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Native vegetation structure and persistence of endangered Tehuantepec jackrabbits in a neotropical savanna in Oaxaca, México

Verónica Farías · Todd K. Fuller

Abstract Because of its crucial importance for the persistence of the endangered Tehuantepec jackrabbit (*Lepus flavigularis*), we identified structural characteristics of native vegetation (1) selected by Tehuantepec jackrabbits to establish home ranges, (2) used within home ranges, and (3) in relation to activity and inactivity periods. A neotropical savanna in the Isthmus of Tehuantepec, Oaxaca, México, offered diversity in native flora and heterogeneity in vegetation structure to the studied population of Tehuantepec jackrabbit. Adults and juveniles differed in habitat use patterns. No effect on habitat selection was detected for sex or season. Jackrabbits established home ranges on grassy habitat with discontinuous overstory of nanche (*Byrsonima crassifolia*) shrubbery and morro (*Crescentia*) trees. Adults underused dense vegetation where predators may ambush them; juveniles avoided dense vegetation and grassland without overstory. Within adults' home ranges, habitat selection favoring grassy habitats with nanche and morro was relatively stronger during the activity period (nocturnal and crepuscular hours) and during one of 2 years which had more rainfall. Scattered trees and open shrubbery likely allowed foraging jackrabbits with both visibility and escape routes used to detect and outrun predators. Moreover, during the inactivity period (diurnal hours) adults and juveniles favored nanche shrubbery that provided resting jackrabbits with shelter to hide from predators. Clearly, structure and diversity of native vegetation in the savanna needs to be preserved for conservation of Tehuantepec jackrabbits because deteriorated habitat may pose higher predation rates for a jackrabbit population in risk of extirpation.

Keywords *Lepus flavigularis* · Habitat selection · Vegetation structure · Leporid conservation · México · Tehuantepec jackrabbit

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Introduction

Vegetation structure is a crucial factor that compromises jackrabbit habitat selection, because it affects the quality, the heterogeneity, and the seasonal availability of food and cover resources, and is directly related to predation risk (Jennings et al. 2003; Marín et al. 2003; Smith et al. 2004, 2005). Studies show that *Lepus* species respond with flexibility in their utilization of available vegetation for food and shelter, but when habitat diversity is low jackrabbits may be more limited in terms of cover (Lechleitner 1958; Tapper and Barnes 1986; Longland 1991; Daniel et al. 1993; Hulbert et al. 1996a, b; Jennings et al. 2003; Smith et al. 2004). Jackrabbits favor vegetation structures that provide them with both the visibility to detect predators and the protective cover to reduce chances of being detected by predators (Lechleitner 1958; Longland 1991; Daniel et al. 1993; Marín et al. 2003; Smith et al. 2004). Furthermore, to reduce predation risk, habitat selection may also depend on whether leporids are active or inactive (Tapper and Barnes 1986; Moreno et al. 1996; Stott 2003; Smith et al. 2004).

The critically endangered Tehuantepec jackrabbit *(Lepus flavigularis)* survives along neotropical savanna and grassy dunes on the shores of a salt-water lagoon connected to the Gulf of Tehuantepec in Oaxaca (López-Forment 1989; Lorenzo et al. 2006). Only four populations of *L. flavigularis* are known to remain (López-Forment 1989; Lorenzo et al. 2006), and their small size is presumably a consequence of habitat loss and fragmentation, with undesirable consequences such as genetic isolation, overexploitation, competition with livestock, and exposure to exotic diseases and increased abundances of native predators tolerant to deteriorated habitats and human activities, i.e., coyotes *(Canis latrans)* and gray foxes *(Urocyon cinereoargenteus)*. Survival of Tehuantepec jackrabbit populations is strongly linked to preservation of their remnant habitat because jackrabbits seek shelter and concealment under native shrubs and grasses, feed mainly on native grasses and forbs (Anderson and Gaunt 1962; Flux and Angermann 1990), and show low tolerance to habitat deterioration (Lorenzo et al. 2006).

The former distribution of Tehuantepec jackrabbits is not documented in detail, but Nelson (1909) estimated the historic range along the Mexican Pacific coast on the Isthmus of Tehuantepec from Salina Cruz in Oaxaca to Tonalá in Chiapas, an area of perhaps 5,000 km^2. According to López-Forment (1989) and Lorenzo et al. (2006), the estimated occupied range of Tehuantepec jackrabbits is perhaps no more than 82 km^2. Remnant habitat occupied by *L. flavigularis* is not included within protected natural lands in México and exists at present on the periphery of the historic range (Nelson 1909; Anderson and Gaunt 1962); most likely, where anthropogenic disturbances have been low during this and past decades as with other endangered mammals (Lomolino and Channell 1995). Priorities for conservation of the Tehuantepec jackrabbit include assessment of the vegetation structure characteristics that the species selects for home range establishment, and vegetation arrangements favored within home ranges.

Our goals were to investigate habitat use patterns of Tehuantepec jackrabbits and to identify the structural characteristics of vegetation selected by radiomarked juvenile and adult individuals in a neotropical savanna in Oaxaca. Radiotracking allowed definition of the range used by each individual and investigation of habitat selection at different spatio-temporal scales via compositional analyses (Aebischer et al. 1993). We predicted that habitat selection for home range establishment and within home ranges of Tehuantepec jackrabbits would be different from random; our expectations were that jackrabbits would select the native vegetation structure of grassy habitats with a sparse overstory of shrubs and trees, and would avoid dense vegetation. We also expected that habitat patterns of Tehuantepec

jackrabbits would show an effect due to the marked seasonality (dry compared to wet season) in the study area.

Methods

Study area

We studied the Tehuantepec jackrabbit population on the northeastern rim of Superior and Inferior Lagoon, Oaxaca, Mexico. The study area encompassed 10 km² of a neotropical savanna locally known as Llano Contreras (16°22′ N, 94°37′ W). Grama (*Bouteloua* spp.) and paspalum (*Paspalum* spp.) are common grasses, morro (*Crescentia*) trees and nanche (*Byrsonima crassifolia*) shrubbery are sparse and dominant, and vegetation along stream-beds is dense and composed of thorny shrubs and trees (Pérez-García et al. 2001). Local people practice subsistence fishing, hunt wildlife for food, and raise free-ranging cattle, horses, sheep, and goats. Climate is tropical with mean annual temperature of 25°C, and mean annual rainfall of 800 mm (García 1964). The rainy season is from May to October with a summer drought in August, whereas the dry season extends from November to April and is severe during late winter and early spring (Zizumbo and Colunga 1982). Monthly reports on precipitation and temperature parameters were obtained for the weather station at Juchitán de Zaragoza, Oaxaca, from the Mexican National Meteorological Service. Total rainfall from May 2001–April 2002 was 33.90 mm compared to 40.83 mm for May 2002–April 2003.

Radiotracking and home range estimation

Handling and radiotracking of jackrabbits, and home range estimation, are described fully elsewhere (Farías et al. 2006). Tehuantepec jackrabbits were captured by hand in nets, aged, sexed, and fitted with 20-, 30-, or 40-g VHF radiocollar transmitters (M2900 Advanced Telemetry Systems Inc., Isanti, Minnesota) with motion and mortality sensors and whip antennae. Research complied with current Mexican laws and was conducted under authorization of the Secretaría de Medio Ambiente y Recursos Naturales, México, and under a protocol approved by the Institutional Animal Care and Use Committee at The University of Massachusetts, Amherst, USA. Capture and handling of jackrabbits followed guidelines approved by the American Society of Mammalogists (ASM 1998). During telemetry sessions we avoided interfering with the individual's behavior by following radiosignals on horseback. Horses grazed the study area and jackrabbits were habituated to their presence. During daytime, we homed-in on individuals hidden in vegetation (White and Garrott 1990). During nighttime, we observed jackrabbits with a handheld spotlight (Truper, México) which allowed illumination distances up to 50–70 m; active jackrabbits continued feeding or interacting socially. Observers recorded the time (hour and minutes) when the radiotracked individual was first sighted, then waited a few minutes until the jackrabbit walked away to log the Universal Transverse Mercator (UTM) coordinates for the location of first sighting using a global positioning system receiver (eTrex Venture, Garmin, Kansas; accuracy 3–15 m).

Home range was defined as 95%, and core area as 50%, fixed-kernel estimates with least-squares cross-validation (Worton 1989; Seaman and Powell 1996; Powell 2000), which were calculated using ArcView GIS [version 3.2, Environmental Systems Research Institute Inc. (ESRI), Redland, California] with the Spatial Analyst (ESRI) and the Animal

Movement Analysis (Hooge and Eichenlaub 1997) extensions. Estimates are reported as means with *SE*s throughout this paper.

Two different home range estimates were considered: (1) overall estimates were calculated using all collected locations between 1 May 2001 and 30 April 2003 for each individual, and (2) seasonal estimates were calculated using locations collected during four seasons defined as: (a) wet 2001 (May 2001–October 2001); (b) dry 2002 (November 2001–April 2002); (c) wet 2002 (May 2002–October 2002); and (d) dry 2003 (November 2002–April 2003). We obtained overall estimates for 17 adults and 18 juveniles, using 22 to 143 locations for adults and 10 to 51 locations for juveniles. Fifty seasonal estimates were calculated for 32 jackrabbits (Farías et al. 2006).

Habitat composition

According to the structure of native vegetation, we distinguished five habitats: (1) Nanchal was sparse shrubbery dominated by *Byrsonima crassifolia* with a grass-forb understory; (2) Morro was composed of scattered shrubs and trees dominated by *Crescentia* and had a grass-forb understory—compared to Nanchal, Morro was a more open habitat found in lowlands that could get flooded after several days of heavy precipitation; (3) Grassland was composed of grasses and forbs and had no overstory; (4) Riparian was dense vegetation occurring along streambeds and composed of thorny shrubs, trees, and lianas; and (5) Thicket was found as patches of a nearly continuous overstory of thorny shrubs and trees. Our study area ended to the south on a sandy beach at the shores of the salt-water lagoon (Fig. 1). Jackrabbits did not use the sandy beach; therefore, it was excluded in the habitat use analysis.

We created a digitized habitat map of the study area to determine proportions of the five habitats using ArcView GIS with the Spatial Analyst extension and the Geoprocessing Wizard (ESRI). We delineated habitat boundaries by walking along edges and logging the UTM coordinates with a global positioning system receiver (eTrex Venture, Garmin,
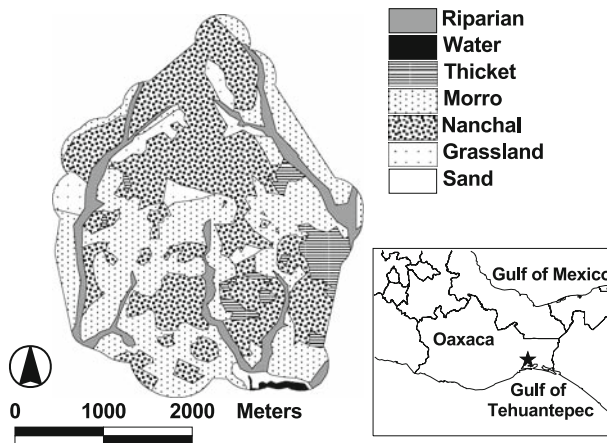

Fig. 1 We determined Nanchal, Morro, Grassland, Riparian, and Thicket as the available habitats for Tehuantepec jackrabbits (*Lepus flavigualris*) in a neotropical savanna of the Isthmus of Tehuantepec, Oaxaca, México, between May 2001 and April 2003. The study area ended to the south on a sandy beach at the shores of a saltwater lagoon. The star represents the location of the study area in the Isthmus of Tehuantepec, Oaxaca, México

Kansas; accuracy 3–15 m), and then converted the point data into habitat polygons. Habitat proportions for individual's home ranges, core areas, and locations were determined by overlapping the kernel estimates and point data onto the habitat map.

Habitat use analysis

We conducted compositional analysis (Aebischer et al. 1993) using the beta version of Resource Selection Analysis software for Windows 95 NT (RSW, Leban 1999) and multivariate analysis of variance (MANOVA) with SPSS 8.0 multivariate general linear model (GLM). We calculated the log-ratio differences between the used and available habitat compositions with RSW. MANOVA was used to test for effects of sex, age, season, and year. Individuals were treated as experimental units in the analysis of overall estimates; but, because 10 adults and one juvenile had 2–4 estimates that corresponded to different seasons, home ranges were the experimental units in the analysis of seasonal estimates (Farías 2004).

Wilk's lambda statistic was tested simultaneously over all habitats for random use, and was compared with the F distribution and P value. If significant differences were detected between habitat use and availability, habitat selection was indicated (Aebischer et al. 1993) and contrasts comparing individual habitats were assessed with Student's t tests (Erickson et al. 2001). Habitats were ranked in order of use by calculating the log-ratio differences for all possible pairs and were displayed in a matrix with the aid of RSW, and for a given pair the mean log-ratio difference was based only on the home ranges containing both habitats (Aebischer and Robertson 1992). The proportion of a missing habitat within a home range was set to 0.001, one order of magnitude less than the detectable minimum in our data (Aebischer et al. 1993).

We investigated habitat use of Tehuantepec jackrabbits by comparing utilized with available habitats according to three spatio-temporal scales (Aebischer et al. 1993; Garshelis 2000). The first scale determined if jackrabbits selected or avoided certain habitats to establish a home range by comparing habitat composition in (1) overall and (2) seasonal estimates with available habitat in the study area. Habitat use of each individual was the habitat composition of its home range (Johnson 1980). To assess available habitat (Erickson et al. 2001) in our study area, we used ArcView GIS with the Spatial Analyst, the Geoprocessing Wizard, the Animal Movement, and the first Tools (ESRI) extensions. We created a polygon theme that encompassed the 50 seasonal home ranges of study animals, and merged it with a point theme that included jackrabbit locations collected from May 2001 through April 2003. The merged themes were converted into a point theme from which the 100% minimum convex polygon with a 200-m buffer was estimated, and habitat proportions were calculated. The sum of proportions of Nanchal, Morro, Riparian, Grassland, and Thicket defined the available habitat in our study area (Fig. 1).

The second spatio-temporal scale determined if habitat use within home ranges of jackrabbits was nonrandom. For each individual, available habitat was determined by habitat proportions within home range estimates, and habitat use by the distribution of locations (Aebischer and Robertson 1992). We excluded Thicket because jackrabbits avoided it when establishing home ranges, and was absent in the locations distributions of most adults and juveniles. For analysis of juvenile's habitat use, we also excluded Riparian and Grassland; Grassland was avoided when establishing home ranges, was absent in 66% of locations distributions and 50% of home ranges, and Riparian was avoided and absent in 88% and 55%, respectively.

The third scale distinguished variation in habitat selection within home ranges according to activity patterns of jackrabbits. For each individual, available habitat was determined by habitat composition within home ranges. Habitat use was determined by habitat proportions associated with locations collected during each period of activity or inactivity (Revilla

et al. [2000](#)). Nanchal, Morro, and Grassland were analyzed for adults, and Nanchal and Morro were analyzed for juveniles. The assessment of the length of activity and inactivity periods of radiomarked jackrabbits is described fully elsewhere (Farías et al. [2006](#)).

Results

Habitat composition

Nanchal and Morro were the most common habitats in the study area and in the home ranges of Tehuantepec jackrabbits (Figs. [1](#), [2](#)). Nanchal was present in all home range and core area estimates, and Morro was present in all home ranges; both habitats showed the highest mean percentages in the locations distribution of individuals (Fig. [2](#)). Riparian was present in 82% of the overall home ranges of adults, but was absent in core areas and locations distribution of almost all individuals, and in 55% of juvenile home ranges. In contrast, Grassland represented just 5.5% of the available habitat and was present in 100% of the overall home ranges of adults, but was absent in 50% of juvenile home ranges. Thicket was the least common habitat, and was absent in 42% and 61% of the overall home ranges of adults and juveniles, respectively.

Home range establishment

Compositional analysis of overall home range estimates of Tehuantepec jackrabbits indicated that differences in log-ratios of use and availability (GLM, Wilk's $\lambda = 0.287$, $F_{[4,\ 28]} = 17.390$, $P = 0.000$) differed between ages (Wilk's $\lambda = 0.661$, $F_{[4,\ 28]} = 3.596$, $P = 0.017$) but not between sexes ($P = 0.433$); therefore we treated data for adults and juveniles separately.

Adult jackrabbits showed nonrandom use of available habitats for establishment of overall (Wilk's $\lambda = 0.334$, $F_{[4,\ 13]} = 6.216$, $P = 0.005$) and seasonal home ranges (GLM,
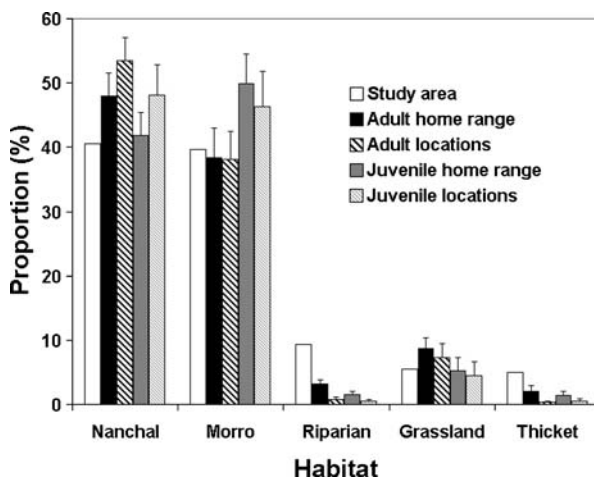

Fig. 2 Proportions of available habitats in the study area (*white bars*) compared to proportions of habitats within home ranges and locations of adult (*black bars*) and juvenile (*gray bars*) Tehuantepec jackrabbits (*Lepus flavigularis*). Values are percentage means with standard errors from 17 adults and 18 juveniles

Wilk's $\lambda = 0.444$, $F_{[4, 24]} = 7.527$, $P = 0.000$) with no effects of sex ($P = 0.327$), season ($P = 0.893$), or year ($P = 0.751$). Habitat rankings were consistent for overall and seasonal estimates in which Nanchal was followed by Morro and Grassland, but relative to one another their utilization was similar except for Nanchal being significantly more used than Morro in seasonal estimates (Table 1). Riparian was followed by Thicket, but relative to one another the difference in their utilization was not significant, and both were signifi-cantly underused relative to the top ranking habitats.

Juvenile jackrabbits showed habitat selection for the establishment of overall (GLM, Wilk's $\lambda = 0.214$, $F_{[4, 14]} = 12.832$, $P = 0.000$) and seasonal home ranges (GLM, Wilk's $\lambda = 0.169$, $F_{[4, 13]} = 16.011$, $P = 0.000$) with no effects of sex ($P = 0.827$) or season ($P = 0.222$) detected. Habitat rankings and differences in their utilization were the same for overall and seasonal estimates, because most (17 of 18) juveniles were radiotracked only for one season. Morro was followed by Nanchal but their relative utilization was similar,

Table 1 Simplified matrices of ranked habitat selection of 17 adult Tehuantepec jackrabbits (*Lepus flavigu-laris*) in Oaxaca, México, from May 2001 to April 2003, according to compositional analyses of (a) individual home range compared to available habitat in study area, and (b) distribution of individual's locations com-pared to available habitat in home range

Estimate[a]		Nanchal	Morro	Riparian	Grassland	Thicket	Rank[b]
(a) Home range establishment							
Overall	Nanchal		1	3	1	3	5
Seasonal			3	3	1	3	5
Overall	Morro	−1		3	−1	3	3
Seasonal		−3		3	1	3	4
Overall and Seasonal	Riparian	−3	−3		−3	2	2
Overall	Grassland	−1	1	3		3	4
Seasonal		−1	−1	3		3	3
Overall and Seasonal	Thicket	−3	−3	−2	−3		1

Estimate[a]		Nanchal	Morro	Riparian	Grassland		Rank[d]
(b) Within home range[c]							
Overall	Nanchal		−1	3	3		3
Seasonal Year 1			2	3	3		4
Seasonal Year 2			−1	3	3		3
Overall	Morro	1		3	3		4
Seasonal Year 1		−2		2	1		3
Seasonal Year 2		1		3	3		4
Overall	Riparian	−3	−3		−1		1
Seasonal Year 1		−3	−2		−1		1
Seasonal Year 2		−3	−3		−3		1
Overall	Grassland	−3	−3	1			2
Seasonal Year 1		−3	−1	1			2
Seasonal Year 2		−3	−3	3			2

The sign represents direction, number 1 indicates no significant difference, number 2 indicates a Student's t statistic at $P < 0.10$, and number 3 represents a significant Student's t statistic at $P < 0.05$

[a] Overall is the 95% fixed kernel home range estimated with all locations during the 2 years of radiotracking for each jackrabbit, and seasonal is the 95% fixed kernel home range estimated with seasonal locations for each jackrabbit. Ten jackrabbits had 2–4 seasonal estimates

[b] 1, lowest; 5, highest

[c] Thicket was excluded from within home range analyses because jackrabbits avoided Thicket for home range establishment

[d] 1, lowest; 4, highest

Table 2 Simplified matrices of ranked habitat selection of 18 juvenile Tehuantepec jackrabbits (*Lepus flavigularis*) in Oaxaca, México, from May 2001 to April 2003, according to compositional analyses of individual home range estimates (overall and seasonal) compared to available habitat in study area

Estimate[a]		Nanchal	Morro	Riparian	Grassland	Thicket	Rank[b]
Home range establishment							
Overall and Seasonal	Nanchal		−1	3	3	3	4
Overall and Seasonal	Morro	1		3	3	3	5
Overall	Riparian	−3	−3		−1	−1	1
Seasonal		−3	−3		−1	1	2
Overall and Seasonal	Grassland	−3	−3	1		1	3
Overall	Thicket	−3	−3	1	−1		2
Seasonal		−3	−3	−1	−1		1

The sign represents direction, number 1 indicates no significant difference, and number 3 represents a significant Student's *t* statistic at $P < 0.05$

[a] Overall is the 95% fixed kernel home range estimated with all locations during the 2 years of radiotracking for each jackrabbit, and seasonal is the 95% fixed kernel home range estimated with seasonal locations for each jackrabbit. One juvenile jackrabbit had two seasonal estimates

[b] 1, lowest; 5, highest

and both were more used relative to Grassland, Riparian, and Thicket, which had similar relative use (Table 2).

Habitat selection within home ranges

Adult jackrabbits showed habitat selection within overall home ranges (GLM, Wilk's $\lambda = 0.421$, $F_{[3, 14]} = 6.416$, $P = 0.006$). Nanchal was followed by Morro but did not differ in relative utilization, and were significantly more used than Grassland and Riparian which were similar in relative use (Table 1).

Within seasonal home ranges of adults, habitat selection was indicated (GLM, Wilk's $\lambda = 0.278$, $F_{[3, 21]} = 18.165$, $P = 0.000$) with a year effect ($P = 0.011$) but no sex ($P = 0.252$) or season ($P = 0.316$) effects. Adult Tehuantepec jackrabbits were relatively more selective in habitat use during the second year of study, and habitat rankings were clearly less marked during May 2001–April 2002 than for May 2002–April 2003. During the first year (GLM, Wilk's $\lambda = 0.084$, $F_{[3/7]} = 25.551$, $P = 0.000$), Nanchal was followed by Morro but their relative utilization was similar, Grassland was underused relative to Nanchal but not relative to Morro and Riparian, and Riparian was underused relative to Nanchal but not relative to Morro (Table 1). During the second year (GLM, Wilk's $\lambda = 0.430$, $F_{[3/18]} = 7.965$, $P = 0.001$), Morro was followed by Nanchal without differing in their relative utilization. But in contrast with the first year, Nanchal and Morro were used significantly more than Grassland, and Grassland was used significantly more than Riparian.

Although habitat proportions of telemetry locations were different from available habitats in home ranges (Fig. 2), juvenile jackrabbits showed no selection for Nanchal or Morro within overall (Wilk's $\lambda = 0.897$, $\chi^2_{[1, 17]} = 1.966$, $P = 0.160$) and seasonal (Wilk's $\lambda = 0.902$, $\chi^2_{[1, 18]} = 1.952$, $P = 0.162$) home ranges.

Habitat selection during the activity and inactivity periods

During the activity period of adult jackrabbits, habitat composition of locations differed from availability within overall (GLM, Wilk's $\lambda = 0.604$, $F_{[2, 15]} = 4.927$, $P = 0.023$) and seasonal home ranges (GLM, Wilk's $\lambda = 0.582$, $F_{[2, 22]} = 7.913$, $P = 0.003$) with a year effect

Table 3 Simplified matrices of ranked habitat selection of (a) 17 adult Tehuantepec jackrabbits and (b) 18 juvenile Tehuantepec jackrabbits (*Lepus flavigularis*) in Oaxaca, Mexico, from May 2001 to April 2003, according to compositional analyses of distribution of individual's locations in relation to activity patterns compared to available habitat in home range

Estimate[a]		Nanchal	Morro	Grassland	Rank[b]
(a) Adult jackrabbits					
Activity period					
Overall	Nanchal		−2	3	3
Seasonal Year 1			1	3	3
Seasonal Year 2			−3	3	3
Overall	Morro	2		3	2
Seasonal Year 1		−1		1	2
Seasonal Year 2		3		3	2
Overall	Grassland	−3	−3		1
Seasonal Year 1		−3	−1		1
Seasonal Year 2		−3	−3		1
Inactivity period					
Overall	Nanchal		1	3	3
Seasonal			3	3	3
Overall	Morro	−1		3	2
Seasonal		−3		3	2
Overall and Seasonal	Grassland	−3	−3		1

Estimate[a]		Nanchal	Morro	Rank[c]
(b) Juvenile jackrabbits				
Inactivity period				
Overall and Seasonal	Nanchal		3	2
Overall and Seasonal	Morro	−3		1

The sign represents direction, number 1 no significant difference, number 2 indicates a Student's *t* statistic al *P* < 0.10, and number 3 represents a significant Student's *t* statistic at *P* < 0.05

[a] Overall is the 95% fixed kernel home range estimated with all locations during the 2 years of radiotracking for each jackrabbit, and seasonal is the 95% fixed kernel home range estimated with seasonal locations for each jackrabbit. Ten adults and 1 juvenile had 2–4 seasonal estimates

[b] 1, lowest; 3, highest

[c] 1, lower; 2, higher

($P = 0.011$), but no sex ($P = 0.260$) or season ($P = 0.285$) effects detected. For overall estimates, Nanchal was followed by Morro with similar relative utilization, and Grassland was significantly underused relative to Nanchal and Morro (Table 3). For seasonal estimates, habitat rankings were again less marked during the first compared to the second year of study, indicating relative stronger habitat selection during the second year. During the first year (GLM, Wilk's $\lambda = 0.432$, $F_{[2/8]} = 5.281$, $P = 0.035$), Nanchal was followed by Morro without difference in their relative use, and Grassland was underused relative to Nanchal but not to Morro (Table 3). In contrast, during the second year (GLM, Wilk's $\lambda = 0.750$, $F_{[2/19]} = 3.165$, $P = 0.065$), adults used Nanchal significantly more than Morro, and used Morro significantly more than Grassland. Juvenile jackrabbits showed no selection for Nanchal nor Morro within overall (Wilk's $\lambda = 0.997$, $\chi^2_{[1, 17]} = 0.046$, $P = 0.830$) and seasonal (Wilk's $\lambda = 0.998$, $\chi^2_{[1, 18]} = 0.039$, $P = 0.842$) home ranges during the activity period.

During the inactivity period of adult jackrabbits, habitat composition of locations differed from availability within overall (GLM, Wilk's $\lambda = 0.333$, $F_{[2, 15]} = 14.620$, $P = 0.000$) and seasonal home ranges (GLM, Wilk's $\lambda = 0.273$, $F_{[2, 22]} = 29.243$, $P = 0.000$). In contrast with
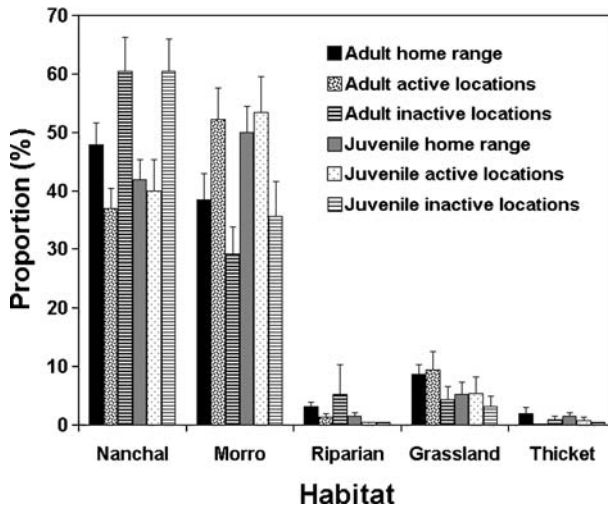
Fig. 3 Habitats proportions within home ranges of adult (*dark bars*) and juvenile (*light bars*) Tehuantepec jackrabbits (*Lepus flavigularis*) compared to habitats proportions associated to telemetry locations collected during periods of activity and inactivity. Values are percentage means with standard errors from 17 adults and 18 juveniles

the activity period, no effects of year ($P = 0.472$) were detected. No sex ($P = 0.186$) or season ($P = 0.779$) effects were detected either. Nanchal and Morro were the top ranking habitats and adults used them significantly more than Grassland within overall home ranges (Table 3). Habitat rankings were more marked in seasonal home ranges; adults used Nanchal significantly more than Morro and Grassland, and used Morro significantly more than Grassland. Also, juvenile jackrabbits showed significant habitat selection for Nanchal over Morro ($P < 0.029$) within overall (Wilk's $\lambda = 0.744$, $\chi^2_{[1, 17]} = 5.327$, $P < 0.050$) and seasonal (Wilk's $\lambda = 0.759$, $\chi^2_{[1, 18]} = 5.234$, $P < 0.05$) home ranges during the inactivity period (Table 3), and habitat proportions of telemetry locations were different from available habitats in home ranges (Fig. 3).

Discussion

Jackrabbit habitat selection

Our results supported expectations that Tehuantepec jackrabbits would select the native vegetation arrangement of grasslands with sparse overstory of shrubs and trees, and would avoid dense vegetation. A diverse habitat mosaic was available for Tehuantepec jackrabbits provided by the combination of four habitat types with different vegetation structure: Nanchal, Morro, Grassland, and Riparian. Yet, the most common habitats at the study area and in jackrabbit's home ranges, Nanchal and Morro, were clearly favored by individuals at the three spatio-temporal scales evaluated; and most likely, Nanchal and Morro provided Tehuantepec jackrabbits with resources required year round by *Lepus* species: suitable areas to feed, rest, hide, breed, take care of leverets, detect predators, and evade attacks (Lechleitner 1958; Smith et al. 2004). The floral diversity found in Nanchal and Morro are mostly grasses and forbs while the overstory is dominated by a few woody species; nevertheless, high heterogeneity in terms of vegetation structure results from shrubs and trees

combined with native annual grasses and forbs that according to their growing stages have different heights (Pérez-García et al. 2001).

In contrast, continuous dense vegetation was lacking grasses and forbs and likely posed higher predation risk and negligible food resources for Tehuantepec jackrabbits. Both adult and juvenile jackrabbits had a tendency to avoid Thicket and Riparian, probably because these habitat types disguise ambushing predators such as gray foxes. Also, dense vegetation may obstruct fleeing as escape strategy in leporids (Lechleitner 1958; Trapp and Hallberg 1975; Daniel et al. 1993; Moreno et al. 1996). On the other hand, it is most likely that juvenile Tehuantepec jackrabbits avoided grassy habitat lacking the protection of shrubs and trees (Grassland) because they rely on concealment as strategy to escape predation. Hiding may be a strategy commonly used by young herbivores to avoid predation when too young to outrun predators. During a study of the effects of habitat on the vulnerability to predation, Aanes and Andersen (1996) found that the type of habitat a roe deer (*Capreolus capreolus*) fawn used affected the probability of being killed by a red fox (*Vulpes vulpes*); predated fawns used open grassland significantly more than surviving fawns, which used woodland to a greater extent. Similarly, owls (*Bubo virginianus*) killed young snowshoe hares (*Lepus americanus*) more often in open than in closed forest, presumably because closed forest provided protective cover (Rohner and Krebs 1996). Lechleitner (1958) has reported concealment as a behavior to prevent predation in young black-tailed jackrabbits (*Lepus californicus*), a species closely related to *L. flavigularis*. Moreover, we observed that leverets of Tehuantepec jackrabbit had difficulty running with speed on flooded savanna.

Nonetheless, Tehuantepec jackrabbits made occasional use of dense vegetation edges when next to open vegetation. Adult and juvenile jackrabbits were observed hidden on Riparian or Thicket edges adjacent to Nanchal, Morro, or Grassland. Individuals positioned the back of their body toward dense vegetation while the head was facing open vegetation; and when flushed, jackrabbits ran in direction of open vegetation. Likewise, Stott (2003) found European hares squatting at the edge of thickets and facing open areas, apparently to get a good view of any approaching predator.

Jackrabbit habitat selection within home ranges

Tehuantepec jackrabbits meet food and cover requirements within their home ranges as a result of habitat richness in terms of the plant diversity and structural heterogeneity, and do not need to feed in a different area from where they shelter. The high richness of grasses and forbs in neotropical savanna (Pérez-García et al. 2001) suggests that such variety fulfills the diet requirements of Tehuantepec jackrabbits. The heterogeneity of vegetation arrangement offers suitable sheltering and hiding places. Thus, Tehuantepec jackrabbits do not need to travel between resting and foraging areas. Farías et al. (2006) found that home ranges of the studied Tehuantepec jackrabbits were comparable in size and overlapped in location between periods of activity and inactivity. Similarly, studies on European hares (*Lepus europaeus*) show that vegetative heterogeneity allows for both food and shelter to be found in the same range (Kunst et al. 2001; Smith et al. 2005).

Contrary to our expectations, no effects of sex or seasonality on habitat selection were detected. Moreover, Farías et al. (2006) found no effects of sex or seasonality on home range or core area sizes of Tehuantepec jackrabbits. Interestingly, we detected a year effect on habitat selection. Our results suggest that adult Tehuantepec jackrabbits were relatively more selective in habitat use during the second year of study compared to the first year, probably because habitat quality in terms of food availability was improved due to higher

rainfall. Precipitation was more abundant during the second year of study relative to the first year, according to the records from the Mexican National Meteorological Service. The circumstance of habitat selection within home ranges of adults being relatively stronger during the year of higher rainfall corresponded with shrinking home range sizes of adults (Farías et al. 2006). Our results are in accordance with the fact that home ranges of *Lepus* tend to be relatively smaller where resources are relatively more abundant (Boutin 1984; Hewson and Hinge 1990; Wolfe and Hayden 1996).

Jackrabbit habitat selection during activity and inactivity periods

Like many leporids (Cowan and Bell 1986; Flux and Angermann 1990; Moreno et al. 1996; Rohner and Krebs 1996), Tehuantepec jackrabbits were most active during crepuscular and nocturnal hours, and rested during diurnal hours, most probably to minimize daytime predation. Specifically during the activity period, habitat selection favoring Nanchal and then Morro within seasonal home ranges of adults was stronger during the year of study with higher rainfall. Foraging in Nanchal and Morro may be a behavior to diminish or avoid predation risk during the activity period. Tehuantepec jackrabbits select the native vegetative structure of these habitat types possibly to obtain better visibility for detecting predators from a distance, as occurs with other *Lepus* species (Lechleitner 1958; Tapper and Barnes 1986; Daniel et al. 1993). Similarly, Marín et al. (2003) assumed that predation risk was lower in grasslands with scattered shrubs than in dense shrublands for foraging black-tailed jackrabbits in the Chihuahuan desert.

Tehuantepec jackrabbits spent diurnal hours sitting in their forms, and most diurnal activity detected from radiosignals probably resulted from grooming, reingestion and stretching behaviors of jackrabbits without leaving the forms, as observed in other *Lepus* species (Flux 1981). We propose that the shrubby protection of Nanchal was selected by adult and juvenile Tehuantepec jackrabbits during diurnal hours, possibly because it allows resting individuals to be less noticeable to predators and, if detected, to flush and evade pursuing predators between shrubs over short distances, as reported for other *Lepus* species (Lechleitner 1958; Sievert and Keith 1985). Similarly, Tapper and Barnes (1986) found that in farming areas, woodlands and hedges were used most frequently during the inactivity period of *L. europaeus*. Also, Stott (2003) found that most radiolocations of *L. europaeus* during inactivity periods fell on scrub in a wheat and sheep farm in a Mediterranean climatic zone of Australia.

Conservation implications

The native structure and diversity of a continuous grass and forb understory with a discontinuous overstory of shrubs and trees in neotropical savannas needs to be preserved for conservation of Tehuantepec jackrabbit populations. Deteriorated savanna due to induced fires may pose higher predation risk for jackrabbits, particularly for young animals, because native predators such as gray foxes and coyotes may be favored in habitats altered by human activities (Fritzell and Haroldson 1982; Schneider 2001). Also, latest surveys indicated that Tehuantepec jackrabbits have low densities in overgrazed grasslands (Lorenzo et al. 2006). In this study, juvenile Tehuantepec jackrabbits avoided grassy habitat devoid of shrubs and trees, and adults underused it in relation to grassy habitat with sparse woody cover. Similarly, Smith et al. (2004) found in a pastural landscape in Britain that *L. europaeus* avoided short homogeneous vegetation in all seasons, and selected vegetation that provides more cover from predation and weather during the breeding period.

In addition, leporid species may exclude each other when habitat alteration favors more tolerant species that are better adapted to changed conditions (Flux and Angermann 1990). Tehuantepec jackrabbits and cottontail rabbits (*Sylvilagus floridanus*) are sympatric and thus potential competitors; rabbits, but not jackrabbits, are found in deteriorated savanna, while jackrabbits are more abundant than rabbits in preserved savanna (Lorenzo et al. 2006). Correspondingly, in arid regions of North America, black-tailed jackrabbits and white-sided jackrabbits (*Lepus callotis*) may coexist in open grassy plains with mesquite, cacti, and shrubs, but in agricultural lands and spoiled grasslands black-tailed jackrabbits exclude white-sided jackrabbits (Dunn et al. 1982; Bednarz and Cook 1984; Best and Henry 1993; Desmond 2003). Also, declines in number and size of populations of native mountain hares (*Lepus timidus*) coincided with expansion of brown hare (*L. europaeus*) distribution in southern Sweden; with the initiation of relative mild winters in northern Europe, brown hares were able to use clear-cuts and roads in forested areas made available by the lack of deep and lasting snow cover (Thulin 2003; Jansson and Pehrson 2007).

The number of native herbaceous species in savannas from the Isthmus of Tehuantepec is high yet poorly studied, and introduction of exotic grasses and anthropogenic burning are constantly threatening vegetation structure and diversity (Pérez-García et al. 2001). Accelerated fire regimes can have negative impact on the long-term persistence of woody overstory in savanna by impeding seedling establishment and recruitment of young plants, and reducing adult density (McPherson 1997; Gardner 2006). Human disturbance in savannas of the Isthmus of Tehuantepec was relatively low in past decades although native vegetation was continuously transformed into agricultural lands and livestock enclosures (Flux and Angermann 1990; Cervantes 1993). Urbanization and economic development trends in the region are increasing and certainly threatening future survival of Tehuantepec jackrabbits, as well as indigenous livelihoods (García and Garza 2001). During the 2 years of research, our study area suffered an increase in the number of cow and horse corrals that gradually covered the study area and beyond, and the area covered by anthropogenic burning to induce growth of green forage for cattle was greatly extended. When burned, grassy habitat without overstory turned into bare habitat with negligible cover and almost no herbaceous food for jackrabbits. We made direct observations of adult Tehuantepec jackrabbits digging out roots of grasses and forbs to eat them in recently burned savanna. Several days after the burn, green biomass may be available for food, but not for cover. As expected, induced fires in jackrabbit habitat are promoting the expansion of deteriorated grassland by inhibiting the growth and establishment of native bushes and trees.

Despite their uniqueness in plant diversity, those areas with native vegetation inhabited by Tehuantepec jackrabbits are not included within the protected natural lands in Mexico (Pérez-García et al. 2001). Without legal protection, remnant jackrabbit habitat is severely jeopardized by increasing development in the Isthmus and Gulf of Tehuantepec during the coming years (García and Garza 2001). Remnant savannas ought to be devoted to conservation, not only for the endangered Tehuantepec jackrabbit, but for their rich flora and fauna diversity, as well.

Notwithstanding, indigenous peasants recognize the savanna as source of resources such as meat from wild mammals and reptiles, seasonal wild fruits, dry wood for fuel, and plant materials for building houses and fence posts. Educational campaigns to preserve the native vegetation structure in remnant jackrabbit habitat are urgently needed and in all probability would have a positive impact for the conservation of Tehuantepec jackrabbits, for land owners and peasants are interested in the preservation of the rich flora and fauna diversity in their homeland. Particularly, wild fruits from *Byrsonima crassifolia* are so appreciated

that local people preserve Nanchal and educate their children to continue with this practice which undoubtedly is in harmony with conservation of Tehuantepec jackrabbits.

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