

HOME RANGE AND SOCIAL BEHAVIOR OF THE ENDANGERED TEHUANTEPEC JACKRABBIT (*LEPUS FLAVIGULARIS*) IN OAXACA, MEXICO

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We studied the home-range and core-area size and overlap of Tehuantepec jackrabbits (*Lepus flavigularis*) by radiotracking 32 individuals between May 2001 and April 2003 in savanna habitat in the Isthmus of Tehuantepec, Oaxaca, Mexico. Annual home-range and core-area sizes averaged $55 \text{ ha} \pm 8 \text{ SE}$ and $8 \pm 1 \text{ ha}$ for 10 adults of both sexes using the 95% and 50% fixed-kernel isopleths, respectively. Seasonal home ranges varied widely for adults, from 15 to 111 ha for females and from 24 to 166 ha for males. Juvenile males had larger seasonal home ranges than did juvenile females ($\bar{X} = 80$ and 24 ha). For adult jackrabbits, seasonal home ranges were larger during the 1st year compared to those of the 2nd year of study ($\bar{X} = 87$ and 49 ha), particularly for females. Home ranges and core areas of Tehuantepec jackrabbits were comparable in size and overlapped between active periods (nocturnal and crepuscular hours) and inactive periods (diurnal hours). Adults overlapped their home ranges with 1–10 individuals. Home-range overlap among females was greater than among males. Females shared portions of their ranges with other females more frequently than did males with other males. Home-range and overlap analysis suggests that Tehuantepec jackrabbits have polygamous mating behavior and nonterritorial social organization.

Key words: home range, *Lepus flavigularis*, mating, Mexico, overlap, social behavior, Tehuantepec jackrabbit

Understanding the organization of animals in space and time provides significant insight into mating behavior and social organization, both of which are key components of any demographic analysis related to conservation of endangered wildlife (Kernohan et al. 2001; Parker and Waite 1997). We used home-range size and overlap to infer basic sociobiological aspects of the Tehuantepec jackrabbit (*Lepus flavigularis*), information that is urgently needed to further develop management activities aimed to reduce threats to remnant populations (Komdeur and Deerenberg 1997; Powell 2000) of this leporid. The Tehuantepec jackrabbit is a Mexican endemic critically endangered by habitat loss and fragmentation, overhunting, and genetic isolation (Anderson and Gaunt

1962; Flux and Angermann 1990). Four small populations of Tehuantepec jackrabbits survive along savannas and grassy dunes on the shores of Superior and Inferior lagoons, a body of saltwater connected to the Gulf of Tehuantepec in Oaxaca, Mexico (López-Forment 1989; Lorenzo et al. 2006).

Home-range size of other members of the genus *Lepus* shows high intraspecific variability (Flux 1981b; Flux and Angermann 1990), suggesting that social organization of hares and jackrabbits is flexible and that leporids may adjust resource use (Hulbert et al. 1996). For instance, food and cover availability and distribution may influence home-range size for hares (Boutin 1984; Hulbert et al. 1996; Kunst et al. 2001; Macdonald 1983), but population density and social organization regulate sharing of feeding and resting areas (Komdeur and Deerenberg 1997). In addition, hares may show large home ranges when living in harsh environments and smaller home ranges when resources are more abundant (Hewson and Hinge 1990; Hulbert et al. 1996; Wolfe and Hayden 1996). Most hare and jackrabbit species overlap their home ranges (Flux 1981b;

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Hewson and Hinge 1990; Stott 2003; Wolfe and Hayden 1996) and are either polygamous or promiscuous (Flux 1981a; Flux and Angermann 1990; Lechleitner 1958).

Mating behavior and social organization of the Tehuantepec jackrabbit have not been studied. Species most closely related to the Tehuantepec jackrabbit in phylogeny and geographic range, the white-sided jackrabbit (*Lepus callotis*) and the black-tailed jackrabbit (*Lepus californicus*—Cervantes and Lorenzo 1997), are polygamous and have overlapping home ranges (Best and Henry 1993; Lechleitner 1958). However, adult white-sided jackrabbits form pair bonds so strong that pairs stay together and the male defends its mate (Best and Henry 1993). Tehuantepec jackrabbits occur in pairs that commonly are observed fleeing, feeding, or resting together (Cervantes 1993; Vargas 2000), but whether or not mated pairs are formed has not been investigated. In this study, radiotracking of Tehuantepec jackrabbits that inhabit the same area allowed comparison of home-range size and overlap among adults within and between sexes. Our expectations were that spatial arrangement of home ranges would support a hypothesis of polygamous mating behavior for Tehuantepec jackrabbits (Flux and Angermann 1990; Powell 2000). Home-range overlap with more than 1 adult individual of the opposite sex would indicate polygamy, whereas extensive home-range overlap between a single adult female and a single adult male would suggest monogamy (Powell 2000).

MATERIALS AND METHODS

Study area.—We studied the Tehuantepec jackrabbit population on the northeastern rim of Superior and Inferior lagoons in the state of Oaxaca, Mexico. The study area was a 9-km² portion of a savanna locally known as Llano Contreras, 2 km northwest from Montecillo Santa Cruz, municipality of San Francisco del Mar (16°22'N, 94°37'W). Native grasses in the savanna were dominated by grama (*Bouteloua*) and paspalum (*Paspalum*), trees were scattered and dominated by morro (*Crescentia*), and shrublands were sparse and dominated by nanche (*Byrsonima crassifolia*—Pérez-García et al. 2001). Vegetation along streambeds was dense and heterogeneous. 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), and is seasonally variable. 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 relative to the study area were obtained from the weather station at Juchitan de Zaragoza, Oaxaca, from the Mexican National Meteorological Service from May 2001 to June 2002. Unfortunately, data for July 2002 through April 2003 were not available from any of the weather stations near the study area. However, during fieldwork we observed that rainfall was more abundant in the 2nd year relative to the 1st year of study.

Native mammals associated with the Tehuantepec jackrabbit and observed during the study were eastern cottontail rabbits (*Sylvilagus floridanus*), nine-banded armadillos (*Dasyurus novemcinctus*), hooded skunks (*Mephitis macroura*), hog-nosed skunks (*Conepatus leuconotus*), southern opossums (*Didelphis marsupialis*), gray mouse opossums (*Tlacuatzin canescens*), gray foxes (*Urocyon cinereoar-*

gents), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*—Cervantes and Yépez 1995; Ramírez-Pulido et al. 2005). Gray foxes and coyotes are native predators of Tehuantepec jackrabbits.

Capture and handling of jackrabbits.—Jackrabbits were approached at night by a vehicle with observers sitting on the roof or by riders on horseback. Handheld fishing nets were thrown over jackrabbits blinded by spotlights. Nets were circular with a diameter of 3–4 m and with 3 kg of weights attached to the perimeter, and posed no threat of injury for jackrabbits. Captured animals were rapidly transferred from the net to a cotton bag for handling.

We recorded sex, age (juvenile or adult), weight, and standard measurements of Tehuantepec jackrabbits, and attached 20-g, 30-g, or 40-g VHF radiocollar transmitters (M2900 Advanced Telemetry Systems Inc., Isanti, Minnesota). Adult females had a well-developed clitoris shaped like a flat, lanced tongue, and adult males had a well-developed penis with conical tip (Péroux 1995). Compared to adults, juveniles had an immature clitoris or penis. Juvenile females were distinguished from juvenile males by identifying at the base of the clitoris a thin, longitudinal canal that extended to the vulva, whereas juvenile males had a cylindrically shaped penis having a conical tip (Péroux 1995). Transmitters were motion- and mortality-sensitive, with whip antennas. Juveniles weighing less than 500 g were not radiomarked because they were too small to comfortably wear the smallest radiocollars; instead, we attached radiocollars with added elastic to juveniles that weighed 500–2,200 g. We glued a 1-cm piece of elastic to the collar, allowing the collar to expand and eventually fall off as young jackrabbits grew larger (Forsy and Humphrey 1996). Radiocollared adults weighed 2,500–3,700 g. To replace radiocollars with depleted batteries, we recaptured 14 individuals 1 or 2 times.

Research complied with current Mexican laws and was conducted under authorization of the Secretaría de Medio Ambiente y Recursos Naturales, Mexico, and under a protocol approved by the Institutional Animal Care and Use Committee at The University of Massachusetts, Amherst. Capture and handling of jackrabbits followed guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Radiotracking of jackrabbits.—We intensively radiotracked Tehuantepec jackrabbits from May 2001 through April 2003, by foot or on horseback, with a portable receiver (Telonics TR-4, Mesa, Arizona) equipped with a 3-element Yagi antenna. Animals were tracked until observed directly, or if hidden in vegetation during daytime, individuals were located by following the transmitter signal and walking in circles within a radius of <5 m (White and Garrott 1990). During nighttime, we followed radiosignals on horseback and observed jackrabbits with a handheld spotlight (Truper, Mexico) that allowed illumination distances up to 70 m. We observed jackrabbits from distances of 50–70 m to avoid interfering with the individual's behavior. Active jackrabbits continued feeding or interacting socially. Observers recorded the time (hour and minutes) when the radiotracked individual was 1st sighted, then waited until the jackrabbit walked away to get the universal transverse mercator (UTM) coordinates for the location of 1st sighting. UTM coordinates were obtained from a global positioning system receiver (eTrex Venture, Garmin, Kansas); accuracy 3–15 m.

We obtained telemetry locations throughout the 24-h cycle. Every month, we located radiocollared animals daily for 1 week, and 1–3 times per week through the rest of the month. We collected 1 location per animal per telemetry session, and separated consecutive telemetry sessions by at least 24 h.

We captured 79 Tehuantepec jackrabbits from February 2001 to November 2002, and fitted 51 of these with radiocollars. We obtained telemetry locations from the 51 radiocollared individuals, and

estimated home ranges for 32 Tehuantepec jackrabbits of both sexes and different ages.

We estimated home ranges and core areas for 17 adult jackrabbits with ≥ 22 locations, including 9 females and 8 males. We estimated home ranges for 18 juvenile jackrabbits with ≥ 10 locations, including 11 females and 7 males, but core area was estimated only for 9 juveniles with > 20 locations. Ten adult jackrabbits (jackrabbits 1, 5, 9, 12, 13, 15, 18, 20, 21, and 22) and 1 juvenile male (8) had 2–4 home-range estimates across seasons over 2 years of radiotracking. One adult male (1) had 2 annual home-range estimates. Two males (5 and 9), and 1 female (27) were captured and radiotracked as juveniles, then recaptured to replace radiocollars and radiotracked as adults.

Four radiocollared adult females were captured 1–10 km away from Llano Contreras but could not be radiotracked for home-range estimation because of logistic constraints. Fifteen radiocollared jackrabbits died or were lost because of transmitter failure before we obtained home-range estimates. Additionally, 9 radiocollared jackrabbits died during the study period because of predation, poaching, and induced fires (Farías 2004); therefore, these individuals could not be radiotracked throughout the 2 years of study.

Analysis of telemetry data.—We partitioned 2 years of data into 4 seasons to estimate seasonal home ranges and core areas of Tehuantepec jackrabbits. Seasons were defined as wet 2001 (May 2001 through October 2001), dry 2002 (November 2001 through April 2002), wet 2002 (May 2002 through October 2002), and dry 2003 (November 2002 through April 2003). We pooled data from wet and dry seasons to estimate annual home ranges and core-area sizes. Years were defined as year 01 (May 2001 through April 2002) and year 02 (May 2002 through April 2003).

We evaluated the effect of sex, season, and year on size differences in seasonal home ranges and core areas of adults and on size differences in home ranges of juveniles with analysis of variance (ANOVA—Sokal and Rohlf 1981). Size differences in core areas of juveniles were evaluated on the effect of sex and season. Statistical analyses were performed with general factorial univariate ANOVA using SPSS (version 8.0, SPSS Inc., Chicago, Illinois). We compared annual home-range and core-area size between adult females and males with 1-way ANOVA (Sokal and Rohlf 1981).

Active and inactive ranges.—Data from annual home ranges and core areas of adult jackrabbits were separated to estimate home-range and core-area size during active (nocturnal and crepuscular hours) compared to inactive (diurnal hours) periods of Tehuantepec jackrabbits. Active and inactive ranges were compared with 1-way ANOVA.

The length of active and inactive periods was assessed separately by sex and season according to activity patterns from radiocollared Tehuantepec jackrabbits, by plotting mean proportion of active radiosignals against time of the day (Farías 2004). Radiotransmitters were motion sensitive and indicated inactivity when the signal had a stable frequency of 55 pulses per minute, as opposed to activity when the signal had chaotic variation in the frequency. An animal was considered inactive if during a 20-s interval the radiosignal was stable, and active if the signal was chaotic.

Home-range size.—We calculated 95% and 50% fixed-kernel ranges with least-squares cross-validation (Powell 2000; Seaman and Powell 1996; Worton 1989) using the computer software ArcView GIS (version 3.2, Environmental Systems Research Institute Inc. [ESRI], Redlands, California) with the Spatial Analyst (ESRI) and the Animal Movement Analysis (Hooge and Eichenlaub 1997) extensions. A home range was defined as the 95% fixed-kernel isopleth, and a core area as the 50% fixed-kernel isopleth (Powell 2000). Our data are better suited to the kernel method because it is a nonparametric robust

estimator that can compute home-range boundaries with multiple centers of activity based on the complete utilization distribution, it is minimally affected by autocorrelated data and outliers, and home-range estimates stabilize with 30–50 points (Kernohan et al. 2001; Powell 2000). The fixed-kernel method generally appears to have lower bias and better surface fit than the adaptive kernel (Seaman et al. 1999) and is more reliable when estimating the outer contours and centers of activity of the home range (Kernohan et al. 2001). To allow comparisons of our results with other published data (Seaman et al. 1999), we also report minimum convex polygon (MCP) estimates of home-range size (Dixon and Chapman 1980; Mohr 1947) for Tehuantepec jackrabbits. Home-range and core-area sizes are reported as means with *SEs* throughout this paper.

Home-range overlap.—Home-range overlap was calculated as the area shared by 2 neighboring individuals using Minta's (1992) index, where overlap values potentially range between 0 and 1 with a mean overlap of 1 calculated for 2 home ranges of identical size with 100% overlap. ArcView GIS with the Spatial Analyst and the GeoProcessing Wizard (ESRI) extensions were used to calculate shared areas for the 95% fixed-kernel isopleth (home range) and the 50% fixed-kernel isopleth (core area) whenever isopleths of the members of a dyad overlapped.

We compared home-range and core-area overlap indices for female–female, male–male, and female–male dyads of sympatric adults present during each season (wet 2001, dry 2002, wet 2002, and dry 2003). Differences among intrasexual and intersexual overlap indices were evaluated with nonparametric Kruskal–Wallis ANOVA because data were not normally distributed (Sokal and Rohlf 1981). We estimated home-range overlap indices between adult and juvenile individuals present during each season.

RESULTS

Seasonal home-range size.—To estimate seasonal home ranges and core areas we used a mean $\pm SE$ of 32 ± 1 locations for adult females ($n = 15$), 32 ± 1 locations for adult males ($n = 16$), 18 ± 2 locations for juvenile females ($n = 11$), and 27 ± 3 locations for juvenile males ($n = 8$). Percentages of telemetry locations taken during the active period (nocturnal and crepuscular hours) of Tehuantepec jackrabbits were 62% for adult females (20 ± 1 locations), 55% for adult males (17 ± 1 locations), 49% for juvenile females (9 ± 1 locations), and 50% for juvenile males (13 ± 1 locations).

Tehuantepec jackrabbits showed wide variation in their ranges during the 2 years of radiotracking (Tables 1 and 2). For adults, neither sex nor seasonality explained range variability (Fig. 1). Seasonal home-range and core-area sizes of adults averaged 56 ± 8 ha and 9 ± 1 ha for females ($n = 15$), and 66 ± 9 ha and 11 ± 1 ha for males ($n = 16$), respectively, with no significant differences between sexes in size of home range ($F = 0.010$, $d.f. = 1, 23$, $P = 0.922$) or core area ($F = 0.316$, $d.f. = 1, 23$, $P = 0.579$). Home-range size averaged 60 ± 8 ha for the wet season ($n = 14$) compared to 62 ± 9 ha for the dry season ($n = 17$); core-area size averaged 10 ± 2 ha for the wet season compared to 9 ± 1 ha for the dry season, with no significant differences detected in home range ($F = 0.294$, $d.f. = 1, 23$, $P = 0.593$) or core area ($F = 1.161$, $d.f. = 1, 23$, $P = 0.292$) between seasons. Interestingly, seasonal home ranges ($F = 9.365$, $d.f. = 1, 23$, $P = 0.005$) and core areas ($F = 4.966$,

TABLE 1.—Seasonal and annual home-range and core-area size of 17 adult Tehuantepec jackrabbits (*Lepus flavigularis*) in Oaxaca, Mexico, May 2001 to April 2003. Sample size (n) is number of locations; home range and core area are fixed-kernel (FK) and minimum convex polygon (MCP) estimates.

Season	Jackrabbit	n	Females				Males					
			Home range 95%		Core area 50%		Home range 95%		Core area 50%			
			FK (ha)	MCP (ha)	FK (ha)	MCP (ha)	FK (ha)	MCP (ha)	FK (ha)	MCP (ha)		
Wet 2001 ^a	2	31	108	58	15	11	1	35	73	62	13	7
							6	22	102	45	20	17
Dry 2002 ^b	13	32	111	62	17	17	1	31	41	42	8	5
	15	34	75	45	13	12	5	30	37	24	2	7
	18	23	64	42	7	5	11	31	93	47	16	20
Wet 2002 ^c							12	31	166	94	15	21
	13	31	62	38	8	6	1	42	50	23	14	9
	15	32	40	27	6	5	5	34	31	19	8	4
	18	32	85	44	19	11	9	30	75	47	8	11
	20	28	15	10	2	2	12	35	98	59	18	11
	21	33	43	21	10	8	22	28	24	22	2	1
Dry 2003 ^d							24	23	32	16	3	3
	15	38	33	22	6	4	1	35	70	41	13	10
	20	35	22	12	5	4	5	34	66	49	9	5
	21	32	53	35	7	4	9	33	75	43	14	12
	27	34	67	40	6	10	22	30	32	19	7	5
	28	33	33	18	8	3						
30	31	25	21	3	2							
Year 01 ^e							1	70	57	76	11	7
Year 02 ^f	15	70	38	32	4	6	1	77	72	49	12	12
	20	63	21	20	6	3	5	68	47	48	6	5
	21	65	49	33	8	9	9	63	100	79	13	15
	27	48	61	37	10	9	12	46	79	70	12	9
	28	40	36	21	8	4	22	58	34	26	2	5

^a Wet 2001: May–October 2001.

^b Dry 2002: November 2001–April 2002.

^c Wet 2002: May–October 2002.

^d Dry 2003: November 2002–April 2003.

^e Year 01: pooled data from Wet 2001 and Dry 2002 seasons (May 2001–April 2002).

^f Year 02: pooled data from Wet 2002 and Dry 2003 seasons (May 2002–April 2003).

$df = 1, 23, P = 0.036$) of adult jackrabbits were significantly larger during the 1st year of study (87 ± 12 and 13 ± 2 ha, $n = 10$) than the 2nd year (49 ± 5 and 8 ± 1 ha, $n = 21$).

Variation in ranges of juveniles (Table 2) could be explained by larger home ranges of males (80 ± 29 ha, $n = 8$) compared to those of females (24 ± 4 ha, $n = 11$; $F = 11.916$, $df = 1, 11, P = 0.005$), and to larger home ranges during the wet season (64 ± 25 ha, $n = 10$) compared to the dry season (30 ± 6 ha, $n = 9$; $F = 8.002$, $df = 1, 11, P = 0.016$). Home ranges of juveniles were larger during the 1st year of study (66 ± 24 ha, $n = 10$) than the 2nd year (27 ± 8 ha, $n = 9$), although differences were not statistically significant ($F = 3.498$, $df = 1, 11, P = 0.088$). No effect of sex ($F = 3.858$, $df = 1, 5, P = 0.107$) or season ($F = 2.753$, $df = 1, 5, P = 0.158$) was detected on size differences in core area of juvenile jackrabbits, probably because of small sample size. Core-area sizes of juveniles averaged 17 ± 9 ha for males ($n = 5$) and 6 ± 2 ha for females ($n = 4$), and 19 ± 11 ha during the wet season ($n = 4$) and 6 ± 1 during the dry season ($n = 5$).

Annual home-range size.—We pooled data from wet 2001 and dry 2002 seasons to estimate annual (year 01) home-range and core-area sizes for 1 adult male. We pooled data from wet 2002 and dry 2003 seasons to estimate annual (year 02) home-

range and core-area sizes for 10 adults, and used a mean $\pm SE$ of 57 ± 6 locations for adult females ($n = 5$), and 62 ± 5 locations for adult males ($n = 5$). We averaged annual home range and core area from the 10 adults radiotracked from May 2002 through April 2003 (year 02), but did not include estimates from the adult male radiotracked from May 2001 through April 2002 (year 01) because size differences in seasonal ranges were statistically significant between the 1st and 2nd year of study.

Annual home-range and core-area sizes averaged 43 ± 8 ha and 7 ± 1 ha for female adults ($n = 5$), and 66 ± 12 ha and 9 ± 2 ha for male adults ($n = 5$), respectively (Table 1). Although females tended to have smaller annual home-range size (1-way ANOVA, $F = 2.684$, $df = 1, 8, P = 0.140$) and core-area size (1-way ANOVA, $F = 0.791$, $df = 1, 8, P = 0.400$) than males, the lack of statistical significance likely was due to small sample size.

Active and inactive range size.—We used the location data from 10 adult jackrabbits radiotracked from May 2002 through April 2003 (year 02) to estimate home-range and core-area size during active period (nocturnal and crepuscular hours) compared to inactive period (diurnal hours) of Tehuantepec jackrabbits. We used 38 ± 3 locations for females ($n = 5$) and

TABLE 2.—Seasonal home-range and core-area size of 18 juvenile Tehuantepec jackrabbits (*Lepus flavigularis*) in Oaxaca, Mexico, May 2001 to April 2003. Sample size (n) is number of locations; home range and core area are fixed-kernel (FK) and minimum convex polygon (MCP) estimates. For $n < 20$, home-range estimates are 95% FK and 100% MCP, and core area is not estimated.

Season ^a	Females						Males					
	Jackrabbit	n	Home range 95%		Core area 50%		Jackrabbit	n	Home range 95%		Core area 50%	
			FK (ha)	MCP (ha)	FK (ha)	MCP (ha)			FK (ha)	MCP (ha)	FK (ha)	MCP (ha)
Wet 2001	4	12	39	15			3	38	264	184	50	43
	7	11	49	33			5	27	114	63	18	3
Dry 2002	10	24	35	19	8	4	8	34	26	14	2	5
	14	22	36	19	8	3	9	34	59	45	10	5
							16	18	11	9		
Wet 2002							17	33	28	20	4	3
	19	32	12	7	2	1	8	17	84	38		
	23	29	23	15	5	4						
	25	10	16	6								
	26	15	7	4								
Dry 2003	27	14	27	13								
	31	13	16	8			29	14	52	24		
	32	17	8	5								

^a Seasons as in Table 1.

37 ± 4 locations for males ($n = 5$) for the estimation of active range sizes, and 19 ± 3 locations for females ($n = 5$) and 26 ± 3 locations for males ($n = 5$) for the estimation of inactive range sizes.

Activity patterns were determined with 1,698 recordings from radiosignals of 26 adult jackrabbits (16 females and 10 males) radiotracked from May 2001 to April 2003. Tehuantepec jackrabbits began activity at dusk and ceased at dawn (Fariás 2004). The active period for adult females was from 1700 to 0559 h during the wet season, and from 1800 to 0659 h during the dry season. The active period for adult males was from 1800 to 0659 h during the wet season, and from 1900 to 0759 h during the dry season.

Home range and core areas tended to be larger in the active period (nocturnal and crepuscular hours; 53 ± 7 ha and 10 ± 1 ha, respectively) than in the inactive period (diurnal hours; 41 ± 6 ha and 8 ± 2 ha, respectively), but differences were not significant (1-way ANOVA: home ranges, $F = 1.455$, $df. = 1, 18$, $P = 0.243$; core areas, $F = 0.542$, $df. = 1, 18$, $P = 0.471$). However, the average number of locations used for estimates was significantly larger (1-way ANOVA, $F = 22.853$, $df. = 1, 18$, $P = 0.000$) for active ranges (38 ± 2) compared to inactive ranges (22 ± 2). Active and inactive ranges overlapped and were similar in location (Fig. 2).

Seasonal overlap.—Adult jackrabbits overlapped their seasonal home ranges with 1–10 individuals, with mean overlap index of 0.21 ± 0.02 for 75 observed dyads over the 2 years of radiotracking. Female–male overlap occurred for 40 dyads, compared to 20 female–female dyads and 15 male–male dyads. Mean overlap of male–male dyads (0.08 ± 0.02) was significantly less than mean overlap of female–female dyads (0.26 ± 0.03) and female–male dyads (0.23 ± 0.03 ; Kruskal–Wallis ANOVA, $H = 11.670$, $df. = 2, 72$, $P = 0.003$).

Seasonal core-area overlap was uncommon between adults of the same sex, with only 1 male–male dyad (0.24) and 4 female–female dyads (0.08 ± 0.03) overlapping over the

2 years of radiotracking. Female–male dyads had 10 instances of core-area overlap with a mean overlap index of 0.14 ± 0.04 .

We estimated home-range overlap indices between adult and juvenile individuals present during each season, but using only home-range estimates from 9 juveniles with >20 locations (Table 2). Juveniles and adults overlapped their home ranges in 41 instances during the 2 years of radiotracking. Adult females had a mean overlap index of 0.31 ± 0.07 with juvenile females ($n = 8$ dyads) and of 0.26 ± 0.06 with juvenile males ($n = 9$ dyads). Adult males had a mean overlap index of 0.16 ± 0.04 with juvenile females ($n = 13$ dyads) and of 0.25 ± 0.06 with juvenile males ($n = 11$ dyads).

Annual overlap.—Among 10 adult jackrabbits, 18 instances of overlap between neighboring annual home ranges occurred between and within sexes with ≥ 1 individuals, with a mean Minta's index of 0.14 ± 0.03 . Mean overlap for female–female dyads ($n = 3$) was higher (0.29 ± 0.02) than mean overlap for female–male dyads (0.14 ± 0.03 , $n = 10$), whereas mean overlap between male–male dyads ($n = 5$) was the lowest (0.06 ± 0.01 ; Kruskal–Wallis ANOVA, $H = 5.750$, $df. = 2, 15$, $P = 0.056$). Annual core-area overlap between adults was uncommon and low and occurred in only 2 instances; overlap indices were 0.01 for a female–female dyad and 0.07 for a female–male dyad.

DISCUSSION

Variation in home-range size.—Estimates of individual home-range size (15–166 ha) from radiotracked Tehuantepec jackrabbits followed the trend of high intraspecific variation characteristic of the genus *Lepus*, and were comparable to home-range estimates for the closely related black-tailed jackrabbit (16–140 ha—Best 1996). Our results fell within values reported in the literature for other jackrabbits and hares (10–300 ha—Flux and Angermann 1990), and were similar to home-range estimates reported in an overview of radiotelem-

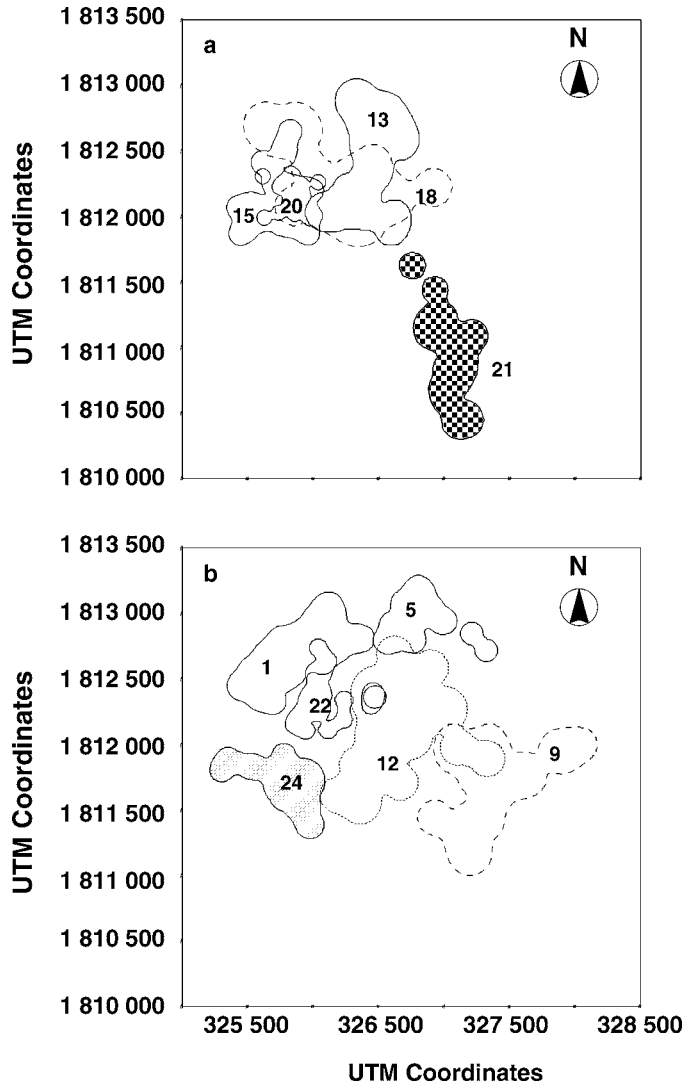


FIG. 1.—Fixed-kernel estimates (95%) of seasonal (wet season 2002) home ranges for a) 5 female and b) 6 male adult Tehuantepec jackrabbits show that home-range overlap among females was greater and more frequent than among males. Numbers inside or next to home ranges indicate animal's identification number.

etry studies on the European hare (*Lepus europaeus*, 26–190 ha—Kunst et al. 2001), a species similar in adult size to the Tehuantepec jackrabbit.

Information about home-range size from other species closely related to Tehuantepec jackrabbits is limited. For instance, home-range estimates for the antelope jackrabbit (*Lepus alleni*) date back to a classic study in Arizona by Vorhies and Taylor (1933), where size varied greatly with habitat and averaged 643 ha, but care should be taken in adopting these values for comparison because home-range size estimates are not based on telemetry data. White-sided jackrabbits have no published home-range size estimates (Bednarz and Cook 1984; Best and Henry 1993; Desmond 2003; Flux and Angermann 1990) for comparison with our results.

Contrary to our expectations, results showed that seasonality did not explain the wide home-range variation for Tehuantepec

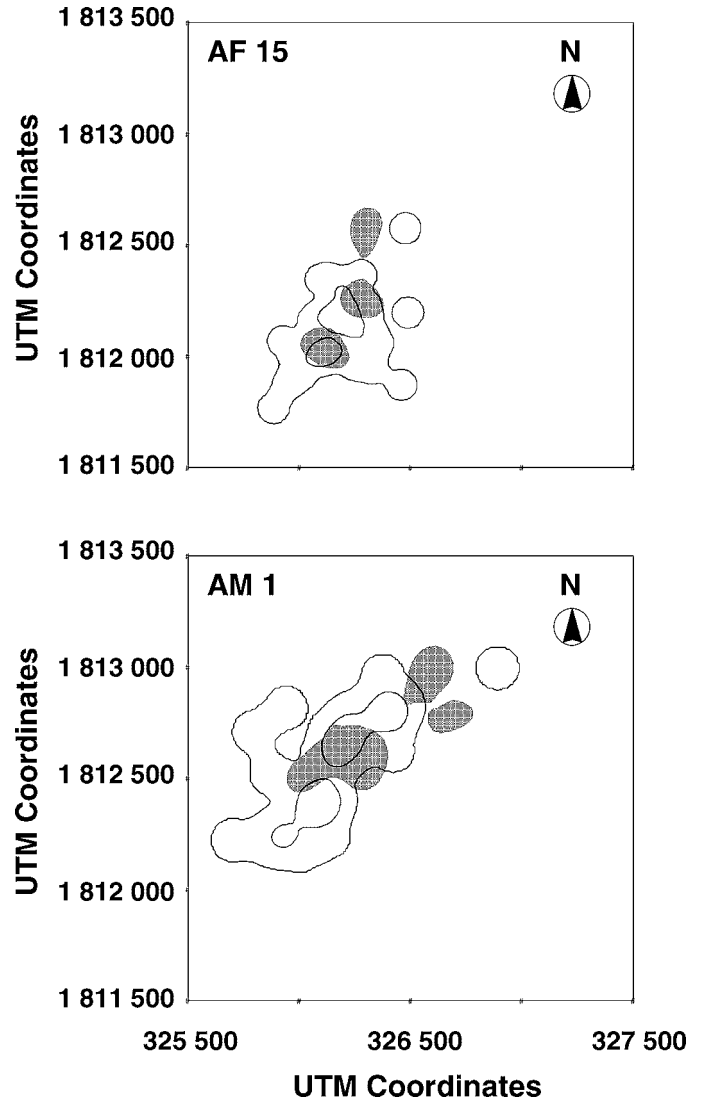


FIG. 2.—Fixed-kernel estimates of active and inactive home-range (95%) and core-area (50%) sizes for an adult female (AF 15) and an adult male (AM 1) Tehuantepec jackrabbit show that the active and inactive ranges were similar in size and location. Outlying closed curves represent active home ranges, whereas interior curves show active core areas. Light shading denotes inactive home ranges, whereas dark shading indicates inactive core areas.

jackrabbits. Similarly, Stott (2003) found that home-range size (149 ha) and overlap of European hares remained large and stable between pre- and postharvest periods in a wheat and sheep farm in the Mediterranean climatic zone of Australia, and Kunst et al. (2001) observed that home-range size (28 ha) for the European hare did not differ between sexes or seasons in a Dutch natural salt-marsh system.

Kunst et al. (2001) found that core-area size for European hares was smallest when food availability was lowest and weather was coldest, which is not expected if home-range size is determined by food supply (Hulbert et al. 1996) but may be explained as a strategy to save energy in poor weather conditions (Kunst et al. 2001). The Tehuantepec jackrabbit inhabits an arid tropical zone as the southernmost species of

Lepus in America (Anderson and Gaunt 1962); the leporid experiences food variability between wet and dry seasons, but is not exposed to extremely cold or dry weather.

Interestingly, home-range size of Tehuantepec jackrabbits was larger during the 1st year than the 2nd year of study. It is likely that weather differences among years affected resource variability in the study area more than seasonality within years, underscoring the need for long-term ecological research for the Tehuantepec jackrabbit. The study area is located in a tropical dry savanna with high richness in grass and forb diversity (Pérez-García et al. 2001), a system where resource availability and distribution seem to vary widely between the wet and dry seasons. Grasses are green and abundant during the wet season and gradually turn brown as the dry season advances. Also, during years of less rainfall grasses turn brown earlier during the dry season, a condition that may facilitate more frequent and intense wildfires.

Cattle grazing also may contribute to the spatial and temporal resource variability faced by the population of Tehuantepec jackrabbits under study. Local people set fires during the dry season to maintain grass shoots for their cattle. Recently burned areas are left with little or no herbaceous cover, and jackrabbits feed from green sprouts that grow within a few days, and from grass roots that are easily excavated. Thus, the patches of green sprouts produced after fires may smooth differences in food availability for jackrabbits between wet and dry seasons. Nevertheless, induced fires and free-ranging cattle reduce plant diversity in the study area (Pérez-García et al. 2001), and survival of Tehuantepec jackrabbits may be threatened in frequently burned and overgrazed habitats (Fariás 2004).

Home-range analysis indicated that differences in spatial behavior may exist between female and male Tehuantepec jackrabbits. Adult males tended to have larger home ranges than adult females, whereas home ranges of juvenile males were larger than those of juvenile females. Also, adult females showed greater variation in home-range size between the 1st and 2nd year of study than did adult males (Table 1).

Active and inactive range size.—Home ranges and core areas of Tehuantepec jackrabbits were comparable in size and overlapped between periods of activity and inactivity (Fig. 2), indicating the importance of native floristic diversity and structure in tropical dry savannas for conservation of this leporid (Fariás 2004). Similarly, Kunst et al. (2001) found that vegetative heterogeneity in a natural salt marsh allows for both food and shelter to be found in the same area, thereby allowing for similarly sized and broadly overlapping night and day ranges of European hares. In contrast, home-range studies of hares in agricultural systems showed larger night ranges than day ranges, with resting and foraging areas often spatially distinct (Hewson and Hinge 1990; Hulbert et al. 1996; Reitz and Léonard 1994; Stott 2003; Tapper and Barnes 1986).

Social behavior.—Overlap analysis from 31 seasonal home ranges of adult jackrabbits of both sexes during 2 years of radiotracking provided sufficient data to infer mating behavior of Tehuantepec jackrabbits. Adults overlapped home ranges with more than 1 individual of the opposite sex, in accordance

with the assumption that Tehuantepec jackrabbits are polygamous. Also, we detected no instance of extensive (>80%) intersexual overlap that would indicate formation of mated pairs (Powell 2000).

Overlap analysis also was consistent with the assumption of a nonterritorial social organization for Tehuantepec jackrabbits. Results suggest a low degree of overlap (Larivière and Messier 1998), but because we did not capture all adult jackrabbits in the study area the possibility exists that we missed animals that had significant overlap. Home ranges of radiotracked adults overlapped with at least 1 and up to 10 individuals, showing that Tehuantepec jackrabbits may not have exclusive use of their home ranges. However, negligible core-area overlap may indicate that at least some portion of the home range is preferentially not shared with other individuals (Crooks and Van Vuren 1996; Fariás 2004). That female–female overlap in home ranges was both more common and more extensive than male–male overlap (Fig. 1) also suggests behavioral differences in spatial organization between sexes.

Conservation implications.—Behavioral information obtained from radiocollared individuals was sufficient to characterize the prevalent mating system (Parker and Waite 1997) for Tehuantepec jackrabbits. Basic knowledge on mating behavior and social organization of this threatened leporid has much to contribute to the analysis of population dynamics and conservation models and provides information for dealing with problems associated with population management for the species' recovery (Komdeur and Deerenberg 1997; Parker and Waite 1997).

Because the effective size of a population depends on the number of sexually mature females and males but also largely on the social behavior of the species (Komdeur and Deerenberg 1997), the effect of mating behavior on gene flow and population growth is linked to population viability (Coté 2003). Also, the degree of random mating influences the genetic diversity transmitted to the next generation (Parker and Waite 1997). In the case of small and isolated populations such as those of the Tehuantepec jackrabbit, the probability of extinction would be higher if their mating behavior was monogamous rather than polygamous, because random mating would increase the effective breeding population size (Coté 2003; Flux and Angermann 1990; Parker and Waite 1997).

Populations of Tehuantepec jackrabbits inhabit savannas and grassy dunes included in lands that are communally owned by local families (ejidos), and where jackrabbits are jeopardized by disturbances such as growing human settlements, cattle-raising activities, frequent fires, and poaching (Fariás 2004). This study obtained information on mating behavior, home-range size, home-range variability in space and time, and home-range overlap needed for the planning and designation of a natural conservation area for the Tehuantepec jackrabbit in Oaxaca, Mexico. Habitat fragmentation and loss are among the most proximate threats for remnant populations of Tehuantepec jackrabbits, and the protection of suitable habitat is essential for the species' survival (Fariás 2004; Flux and Angermann 1990).

RESUMEN

Estudiamos el tamaño y superposición del ámbito hogareño y centro de actividad de la liebre de Tehuantepec (*Lepus flavigularis*) mediante el seguimiento de 32 liebres en el Istmo de Tehuantepec, Oaxaca, México, de Mayo 2001 a Abril 2003, utilizando la radiotelemetría. El tamaño de ámbito hogareño anual y su centro de actividad promediaron $55 \text{ ha} \pm 8 \text{ SE}$ y $8 \pm 1 \text{ ha}$ para 10 liebres adultas de ambos sexos utilizando el estimador kernel fijo del 95% y del 50%, respectivamente. El tamaño del ámbito hogareño estacional de las liebres adultas tuvo una variación de 15 a 111 ha para hembras y de 24 a 166 ha para machos. Los machos juveniles presentaron ámbitos hogareños de mayor tamaño que las hembras juveniles ($\bar{X} = 80$ y 24 ha). Los ámbitos hogareños estacionales de las liebres adultas fueron más grandes durante el primer año de estudio comparado con el segundo año de estudio ($\bar{X} = 87$ y 49 ha), particularmente para las hembras. El ámbito hogareño y su centro de actividad fueron comparables en tamaño y localización entre el periodo de actividad de las liebres (horas nocturnas y crepusculares) y el periodo de inactividad (horas diurnas). Las liebres adultas compartieron sus ámbitos hogareños con 1 a 10 individuos, y la superposición fue mayor entre las hembras que entre los machos. Las hembras compartieron con otras hembras porciones de sus ámbitos hogareños con mayor frecuencia que los machos con otros machos. El análisis de tamaño y superposición de ámbito hogareño sugiere que la liebre de Tehuantepec presenta un sistema de apareamiento poligámico y una organización social en la que los individuos no defienden territorios.

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