredl. Phylogenetic analysis of Chiricahua and Ramsey Canyon leopard frog populations in Arizona.

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Sexual Differentiation in the Distribution Potential of Northern Jaguars (*Panthera onca*)

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Abstract—*We estimated the potential geographic distribution of jaguars in the southwestern United States and northwestern Mexico by modeling the jaguar ecological niche from occurrence records. We modeled separately the distributions of males and females, assuming records of females probably represented established home ranges while male records likely included dispersal movements. The predicted distribution for males was larger than that for females. Eastern Sonora appeared capable of supporting male and female jaguars with potential range expansion into southeastern Arizona. New Mexico and Chihuahua contained environmental characteristics primarily limited to the male niche and thus may be areas into which males occasionally disperse.*

Introduction

One source of the rich biodiversity found in North America's Madrean Archipelago is the meeting of temperate and sub-tropical zones (Felger and Wilson 1994), resulting in the unique overlap of some temperate and tropical species at the edges of their distributions. Among these species are large carnivores that may further contribute to the region's biodiversity through top-down effects and other ecological roles (Berger 1999; Estes et al. 1998; Terborgh et al. 1999). As is the case for large carnivores worldwide (Gittleman et al. 2001), however, predators have declined or disappeared from the Madrean Archipelago largely due to human pressures (Brown 1985; Brown and López González 2001; Phillips and Smith 1996).

The only Neotropical large carnivore with a distribution extending north into the Madrean Archipelago is the jaguar. Jaguars are distributed across parts of Mexico, Central America, and South America (Sanderson et al. 2002), but the rugged and extremely arid conditions at the northern limit of this distribution contrast sharply to lush tropical forests to the south. Currently the northernmost breeding population of jaguars is situated in Sonora, Mexico, about 220 km south of the junction of Arizona and New Mexico with the United States-Mexico border (López González and Brown 2002); how far north this population may have formerly extended is unknown. There are documented records of jaguars killed or photographed in Arizona and New Mexico during the 1900s, and these numbers declined from 51 individuals between 1900-1940 to 11 between 1946-1986 (Brown and López González 2001). No verified jaguars were documented in the United States from 1987 until 1996, and four documented observations during 1996-2003 (J. Childs, personal communication; Childs 1998; Glenn 1996) were presumably individuals that originated in Sonora.

Although it may never be possible to resolve debate about the existence of a breeding jaguar population in the United State, we sought to identify areas in the southwestern United States and northwestern Mexico that jaguars could occupy and that may be areas that jaguars formerly occupied. To estimate the potential distribution of "northern" jaguars (jaguars in the southwestern United States and northwestern Mexico) and identify possible dispersal routes, we employed Geographic Information Systems (GIS) technology and new spatial tools for modeling a species' fundamental ecological niche (Grinnell 1917) from records of occurrence (Stockwell and Peters 1999). Researchers have recently demonstrated powerful conservation biology applications for such predictive models of species' ecological niches (Peterson et al. 2002; Peterson and Robins 2002; Raxworthy et al. 2003), and such tools appear to be particularly useful when spatial and ecological data are limited, as is often the case with large elusive carnivores.

Although little is known about jaguars, knowledge and syntheses about other large carnivore species provide a strong theoretical background for making predictions about jaguars. Dispersal in carnivores is male-biased (Fuller et al. 1992; Rogers 1987; Smale et al. 1997), and male carnivores generally have much larger home ranges than females (Sandell 1989). Among solitary felids, males tend to occupy exclusive territories that may overlap with the home ranges of multiple females but generally do not overlap with other males (Sandell 1989; Sunquist and Sunquist 1989). Male felids can move long-distances in the process of dispersal (Logan et al. 1986; López González 1999), but when female dispersal does occur, distances are much shorter (Logan and Sweanor 2001). Finally, jaguars are sexually dimorphic, and such species tend to have different habitat and food requirements (Aunapuu and

Oksanen 2003). We expected that these sex differences would be important at the landscape scale and therefore considered them in our modeling exercise. We assumed that records of occurrence for jaguar males would include dispersing or non-territorial males in search of areas without male competitors, while records for females were more likely to be from animals with established home ranges in areas with adequate food and shelter resources for reproduction. We therefore predicted that males would show a broader ecological niche than females, and females would have a more restricted niche, as their distribution should be more closely tied to the distribution of resources (Emlen and Oring 1977; Sunquist and Sunquist 1989).

Materials and Methods

We delimited our study area as that encompassing a portion of the southwestern United States, namely the States of Arizona, New Mexico, and the panhandle of Texas, and the northwest Mexican States of Sonora and Chihuahua. The Madrean Archipelago is contained within this arid region, which extended from 25º26' and 36º56' N latitude, and 103º04' and 113º58' W longitude.

We assembled a database of jaguar occurrence records, including museum records, photographic records, and verified kills for the study area. We requested holdings information from North American institutions, including Arizona State University, California Academy of Science, CONABIO, Michigan State University, Museum of Comparative Zoology, Harvard University, Natural History Museum of Los Angeles County, University of Arizona, Southwestern Biology Museum-University of New Mexico, Texas Tech University, University of Kansas, and University of Texas. A complementary bibliographic search included records published in Hall (1981), Leopold (1977), and Brown and López González (2000; 2001). We obtained jaguar records for 2001-2003 in Sonora and Chihuahua through interviews with residents. All occurrence records were verified, ground-truthed, and the geographic location recorded using a Garmin 12XL GPS unit. We included only records with sufficient locality information to plot occurrence points within 25 km^2 accuracy and that included the sex of the individual.

We estimated the distribution of northern jaguars based on the Genetic Algorithm for Rule Set Production (GARP, Sachetti-Pereira 2002; Stockwell and Noble 1999; Stockwell and Peters 1999). The GARP algorithm models the fundamental ecological niche of species, utilizing environmental conditions (e.g., temperature, frost, soil) to predict the distribution of a species that would support a viable population (Anderson et al. 2002a). This algorithm associates points of known occurrence to digital environmental layers by searching for non-random association between the known points against the full extension of the study area for all the environmental characteristics. Through an iterative process of rule selection, rules with increasing predictive accuracy evolve until the algorithm has run 1,000 iterations or reached convergence. The results of these iterations are represented as maps of the predicted geographic distribution of the species in the experiment (Rice et al. 2003; Stockwell and Peters 1999).

We used GARP to model 3 jaguar distributions. One model included records for both males and females, another included only males, and the third included only females. There were 20 environmental layers representing abiotic characteristics for the climate and landscape, including temperature, wetness, vapor pressure, frost days, snow accumulation, radiation, soil type and other geologic features, elevation, aspect, slope, compound topographic index, water flow, and runoff. We derived these layers from raster and vector data from IPCC (http://www.ipcc.ch), USGS Hydro 1k (http://edcdaac.usgs.gov/gtopo3/hydro), and ESRI ArcAtlas (ESRI 1996). Layers were projected into geographic coordinates and resampled to 25 km^2 pixel size to match the resolution of the occurrence data.

The GARP program tested occurrence points for spatial independence and excluded redundant points. For each modeling exercise, we opted for 100 runs with a maximum of 1,000 iterations. We selected a convergence limit of 0.01 and restricted the analysis to an omission of 10% and a tolerance commission of 50%, and we selected the option "best subsets" (Anderson et al. 2003; Anderson et al. 2002b). We selected the 4 best models from each category (males, females, and males and females combined), choosing those with the closest precision value to one, the highest number of records present in the predicted area, and low omission errors for inclusion in analyses (Anderson et al. 2002b). We added these 4 models together as raster overlays in ArcView 3.3 (ESRI, Inc.) to generate a graduated distributional map for each category. We based area measurements and other analyses of the distributional outputs on the overlap among these models, which were essentially binary maps with each pixel or grid cell coded for either the predicted presence or absence of jaguars, with a map for males, females, and both males and females combined. For measurements of area (in km^2), we reprojected GIS data into meters in the Lambert Azimuthal Equal Area projection.

We made a composite grid by combining the binary maps of the predicted male and female distributions with the 20 environmental data grids that were used in building the GARP model, such that each grid cell (or pixel) could have one of 22 different attribute values (20 environmental values plus male presence/absence and female presence/absence). We exported the attribute data for the 22 data layers to a data spreadsheet to conduct ecological niche "visualization" (Rice et al. 2003). We z-standardized all of the environmental variables based on the mean of each, and examined differences between the data for cells that were included in the male and female distributions and cells that were not. We used multivariate discriminant analysis to explore niche specificity and examine if differences in the environmental data allowed grid cells to be classified according to whether or not they were from the predicted distributions.

Finally, we focused on females and compared the predicted female distribution to a land cover map from the USGS North America Landcover Database (http://edcdaac.usgs.gov/glcc) resampled to 25 m^2. Using the grid cell values for land cover and the female distribution, we performed a chi-square analysis to compare land cover types in the female distribution to the land cover types for the entire study area.

Results

We obtained 142 records of jaguar occurrence, 100 male and 42 female records (for a partial list of records with descriptions, see Brown and López González 2001). Records for males came from all 4 States: Arizona (n = 47), Chihuahua (n = 8), New Mexico (n = 6), and Sonora (n = 39), while records of females came only from Arizona (n = 6) and Sonora (n = 36) (figure 1a). We obtained no verifiable records with sufficient locality information from the Texas panhandle, although there are records of jaguars in other parts of Texas (Brown and López González 2001).

The total area of the predicted distribution for jaguars was 367,000 km^2, with an area of 391,000 km^2 predicted based on males only and 145,000 km^2 based only on females. Thus, as expected, male jaguars had a wider distribution than females (figure 1). That the model for both males and females combined yielded a more limited distribution than for males alone suggests that this difference was not simply a function of the sizes of the datasets. The amount of area where the male and female geographic distributions overlapped was 132,000 km^2. This amount was 91% of the predicted female distribution but was only 34% of the range predicted for males. Thus, very little area was uniquely predicted for females compared to males. The female distribution predicted with highest confidence included a 100,000 km^2 contiguous area contained mostly in Sonora's eastern half and some disjointed patches mostly in Arizona. Interestingly, although we obtained no records of females from New Mexico or Chihuahua, scattered areas predicted as parts of the female distribution in these States overlapped with the predicted male distribution (figure 1).

To assess whether values of grid cells from particular groups were readily identifiable, we conducted quadratic discriminant analysis (DA). We divided grid cells into 4 classification groups: (a) the predicted distribution (or "niche") of females, (b) areas not included in the female distribution,

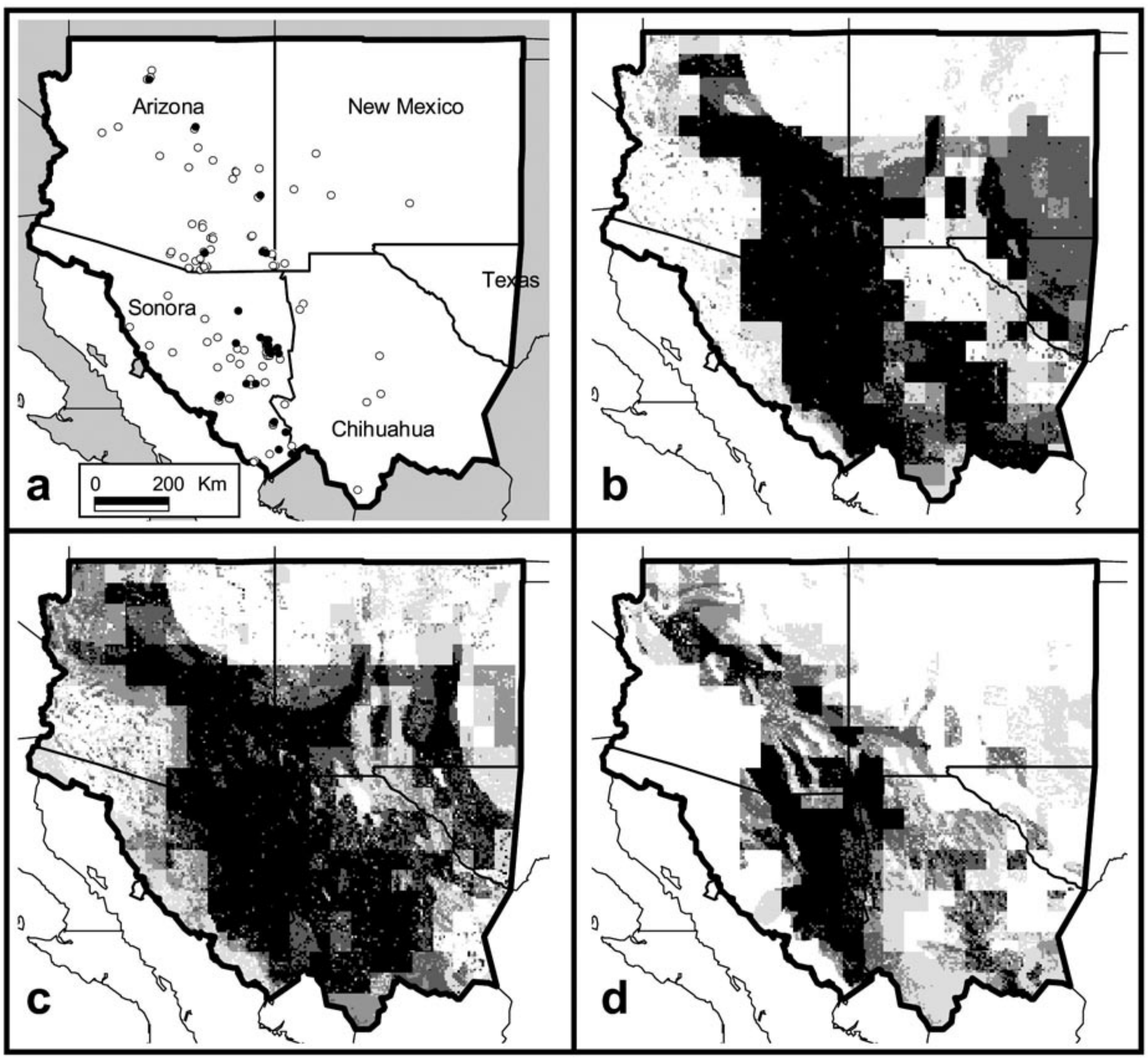

Figure 1—(a) Records of occurrence of male jaguars (open circles) and female jaguars (solid circles) in the study area which included all of Arizona, New Mexico, Sonora, Chihuahua, and the panhandle of Texas, shown in white with a bold outline. In (b), (c), and (d), the predicted distributions are shown in graduated shades representing confidence with black indicating where all 4 best subset models overlapped for distributions based on (b) all occurrence points, (c) male occurrence points only, and (d) female occurrence points only.

(c) the predicted male distribution, and (d) areas not included in the male distribution. DA to classify data for females (figure 1d) into groups a and b correctly assigned 95% of 5,227 cells from the female distribution to group a and correctly assigned 83% of the remaining 36,351 cells to group b. The overall proportion correct was 84%. Similarly, DA on data for males (figure 1c) correctly assigned 93% of 14,798 cells to group c, 78% of 26,780 cells to group d, and had an overall proportion correct of 83%. Thus, DA distinguished cells that were not predicted as part of the distributions from those that were, and it correctly assigned cells that were included in the distributions with a very high probability. In a DA to compare cells from the female distribution (group a) with cells from the male distribution (group c), the overall proportion correctly classified was lower at 68%. For group a, DA correctly classified 83% of cells while only 63% from group c were correctly classified, suggesting that the female ecological niche was narrower than the niche predicted for males.

We could not identify the variables that most contributed to group classification from the discriminant analysis. However, histograms and scatterplots revealed some of the differences for specific environmental variables, including precipitation, elevation, slope, and temperature that were normally distributed. Mean annual precipitation (± SD) averaged across all pixels for the study area was 291 ± 116 mm. For the male distribution, mean precipitation was 347 ± 116 mm; it was slightly higher for the female distribution at 379 ± 115 mm. Mean elevation of the predicted male distribution was 1,481 ± 510 m, similar to the mean of 1,414 ± 619 m for the study area as a whole. For females, mean elevation was lower at 1,216 ± 478 m, but the slopes of both the male (31 ± 31 degrees) and female distribution (31 ± 29 degrees) tended to be steeper than for the study area in general (20 ± 26 degrees). Other general differences were that the predicted jaguar distributions were on average warmer, sunnier, and had older soils than the study area as a whole. Jaguars were not predicted to occur on Sonora's coast, even though there was one male record from there. Jaguars were also not predicted in the very high elevation and cold areas of northern New Mexico and northeastern Arizona.

The primary land cover types in the study area landscape were shrubland (60%), grassland (22%), and forest (17% for all types combined) (figure 2). The remaining land cover types were 1% or less of the landscape. We found significant differences between land cover within the female distribution and the available landscape ($X^2 = 217.62$, df = 8, p = 0.05; figure 2). The predicted distribution of female jaguars was mainly across areas of shrubland, deciduous broadleaf forest, and grassland (figure 2), but deciduous broadleaf forest and mixed forest composed more of the female distribution than expected by chance when compared to the available land cover for the study area. Shrubland was a smaller proportion of the female distribution than expected, and grassland and needleleaf forest were present in proportion to their availability.

Discussion

We expected that differences between the sexes in resource use and competition would be apparent in the ecological niche distributions of jaguars and that female jaguars would have a smaller distribution. We also assumed that for a large carnivore in which males range more widely than females, female occurrence records would be a better indicator of the potential distribution of a viable population than records of males. Our GARP modeling showed that a predicted distribution based on males alone resulted in a broader geographic range and ecological niche than for females. Using the occurrence records for both males and females yielded a model that was intermediate between the males-only and females-only models and that was a blend of the more environmentally restricted females and more generalist males. We derived these distributions from records of occurrence that were mostly from hunted specimens. We do not know if a male and female jaguar in a given area

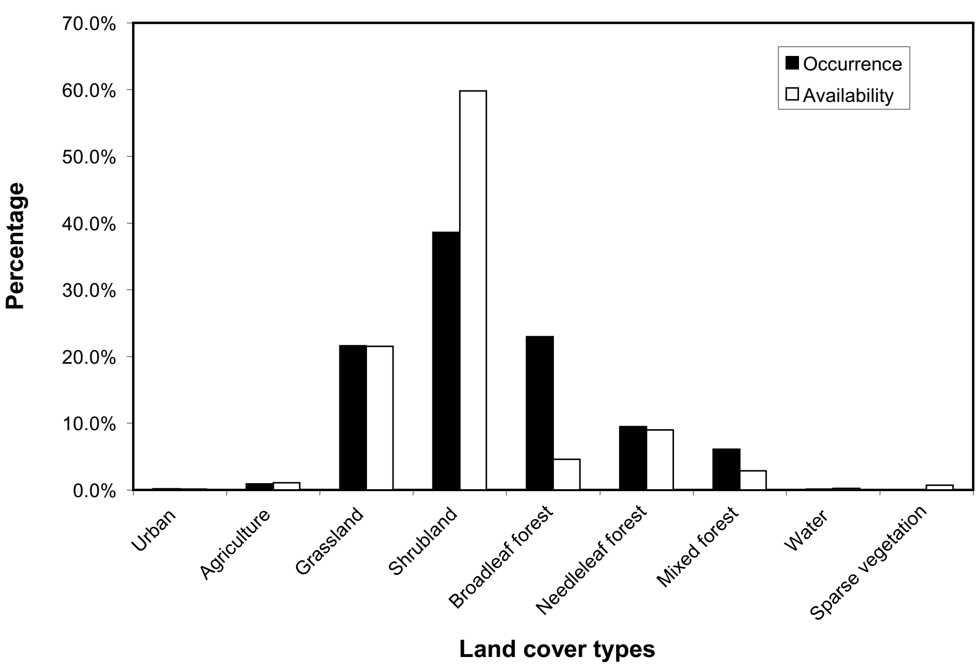

Figure 2—Comparison of female jaguar occurrence (solid bars) versus available land cover types within the study area (open bars). The broadleaf forest category was almost entirely deciduous, but we also grouped into this category the small percentage of evergreen broadleaf (<0.05%) in the landscape. Ranchlands were not included in the category of agriculture.

would have the same detection and capture probability by a hunter. However, the sex ratio of records from Sonora where jaguars are known to occur was almost 1:1, but elsewhere it was heavily skewed towards males.

Our results indicated that the availability of areas meeting females' environmental requirements may be an important factor limiting the distribution of northern jaguars. That jaguars formerly wandered as far north as the Grand Canyon (Brown and López González 2001) suggests that the leading edge of the northern jaguar range has likely retracted to the south, as reaching this location today from the center of the nearest jaguar population would require traveling 750 km. Whether the range of the jaguar is currently decreasing is unclear. However, even in the core population area in Sonora, jaguars are rare and there are conflicts between ranchers and jaguars (López González 2004). Additionally there are almost no protected areas in this area (Arriaga et al. 2000).

Although GARP has been used for a variety of taxa (Anderson et al. 2002a; Peterson et al. 2002; Peterson and Robins 2002; Raxworthy et al. 2003; Rice et al. 2003), this may be the first application to a large carnivore and the incorporation of sex differences using this tool. There are important limits to the interpretation of our results, but we hope this attempt will be just one of many by a wider community of scientists to better understand jaguar requirements and assist with prioritizing conservation efforts. The center of the existing jaguar population lies in the heart of the area that the GARP model predicted based on females, but potentially suitable areas that are currently unoccupied were also predicted within the female distribution. A future challenge for conservation biologists could be determining whether the existing jaguar population could naturally expand into these unoccupied areas and understanding the social, political, and biological requirements for this process to occur. Range expansion could help prevent genetic isolation and extinction of the northern jaguars and also increase chances for long-term survival of this species in the face of global anthropogenic changes. Furthermore, as top predators, jaguars can serve as indicators of the success of land management policies and practices that help maintain biological resources in the United States and Mexico. By maintaining connectivity across subtropical and temperate zones, conservation of jaguars would help conserve a number of other species and preserve the biological integrity of the unique Madrean region.

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