SPATIO-TEMPORAL ECOLOGY AND HABITAT SELECTION OF THE CRITICALLY ENDANGERED TROPICAL HARE (<u>LEPUS FLAVIGULARIS</u>) IN OAXACA, MEXICO

A Dissertation Presented

by

VERONICA FARIAS

Submitted to the Graduate School of the University of Massachusetts Amherst in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

September 2004

Wildlife and Fisheries Conservation



© Copyright by Veronica Farias 2004

All Rights Reserved

SPATIO-TEMPORAL ECOLOGY AND HABITAT SELECTION OF THE CRITICALLY ENDANGERED TROPICAL HARE (<u>LEPUS FLAVIGULARIS</u>) IN OAXACA, MEXICO

A Dissertation Presented

by

VERONICA FARIAS

Approved as to style and content by:

Todd K. Fuller, Chair

Matthew J. Kelty, Member

Paul R. Sievert, Member

Matthew J. Kelty, Department Head Department of Natural Resources Conservation

ACKNOWLEDGMENTS

I would like to deeply thank my advisor, Todd K. Fuller, for his guidance, invaluable support, and generous sharing of knowledge and enthusiasm during all stages of this project. I want to extend my gratitude to the members of my committee, Paul R. Sievert and Matthew J. Kelty, for their helpful comments and suggestions to improve the document.

I am especially grateful to Fernando A. Cervantes for his willing and generous help, advice, and support to materialize my academic goals. He made me a member of the team studying and working at the Mammalogy Laboratory of the Institute of Biology, UNAM. Consuelo Lorenzo and Julieta Vargas are acknowledged for their support and guidance during the project, and for sharing their knowledge on capturing hares.

I want to thank The Wildlife Conservation Society for funding fieldwork through the Research Fellowship Program. WCS funding made possible the acquisition of telemetry equipment and the participation of the local people with the project.

Enrique Martinez Meyer kindly provided advice on ArcView tools. Eduardo Perez-Garcia, Gerrit Davidse, and Mario Sousa kindly provided information about biodiversity and conservation of savannas from the Isthmus of Tehuantepec in Mexico. Andrew Smith is acknowledged for providing information on Red List Assessment for Mexican lagomorphs.

I am grateful for the support provided during fieldwork by Elizabeth Sandoval and Ernestina C. Caamaño. Oscar Retana, Zadya Vargas, Eugenia Santiz, Mario Castañeda, Jonathan Ramirez, Jorge, Felipe, and field assistants who shared great adventures during capture efforts.

This research would not have been possible without the help of the people from Montencillo Santa Cruz, Oaxaca, particularly the Gutierrez Vazquez family. My special

iv

thanks to Na Magdalena and Ta Rube, and their family, Dominga and Juan, Leiber and Cheya, Bertha and Ismael, Maria and Colocho, Roberto, Rosa Maria, and their children.

I thank the civil authorities from Municipalities of Guamuchil and San Francisco del Mar Pueblo Nuevo (SFMPN), Oaxaca, who kindly permitted field research to be conducted on their properties. The Ecology Regent of SFMPN joined during two nights of capture efforts in April 2002 and provided a vehicle. COVOMA is thankfully acknowledged for their friendship and help during fieldwork, and for providing links of cooperation with the civil authorities of Municipality of Juchitan de Zaragoza, Oaxaca, to whom I am also grateful for their support and interest in the project.

I would like to thank Hector A. Malagon, who provided advice on leporid handling and tissue sampling. Thanks to Angel P. Utrilla for his advice to sex domestic rabbits, which proved invaluable to sex tropical hares in the field.

Consejo Nacional de Ciencia y Tecnologia (CONACYT), Mexico, and the Fulbright Program of the Institute of International Education, USA, supported me during the completion of the graduate degree.

This research was conducted under permit 2094 of Secretaria de Medio Ambiente y Recursos Naturales (SEMARNAT), Mexico, and under protocol number 22-02-07 from the Institutional Animal Care and Use Committee (IACUC) at The University of Massachusetts, Amherst, USA.

ABSTRACT

SPATIO-TEMPORAL ECOLOGY AND HABITAT SELECTION OF THE CRITICALLY ENDANGERED TROPICAL HARE (LEPUS FLAVIGULARIS) IN OAXACA, MEXICO

SEPTEMBER 2004

VERONICA FARIAS, BIOLOGIST, NATIONAL AUTONOMOUS UNIVERSITY OF MEXICO M.Sc., UNIVERSITY OF MASSACHUSETTS AMHERST Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Todd K. Fuller

I studied the spatio-temporal ecology, habitat selection, and survival of tropical hares *Lepus flavigularis* in Oaxaca, Mexico. Home range size and overlap were estimated to insight into tropical hare's mating behavior and social organization. Habitat selection and survival rates were determined to identify key habitat types and cause-specific mortality for conservation actions. I radio-tracked 51 hares in a savanna of the Isthmus of Tehuantepec, from February 2001 to July 2003. Annual home ranges and core areas of adults averaged 0.56 and 0.09 km2, respectively. Seasonal home ranges of adults varied from 0.22 to 1.11 km2 for females, and from 0.24 to 1.66 km2 for males. Seasonal core areas varied from 0.03 to 0.19 km2 for females, and from 0.02 to 0.20 km2 for males. Juvenile home range overlap with more than one individual suggests tropical hares show a polygamous mating behavior, and a non-territorial social organization. Hares selected home ranges with relatively more grassy and sparse shrubby habitats and less dense vegetation. Hares rested during daytime, and favored savanna with bushes of *Byrsonima crassifolia* that probably provided cover from predators.

Hares foraged during crepuscular and nocturnal hours, and favored savanna with scattered trees of *Crescentia spp*. that allowed visual detection of predators. No effects of sex and season on range size or habitat selection were detected. Annual survival for adults was 0.43, and survival during the wet season (0.56) was lower than during the dry season (0.79), particularly for females. Survival of juvenile females was low during the dry (0.06) and wet (0.15) seasons when compared to juvenile males survival (0.35 and 0.48). Predation was the major cause of mortality with 67% of adult and 94% of juvenile deaths. Induced fires and poaching accounted for 20% and 13% of adult deaths, respectively. Preservation of native vegetation structure in savannas is needed for tropical hare conservation.

Key words: compositional analysis, conservation, demographic parameters, habitat selection, home range, Lepus flavigularis, mating behavior, Mexico, mortality, radio-telemetry, social organization, survival, Tehuantepec jackrabbit, tropical hare.

PREFACE

Mexico is a center of lagomorph diversity because it is one of the countries with the most leporid species, and also has a high proportion of endemic species. Eight out of 15 rabbit and hare species are unique to Mexico, but with the exception of the volcano rabbit, *Romerolagus diazi*, our ecological knowledge of endemic rabbits and hares is poor. Preserving Mexico as a center of lagomorph diversity is a conservation priority because the eight Mexican endemisms are classified as near threatened, threatened, or endangered. When I began this research, ecological information on Mexican leporids was urgently needed for conservation plans, and particularly so for the tropical hare, *Lepus flavigularis*. The tropical hare is the most endangered of five species of hares in Mexico and is one of the most endangered mammals in the world.

Previous studies on the tropical hare were limited to karyotype analysis, histology of ovaries and vagina, phylogenetics, and surveys. Through this research, I aimed to produce scientific information on home range size and overlap, habitat selection, survival and mortality, and preliminary data on reproduction and density of tropical hares, or in other words, basic ecological data needed for conservation actions.

Tropical hares are jeopardized by habitat loss and fragmentation, genetic isolation, and poaching. Three populations survive along savannas and grassy dunes on the shores of a salt-water lagoon connected to the Gulf of Tehuantepec, Oaxaca, Mexico. My study area, a savanna locally named Llano Contreras, is 2 km northwest from Montecillo Santa Cruz, a Zapotec settlement of about 70 households in one of the most marginalized rural areas of Mexico.

When I started fieldwork, local people wondered why university professors and students would come from Mexico City to study the hare, but soon they got involved in the

viii

project by helping during capture efforts, which were lots of fun for adults and kids. I believe that local people need to be informed of wildlife conservation issues in their homelands in order to accept and integrate conservation efforts into strategies implemented in the region. By the end of the fieldwork, local people had named the radio-marked hares, and kids would ask if "Bolalari" was still alive.

This dissertation is presented as a series of chapters intended to be published as scientific papers in journals. Chapter 1 reports estimates on home range size and overlap and insights into the tropical hare mating behavior and social organization. Chapter 2 investigates habitat selection of tropical hares to identify vegetation types that need to be targeted for conservation. Chapter 3 estimates survival and mortality rates of adult and juvenile hares, to identify mortality factors that threaten the survival tropical hare populations. Chapter 4 summarizes available information on tropical hare biology, and generates guidelines relevant for developing potential conservation strategies. My main recommendations are to inform local people about the endangerment of tropical hares, to propose a natural area for hare conservation, and to continue research on tropical hare populations.

CONTENTS

CKNOWLEDGMENTS	iv
BSTRACT	vi
REFACE v	iii
IST OF TABLES x	iv
IST OF FIGURES x	vi

CHAPTER

1.	SPATIAL ECOLOG TROPICAL HARE	Y INSIGHTS INTO THE MATING SYSTEM OF THE	1
	Abstract Introduction Methods		1 1 3
	Study Captu Radio Home Home Seaso Rangi	Areare of Animals-TrackingRange and Core Area SizesRange and Core Area Overlapsnal Shifting of Rangesng Distance	3 4 5 6 7 8 8
	Results		9
	Radio Home	-Tracking	9 10
		Annual RangesSeasonal Ranges	10 10
	Overla	ap Analysis	11
		Annual Overlap	11 12
	Seaso Rangi	nal Shifting of Rangesng Distance	13 13

	Discussion	14
	Spatial Organization	14 16
	Literature Cited	18
2.	HABITAT SELECTION OF THE TROPICAL HARE	29
	AbstractIntroductionMethods	29 30 31
	Study AreaCapture of AnimalsRadio-Tracking and Home Range EstimationHabitat Use AnalysisHabitat Selection for the Establishment of Home RangesHabitat Selection within Home RangesHabitat Selection for Inactive and Active PeriodsActivity PatternsHabitat Type of Mortality Sites	31 32 33 35 36 37 38 38 38 39
	Results	40
	Home Range EstimatesHabitat Use AnalysisHabitat Selection for the Establishment of Home RangesHabitat Selection within Home RangesHabitat Selection for Inactive and Active PeriodsActivity PatternsHabitat Type of Mortality Sites	40 40 41 42 42 43 44
	Discussion	44
	Home Range Establishment Habitat Selection within Home Ranges Habitat Selection for Inactive and Active Periods Habitat Selection for Inactive and Active Periods Activity Patterns Conservation Implications Literature Cited Literature Cited	44 45 46 47 47
		51

3.	POPULATION ECOLOGY OF THE TROPICAL HARE	69
	AbstractIntroductionMethods	69 70 71
	Study Area	71
	Capture of Animals	72
	Age Assessment of Young Hares	73
	Radio-Tracking	74
	Survival Rates and Mortality Causes	76
	Density	77
	Population Characteristics	78
	Results	79
	Survival Rates and Mortality Causes	79
	Density	81
	Population Characteristics	81
	Population Effects	82
	Discussion	85
	Adult and Juvenile Survival	85
	Seasonal Survival and Predation	86
	Predation Mortality	88
	Poaching and Induced-Fire Mortality	88
	Conservation Implications	89
	Literature Cited	92
4.	CONSERVATION OF TROPICAL HARE POPULATIONS	102
	Abstract	102
	Introduction	102
	Results	103
	Geographic Range, Extent of Occurrence, and Area of	
	Occupancy	103
	Habitat Use	104
	Home Range and Temporal Ecology	105
	Survival and Cause-Specific Mortality	106
	Preliminary Data on Reproduction, Sex Ratios, and Density	106
	Threats for Tropical Hare Populations	107
	Conservation Actions in Place	108

Discussion
Guidelines for Conservation of Tropical Hares
Literature Cited
BIBLIOGRAPHY113

LIST OF TABLES

Table]	Page
1.1	Annual home range and core area sizes (ha) of adult tropical hares (<i>Lepus flavigularis</i>) in Llano Contreras, Oaxaca, Mexico, from May 2001 thru April 2003	22
1.2	Seasonal home range and core area sizes (ha) of adult female tropical hares (<i>Lepus flavigularis</i>) in Llano Contreras, Mexico, from May 2001 thru April 2003	23
1.3	Seasonal home range and core area sizes (ha) of adult male tropical hares (<i>Lepus flavigularis</i>) in Llano Contreras, Mexico, from May 2001 thru April 2003	24
2.1	Proportion (%) of habitat types (N = Nanchal, M = Morro, G = Grassland, S = Scrub) in seasonal home ranges (95% fixed kernel in km2) and telemetry locations of 17 adult tropical hares in Llano Contreras, Oaxaca, Mexico \dots	56
2.2	Proportion (%) of habitat types (N = Nanchal, M = Morro, G = Grassland, $S = Scrub$) in seasonal home ranges (95% fixed kernel in km2) and telemetry locations of 18 juvenile tropical hares in Llano Contreras, Oaxaca, Mexico	57
2.3	Compositional analysis of relative use of habitat types (N = Nanchal, M = Morro, G = Grassland, S = Scrub) by radio-marked tropical hares (<i>Lepus flavigularis</i>) in Llano Contreras, Oaxaca, Mexico, from May 2001 to April 2003	58
2.4	Proportion of habitat types for predator-caused mortality sites compared to the proportion of habitat use by radio-marked tropical hares, relative to the proportion of available habitat types in the 9.09-km2 study area polygon	59
3.1	Gain in body weight of six young tropical hares (<i>Lepus flavigularis</i>) captured and recaptured in Llano Contreras, Oaxaca, Mexico	96
3.2	Interval and annual survival rates for 25 adult (13 F, 12 M) radio-marked tropical hares (<i>Lepus flavigularis</i>) monitored at Llano Contreras, Oaxaca, Mexico, from February 2001 to July 2003	97
3.3	Cause-specific mortality rates of 51 radio-marked tropical hares (<i>Lepus flavigularis</i>) monitored at Llano Contreras, Oaxaca, Mexico, from February 2001 to July 2003 (n = 31 mortalities)	98

3.4	Interval survival rates for 35 juvenile (21 F, 14 M) radio-marked tropical hares (<i>Lepus flavigularis</i>) monitored at Llano Contreras, Oaxaca, Mexico, from February 2001 to July 2003
3.5	Proportion of adult female tropical hares (<i>Lepus flavigularis</i>) that were pregnant or lactating when captured at Llano Contreras, Oaxaca,
	Mexico
3.6	Hypothetical change for a population of 100 adult and juvenile female tropical hares (<i>Lepus flavigularis</i>). Average annual rate of change (?) equals 1.10 (i.e., 109.6/100), with a stable age distribution of 27% and 61% adults (i.e., 27/[27+73] and 33/[33+21]) during the wet and dry season, respectively 101

LIST OF FIGURES

Figure		Page
1.1	Location of the study area and the three populations of tropical hare	25
1.2	Home range overlap between pairs of adult tropical hares	26
1.3	Home ranges of adult female and male tropical hares	27
1.4	Core areas of adult female and male tropical hares	. 28
2.1	Historic distribution of the tropical hare	60
2.2	Tropical hare, Nanchal, Morro, Grassland, and Scrub	61
2.3	Study area polygon with available habitat types	62
2.4	Seasonal activity patterns from adult tropical hares	63
2.5	Habitat use in home ranges of adult and juvenile tropical hares compared to habitat availability in study polygon	64
2.6	Habitat use in telemetry locations of adult hares compared to habitat availability in home ranges	65
2.7	Habitat use in telemetry locations of juvenile hares compared to habitat availability in home ranges	66
2.8	Habitat use in telemetry locations of adult tropical hares during the inactive period compared to availability in home ranges	. 67
2.9	Habitat use in telemetry locations of adult tropical hares during the active period compared to availability in home ranges	68

CHAPTER 1

SPATIAL ECOLOGY INSIGHTS INTO THE MATING SYSTEM OF THE TROPICAL HARE

<u>Abstract</u>

The home range and core area size and overlap of tropical hares (*Lepus flavigularis*) in Oaxaca, Mexico, were studied by radio-tracking between May 2001 and April 2003. Annual home range and core area sizes averaged 55.5 ha (range = 27.6 - 99.7 ha) and 8.5 ha (range = 2.1 - 13.3 ha) for adult tropical hares of both sexes (n = 10) using the 95% and 50% fixed kernel isopleths, respectively. Seasonality did not influence range size for adult tropical hares: seasonal home ranges varied from 21.6 to 111.1 ha for females (n = 15) and from 23.8 to 165.9 ha for males (n = 16). Females shared with females portions of their ranges more than did males with males. Overlap with more than one individual suggests that tropical hares have a polygamous mating behavior, and a non-territorial social organization.

Key words: home range, *Lepus flavigularis*, mating behavior, Mexico, radio-telemetry, social organization, tropical hare.

Introduction

The tropical hare (*Lepus flavigularis*) is endemic to Oaxaca, Mexico, where only three small populations survive (Fig. 1.1). The species is jeopardized by habitat loss and fragmentation, as well as over-hunting, and the three isolated populations occur at sites not included within protected natural areas in Mexico (Chapman et al., 1990). Basic ecological information on the tropical hare is urgently needed to further develop management activities that will reduce threats to the species (CSBG, 1996).

Research on spatial ecology for populations of endangered wildlife has relied on home range analysis to infer aspects of social organization of study animals (Powell, 2000; Kernohan et al, 2001). Understanding spacing behavior and home range variation provides significant insight into a species' mating patterns and social behavior (Powell, 2000), both key components of any demographic analysis related to conservation. Home range size and spacing are influenced by population density and social organization (Komdeur and Deerenberg, 1997), and may vary with the availability and distribution of resources (Macdonald, 1983) or habitat quality (Ford, 1983). Therefore, knowledge of the social behavior of secretive wildlife may be enhanced with spatial ecology research (Parker and Waite, 1997).

Home range and core area size within the genus *Lepus* show high intraspecific variability (Hewson and Hinge, 1990; Wolfe and Hayden, 1996), probably because the social organization of hares is flexible and hares are adaptable in the use of food types in available habitats (Hulbert et al., 1996). Mountain hares (*Lepus timidus*) have large home ranges when living in harsh environments and smaller home ranges where resources are more abundant (Hewson and Hinge, 1990; Wolfe and Hayden, 1996). Also, snowshoe hares (*Lepus americanus*) may respond to a short-term increase of food by decreasing home range size (Boutin, 1984). Food and cover availability may regulate home range size for hares, but social behavior regulates sharing of feeding areas and spatial overlap (Boutin, 1984; Hulbert et al., 1996).

In home range studies, extensive overlap between mated pairs suggests monogamy, and range overlap between sexes with more than one individual of the opposite sex suggests polygamy (Powell,2000). No overlap within sexes suggests

territoriality (Powell, 2000). Home range studies indicate that hares are not territorial and their home ranges overlap (Flux, 1981a; Hewson and Hinge, 1990; Wolfe and Hayden, 1996), while behavioral observations suggest that most hares are either polygamous or promiscuous (Lechleitner, 1958; Flux, 1981b). In contrast, the white-sided hare (*Lepus callotis*), a species closely related to the tropical hare (Flux and Angermann, 1990; Cervantes and Lorenzo, 1997), is probably monogamous (Bednarz, 1977; Dunn et al., 1992; Best and Hill, 1993). Although it is common to observe pairs of tropical hares fleeing, feeding, or resting together throughout the year (Cervantes, 1993; Vargas, 2000), the sex and age of the observed dyads has not been determined and the mating strategy of the tropical hare is not well understood.

I conducted radio-tracking research to estimate home range and core area sizes and overlap, and analyzed the spatial relationships of the tropical hare population on the northeast rim of the Inferior Lagoon, Isthmus of Tehuantepec, Oaxaca, Mexico. Radiotracking of sympatric tropical hares allowed comparison of range size and overlap among adult individuals of the same and different sex to see if tropical hares are polygamous and share territories. I tested the following predictions: 1) home range size does not differ between sexes; 2) overlap occurs with more than one individual, indicating polygamy.

<u>Methods</u>

Study Area

The 16-km² study area of Llano Contreras is 2 km northwest from the locality of Montecillo Santa Cruz, Municipality of San Francisco del Mar Pueblo Nuevo, Oaxaca, Mexico, on the northeast rim of the Inferior Lagoon connected to the Gulf of Tehuantepec (Fig. 1.1). The study area encompassed savanna with native grasses

dominated by grama (*Bouteloua spp.*) and paspalum (*Paspalum spp.*), scattered trees dominated by morro (*Crescentia spp.*), sparse shrublands of nanche (*Byrsonima crassifolia*), and dense heterogeneous vegetation along streambeds (Perez-Garcia et al., 2001). Local people practice subsistence fishing and hunting and raise free-ranging cattle, horses, sheep, and goats in the study area. Climate is tropical with mean annual temperature of 25°C, mean annual rainfall of 800 mm (Garcia, 1964), and marked seasons. The rainy season is from May to October with an intra-estival drought in August, and the dry season is from November to April and is severe during late winter and early spring (Zizumbo and Colunga, 1982).

Capture of Animals

I captured 79 tropical hares by throwing handheld fishing nets over them. Nets were circular with a diameter of 3 to 4 m with 4 kg of weights attached to the perimeter. Hares were approached at night by a vehicle equipped with roof-mounted spotlights (Griffith, 1970) or by two persons riding horses with handheld spotlights. Captured hares were rapidly transferred from nets to a cotton bag.

I recorded sex, age (juvenile or adult), weight, standard measurements (total length, tail length, foot length, and ear length), and attached 20-g, 30-g, or 40-g VHF radio-collar transmitters (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA). Juveniles weighing less than 500 g were not collared because they were too small to comfortably wear one of the smallest radio-collars. Juveniles weighing \geq 500 g wore radio-collars with glued elastic added to allow the collar to expand and eventually fall off as hares grew larger (Forys and Humphrey, 1996). Female hares were sexed by identifying at the base of the clitoris a thin longitudinal canal that extends to the vulva.

Adult females have a well developed clitoris shaped like a flat, lanced tongue (Peroux, 1995). Adult females were palpated for embryos, and lactation was recorded (Peroux, 1995). Males were identified by the presence of a cylindrically shaped penis having a conic tip (Peroux, 1995). Individuals with external genitalia development and body weight ≥ 2500 g were considered adults. Six circular (2-mm diameter) clippings of skin from the ear were collected from captured hares and stored for subsequent genetic analysis. Fourteen hares were recaptured one or two more times to replace radio-collars with failing batteries. Capture efforts started on February 2001 and continued through November 2002. Forty-seven percent (24 of 51) of the radio-tracked animals were captured during February and April 2002. Capture and research activities were conducted in accordance with the approval of the Mexican Secretariat of Environment and Natural Resources (SEMARNAT), and from the Institutional Animal Care and Use Committee (IACUC) at The University of Massachusetts, Amherst, USA. (IACUC protocol number 22-02-07).

Radio-Tracking

Tropical hares of both sexes and different ages were radio-tracked from February 2001 through July 2003. Transmitters with a life span of 6 to 12 months had whip antennas and were motion- and mortality-sensitive. Radio-collared hares were followed on foot or by horseback, and located using a portable receiver (Telonics TR-4) equipped with a three-element Yagi antenna until observed directly. Hares hidden in vegetation were located by walking around the hare's location within a diameter of ≤ 5 m. (White and Garrot, 1990). Universal Transverse Mercator (UTM) coordinates were obtained using a portable Global Positioning System (GPS) unit (Garmin eTrex) with a precision

of 3 to 15 m (Garmin eTrex Manual). Locations were recorded when 6 to 12 satellites were available to increase the precision of the UTM coordinates.

Locations were taken throughout the 24-hour cycle. Every month, I located collared animals daily for one week, and the rest of the month I located animals one to three times per week. I collected one location per animal per telemetry session, except when some radio-collars malfunctioned or when radio-marked animals died. Consecutive telemetry sessions were separated by at least one day.

Home Range and Core Area Sizes

I analyzed telemetry data collected between May 2001 and April 2003 inclusive, and partitioned data into four seasons: wet 2001 (May 2001 thru Oct 2001), dry 2002 (Nov 2001 thru Apr 2002), wet 2002 (May 2002 thru Oct 2002), and dry 2003 (Nov 2002 thru Apr 2003) to estimate seasonal ranges and core areas for hares with \geq 22 fixes collected on separate days. Annual estimates for home ranges and core areas were calculated for adult females and males by pooling wet 2002 and dry 2003 data.

I calculated 95% and 50% fixed kernel ranges with least-squares cross-validation (Worton, 1989; Seaman and Powell, 1996; Powell, 2000) using the computer software ArcView 3.2 (Environmental Systems Research Institute Inc. (ESRI), Redlands, CA) with the Spatial Analyst (ESRI) and the Animal Movement Analysis (Hooge and Eichenlaub, 1997) ArcView extensions. A home range was defined as the 95% fixed kernel isopleth, and a core area as the 50% fixed kernel isopleth (Powell, 2000). The kernel is a nonparametric robust estimator that can compute home range boundaries with multiple centers of activity based on the complete utilization distribution, is minimally affected by autocorrelated data and outliers, and home range estimates stabilize with 30

to 50 points (Powell, 2000; Kernohan et al., 2001). 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).

Because most telemetry studies use the minimum convex polygon method (MCP; Mohr, 1947) to report home range size (Seaman et al., 1999), I calculated home range and core area size using the 95% and 50% MCP respectively with the harmonic mean method (Dixon and Chapman, 1980) to allow comparisons of my results with other published data. Nevertheless, I believe my data are better suited to the kernel method because MCP methods are sensitive to sample size and outliers and cannot calculate contours and multiple centers of activity (Kernohan et al., 2001).

I evaluated home range and core area size differences between adult females and adult males, and between wet and dry seasons, with Mann-Whitney U tests because data were not normally distributed (Sokal and Rohlf, 1981).

Home Range and Core Area Overlaps

Overlap was calculated as the area shared by two neighboring adult individuals using Minta's (1992) index, where overlap values potentially range between 0 and 1 with a mean overlap of 1 calculated for two home ranges of identical size exhibiting 100% overlap. ArcView 3.2 (ESRI) with the Spatial Analyst (ESRI) and the GeoProcessing Wizard (ESRI) ArcView 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 (Minta, 1992).

I compared home range and core area overlap indices for female-female, malemale, and female-male dyads with annual range estimates and for dyads present during each specific season (wet 2001, dry 2002, wet 2002, and dry 2003). Differences among dyad overlap was evaluated with nonparametric Kruskal-Wallis ANOVA tests because data were not normally distributed (Sokal and Rohlf, 1981).

The analysis of home range overlap failed to satisfy the assumption that all animals in the study area were monitored, because I could not capture all adult hares. Results may indicate minimum degree of overlap (Lariviere and Messier, 1998) because the possibility exists that I missed hares that had significant overlap.

Seasonal Shifting of Ranges

Range estimates from individuals with more than one seasonal home range were used to determine range shifting from season to season. I calculated Minta's overlap index between every two consecutive seasonal ranges of the same individual. Individuals were the unit of measurement, and when more than one overlap index was available for any individual data were averaged. I compared range shifting between adult females and males with a one-way ANOVA.

Ranging Distance

I calculated the maximum distance between two telemetry location points for tropical hares with \geq 15 locations, and defined it as the ranging distance (Sievert and Keith, 1985). I conducted a two-way analysis of variance ANOVA on the effect of sex and age on ranging distances of tropical hares.

Results

Radio-Tracking

From February 2001 through July 2003, 51 tropical hares of both sexes and different ages were radio-tracked. I obtained telemetry data to calculate home range and core area size estimates from 24 tropical hares: 9 adult females, 4 juvenile females, 8 adult males, and 5 juvenile males, with repeated measures of 10 individuals across seasons, over the two years of radio-tracking. Two males were captured and radio-tracked as juveniles and then recaptured and radio-tracked as adults.

Annual ranges were calculated for adult animals radio-tracked for periods of 7 to 12 months within a year by pooling seasonal data. I obtained annual home range and core area estimates for 5 adult female and 5 adult male hares during year 2002-2003 (May 2002 to April 2003). Number of locations used to estimate annual home ranges for each hare ranged from 40 to 70 for females with mean (\pm SD) 60 \pm 15 (n = 5), and from 46 to 77 for males with mean 62 \pm 12 (n = 5).

Seasonal home ranges and core areas were calculated for sympatric hares radiotracked for periods of 3 to 6 consecutive months. For adult hares, number of locations used to estimate seasonal home ranges varied from 23 to 38 for females with mean 33 ± 4 (n = 15), and from 22 to 42 for males with mean 32 ± 5 (n = 16). Number of locations of juvenile home ranges varied from 22 to 32 for females with mean 27 ± 5 (n = 4), and from 27 to 38 for males with mean 33 ± 4 (n = 5).

Fourteen hares were radio-tracked during only one season, six hares were radiotracked during two seasons, and two hares were radio-tracked during three and four seasons. Two male hares were captured and radio-tracked as juveniles for one season and recaptured and radio-tracked as adults for two and three seasons.

Home Range and Core Area Sizes

Annual Ranges

Though females tended to have smaller home range and core area size than males, no significant statistical differences were found. Annual home range and core area sizes averaged 55.5 ± 7.3 ha and 8.5 ± 1.2 ha for adult tropical hares of both sexes (n = 10), using the 95% and 50% fixed kernel isopleths respectively. Home range and core area sizes are reported as mean with standard errors throughout this paper.

Average annual home range for adult females was 44.7 ± 6.8 ha (n = 5) and for adult males was 66.3 ± 11.7 ha (U = 6, n₁ = n₂ = 5, *p* = 0.222). Average annual core area for adult females was 7.8 ± 1.4 ha and for adult males was 9.2 ± 2.2 (U = 8, n₁ = n₂ = 5, *p* = 0.421) (Table 1.1).

Seasonal Ranges

Seasonal home range and core area sizes varied widely for adult female (Table 1.2) and male (Table 1.3) tropical hares. Seasonal home range size for adult tropical hares ranged from 21.6 to 111.1 ha for females (n = 15) and from 23.8 to 165.9 ha for males (n = 16) according to the 95% fixed kernel isopleth.

Adult females tended to have larger seasonal home ranges during the first year (May 2001 to April 2002) than during the second year (May 2002 to April 2003) of study. The home range size for one radio-tracked hare during the wet 2001 season was 107.63 ha, and was the double compared to the average 54.8 ± 10.4 ha for five radio-tracked hares during the wet 2002 season, but with no statistical differences. Adult

females had larger mean home range size $(83.2 \pm 14.3 \text{ ha})$ for the dry 2002 season (n = 3) than mean home range size $(38.8 \pm 7.2 \text{ ha})$ for the dry 2003 season (n = 6) (One-way ANOVA, F = 9.974, *p* = 0.16).

Adult males showed little tendency for larger seasonal home ranges during the first year compared to the second year of study. Mean home range sizes of adult males were 87.4 ± 14.1 ha for the wet 2001 season (n = 2), and 51.5 ± 29.5 ha for the wet 2002 seasons (n = 6), with no statistical differences. Mean home range sizes of adult males were 84.4 ± 30.0 ha for the dry 2002 season (n = 4), and 60.4 ± 9.8 ha for the dry 2003 seasons (n = 4), with no statistical differences.

Seasonal core area size for an adult female was 14.8 ha for the wet 2001 season, and mean core area sizes for adult females were 9.2 ± 2.7 ha for the wet 2002 season, 12.1 ± 3.0 ha for the dry 2002 season, and 5.8 ± 0.7 ha for the dry 2003 season. Adult males had larger mean core area size $(16.3 \pm 3.5 \text{ ha})$ during the wet 2001 season than during the wet 2002 season $(8.8 \pm 2.6 \text{ ha})$, with significant differences (One-way ANOVA, F = 92.577, p = 0.000). Mean home range size of adult males was 10.2 ± 3.3 ha during the dry 2002 season, and 10.8 ± 1.6 ha during the dry 2003 season.

Home range size for juvenile tropical hares ranged from 11.5 to 35.9 ha for females (n = 4), and from 26.0 to 263.8 ha for males (n = 5). Core area size for juvenile tropical hares ranged from 1.5 to 7.9 ha for females, and from 2.4 to 50.1 ha for males.

Overlap Analyses

Annual Overlap

Annual overlap indices were calculated between adult tropical hares with annual home range estimates for year 2002-2003 (May 2002 to April 2003; 5 females and 5

males). Mean annual overlap in home ranges was 0.14 ± 0.03 (SE) between 18 dyads of tropical hares. Intersexual overlap occurred in 10 instances and intrasexual overlap in 8. 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), and mean overlap between male-male dyads (n = 5) was the lowest with a mean of 0.06 ± 0.01 (H = 5.75, df = 2, n = 18, p = 0.056).

Annual core area overlap between adult hares was rare and low and occurred in only two instances; overlap indices were 0.01 for a female-female dyad and 0.07 for a female-male dyad.

Within Season Overlap

Seasonal home range overlap occurred between and within sexes among one or more individuals, with mean overlap of 0.21 ± 0.02 between all dyads of adult hares (n = 75) over the two years of radio-tracking (Fig 1.2). Female-male overlap occurred for 40 dyads, compared to 20 female-female dyads and 15 male-male dyads. Mean overlap of male-male home dyads (0.08 ± 0.02) was significantly less than mean overlap of femalefemale dyads (0.26 ± 0.03 and female-male dyads (0.23 ± 0.03) (H = 11.67, df = 2, n = 75, p = 0.003). Adult males overlapped the home ranges of other adult males more on the outer boundaries and less on the inner areas, in comparison to adult females (Fig. 1.3)

Seasonal core area overlap was uncommon between adult hares of the same sex (Fig. 1.4), with only one male-male dyad (0.24) and four female-female dyads (0.08 \pm 0.03) overlapping over the two years of radio-tracking. Female-male dyads had 10 instances of core area overlap with a mean overlap of 0.14 \pm 0.04.

Juvenile home ranges overlapped home ranges of adult hares in 41 instances during the two years of radio-tracking. Juvenile home ranges overlapped home ranges of adult female hares with a mean overlap of 0.31 ± 0.07 for female-juvenile female dyads (n = 8), and of 0.26 ± 0.06 for female-juvenile male dyads (n = 9). Home range overlap between juveniles and adult males had a mean overlap of 0.16 ± 0.04 for male-juvenile female dyads (n = 13) and of 0.25 ± 0.06 for male-juvenile male dyads (n = 11). Core area overlap between juvenile and adult hares occurred in 9 instances with a mean overlap of 0.12 ± 0.03 . Juvenile hares had a mean overlap of 0.29 ± 0.09 for home ranges (n = 5), and of 0.28 ± 0.17 for core areas (n = 2).

Seasonal Shifting of Ranges

Seasonal shift in location of home range for adult hares was considerable, with males showing less home range stability than females. Mean overlap from season to season was higher for home ranges of adult females $(0.62 \pm 0.03, n = 5)$ than for adult males $(0.52 \pm 0.04, n = 5)$ (p = 0.088), and mean overlap for core areas were 0.36 ± 0.14 for adult females, and 0.25 ± 0.10 for adult males (p = 0.378).

Ranging Distance

I found a sex effect (F = 10.25, p = 0.003) and no age effect (F = 0.07, p = 0.797) on ranging distance. The mean ranging distance for males (1699 ± 170 m, n = 17) was farther than for females (1025 ± 118 m, n = 18). Juvenile males had the farthest mean ranging distance (1869 ± 293 m, n = 9), while juvenile females had the smallest (799 ± 106 m, n = 9). Adult males had a mean ranging distance of 1517 ± 193 m (n = 8) vs 1251 ± 188 m (n = 9) for adult females.

Discussion

Spatial Organization

Estimates of individual home range size (22 to 166 ha) for *Lepus flavigularis* were similar to values reported for the black-tailed jackrabbit (*Lepus californicus*) (16 to 140 ha) (Dunn et al., 1982; Best, 1996), a species closely related to the tropical hare (Flux and Angermann, 1990; Cervantes and Lorenzo, 1997), and fell within reported values in the literature for the genus *Lepus* (10 to 300 ha) (Flux and Angermann, 1990).

Home range and core area sizes of *Lepus flavigularis* are highly variable and may reflect behavioral acclimation to resource abundance and distribution in the study area (Hulbert et al., 1996; Komdeur and Deerenberg, 1997). Savannas from the Isthmus of Tehuantepec are rich in grass and forb diversity (Perez-Garcia, et al., 2001), and the tropical hare population in Llano Contreras may confront variable food and cover availability through space and time. Hulbert et al. (1996) found that mountain hares (*Lepus timidus*) living in a diverse landscape had range sizes varying from 5 to 116 ha according to resource availability within habitat type. Mean home range size for moorland hares was about double (17 ha) that of forest hares (10 ha) and pasture hares (7 ha) (Hulbert et al., 1996). However, I ran a multiple regression analysis to test for a relationship between habitat composition and home range size, and found correlation, suggesting that home range size variability is due to other factors.

Seasonality did not significantly influence range size of tropical hares, although the wet and dry seasons are marked in the study area. One possible explanation is that despite differences in weather conditions between seasons, tropical hares can adapt to obtain adequate food supplies and shelter throughout the year. Human activities

contribute to the spatial and temporal variability of resource abundance for tropical hares in Llano Contreras. Local people set fires to maintain grass shoots to feed their cattle. After the rains, grasses are tall but gradually loose their greenness as the dry season advances. The savanna is burned at the end of the dry season to allow sprout growth as soon as the first rains arrive. Also, tall grasses are burned during the dry season to maintain easy walking access on the savanna for local people that capture wildlife and collect fruits and wood. This practice provides tropical hares with patches of green biomass in the savanna throughout the dry season. Tropical hares also use the recently burned areas by easily digging out grass roots and eating green sprouts that grow within a few days.

Home range and core area did not differ statistically in size between adult female and male hares during the seasons or for annual estimates, though adult males tended to have larger ranges than adult females. A second tendency showed adult males to have less home range stability from season to season than adult females. Males also had larger ranging distances than females, and juvenile males showed the largest ranging distances. Sex may not significantly influence range size in tropical hares, but may influence movement patterns within range boundaries (Crooks and Van Vuren, 1996).

The analysis of home range overlap failed to satisfy the assumption that all of the hares in the study area were monitored, thus results indicate minimum degree of overlap (Lariviere and Messier, 1998) because the possibility exists that I did not include hares that had significant overlap. Nevertheless, the overlap analysis may provide valuable insights into the mating behavior of the tropical hare. High (\geq 80 %) home range overlap between female-male dyads that would indicate formation of mated pairs of tropical hares

was not detected. Intersexual overlap occurred with more than one individual of opposite sex, in accordance with the assumption that mated pairs are not formed. The presence of overlap shows that tropical hare may not have exclusive use of home ranges (Crooks and Van Vuren, 1996), although females shared portions of their ranges more than males. Also, during telemetry sessions I observed groups of 2 to 7 tropical hares feeding in the same patch of grass. However, negligible core area overlap may indicate that at least some portion of the home range is preferentially not shared with other hares.

Because intersexual overlap with more than one individual is associated with promiscuous mating systems (Greenwood, 1980), study results are consistent with a polygamous mating behavior and non-territorial social organization for *Lepus flavigularis*.

Conservation Implications

Mating behavior may affect gene flow and population growth, which are linked to the probability of population extinction (Cote, 2003). Basic knowledge on mating behavior in natural populations of tropical hare has much to contribute to their conservation (Parker and Waite, 1997). Mating systems place constraints on which individuals can breed and thus affects reproductive success of individuals and population growth (Komdeur and Deerenberg, 1997). When population size is small, the probability of extinction may be higher for monogamous than for polygamous species (Cote, 2003) as random mating increases the effective breeding population size (Parker and Waite, 1997). Insights into the mating behavior of *Lepus flavigularis* can make a significant contribution as a tool for predicting the potential effects of conservation actions on population size (Cote, 2003). Social systems are not fixed features of species but often show intraspecific variation that has conservation relevance (Komdeur and Deerenberg, 1997). Study results showed that seasonality did not explain the wide home range variation for *Lepus flavigularis*, and probably range variation may reflect individual behaviors of hares to adapt to resource availability. Home range variation was not explained by sex either, nevertheless study results suggest that further research is needed to address differences in spatial behavior of female and male tropical hares.

Literature Cited

- Bednarz, J. 1977. The white-sided jackrabbit in New Mexico: distribution, numbers, and biology in the grasslands of Hidalgo County. Unpublished manuscript. New Mexico Department of Game and Fish, USA. 33 pp.
- Best, T. L. 1996. Lepus californicus. Mammalian Species 530: 1-10.
- Boutin, S. 1984. Effect of late winter food addition on numbers and movements of snowshoe hares. Oecologia 62:393-400.
- CBSG, 1996. International Workshop for the Conservation of Mexican Lagomorphs in Danger of Extinction. Inform. Apple Valley, MN 55124 USA: IUCN/SSC Conservation Breeding Specialist Group.
- Cervantes, F. A. 1993. Lepus flavigularis. Mammalian Species 423:1-3.
- Cervantes, F. A., and C. Lorenzo. 1997. Morphometric differentiation of rabbits (*Sylvilagus* and *Romerolagus*) and jackrabbits (*Lepus*) of Mexico. Gibier Faune Sauvage 14:405-425.
- Chapman, J. A., J. E. C. Flux, A. T. Smith, D. J. Bell, G. G. Ceballos, K. R. Dixon, F. C. Dobler, N. A. Formozov, R. K. Ghose, W. L. R. Oliver, T. Robinson, E. Schneider, S. S. Stuart, K. Sugimurua, and Z. Changlin. 1990. Conservation action needed for rabbits, hares, and pikas. Pp. 154-168 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.). Chapter 14. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Cotè, I. M. 2003. Knowledge of reproductive behavior contributes to conservation programs. Pp. 77-92 in Animal behavior and wildlife conservation (Festa-Bianchet, M. and M. Apollonio, eds.) Chapter 6. Island Press. Washington, D. C. 380 pp.
- Crooks, K. R, and D. Van Vauren. 1996. Spatial organization of the island fox (*Urocyon littoralis*) on Santa Cruz Island, California. Journal of Mammalogy 77:801-806.
- Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

- Dunn, J. P., J. A. Chapman, and R. E. Marsh. 1982. Jackrabbits: *Lepus californicus* and allies. Pp. 124-145 in Wild mammals of North America: biology, management, and economics (Chapman, J. A. and G. A. Feldhamer, eds). The Johns Hopkins University Press. Baltimore, Maryland. 1147 pp.
- Flux, J. E. C. 1981a. Field observations of behavior in the genus *Lepus*. Pp. 377-394 in: Proceedings of the World Lagomorph Conference (Myers, K. and C. D. Mac Innes, eds.). August 12-16, 1979. University of Guelph, IUCN/SSC, World Wildlife Fund. Ontario, Canada. 983 pp.
- Flux, J. E. C. 1981b. Reproductive strategies in the genus *Lepus*. Pp. 155-174 in: Proceedings of the World Lagomorph Conference (Myers, K. and C. D. Mac Innes, eds.). August 12-16, 1979. University of Guelph, IUCN/SSC, World Wildlife Fund. Ontario, Canada. 983 pp.
- Flux, J. E. C., and R. Angermann. 1990. The hares and jackrabbits. Pp. 61-94 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.) Chapter 4. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Ford, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist 23:315-326.
- Forys, E. A., and S. R. Humphrey. 1996. Home range and movements of the Lower Keys Marsh Rabbit in a highly fragmented habitat. Journal of Mammalogy 77:1042-1048.
- García, E. 1964. Modificaciones al sistema de clasificación climática de Kopen (para adaptarlo a las condiciones de la República Mexicana). Instituto de Geografía, UNAM. México, D. F., México.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140-1162.
- Griffith, R. E., and J. Evans. 1970. Capturing jackrabbits by night-lighting. Journal of Wildlife Management 34:637-639.
- Hewson, R., and M. D. C. Hinge. 1990. Characteristics of the home range of mountain hares *Lepus timidus*. Journal of Applied Ecology 27:651-666.
- Hulbert, I. A. R., G. R. Iason, D. A. Elston, and P. A. Racey. 1996. Home-range sizes in a stratified upland landscape of two lagomorphs with different feeding strategies. Journal of Applied Ecology 33:1479-1488.

- Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to arcview. Ver 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA.
- Kernohan, B. J, R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 125-166 in: Radio tracking and animal populations. (Millspaugh J. J. and J. M Marzluff eds.) Chapter 5. Academic Press. San Diego, California. 474 pp.
- Komdeur, J., and C. Deerenberg. 1997. The importance of social behavior studies for conservation. Pp.262-276 in Behavioral approaches to conservation in the wild. (Clemmons, J. R. and R. Buchholz, eds.) Chapter 11. Cambridge University Press. Cambridge, United Kingdom. 380 pp.
- Larivière, S., and F. Messier. 1998. Spatial organization of a prairie striped skunk population during the waterfowl nesting season. Journal of Wildlife Management 62: 199-204.
- Lechleitner, R. R. 1958. Certain aspects of behavior of the black-tailed jack rabbit. The American Midland Naturalist 60:145-154.
- Macdonald, D. W. 1983. The ecology of carnivore social behaviour. Nature 301:379-384.
- Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. Ecological Applications 2:178-188.
- Mohr, C. O. 1947. Table of equivalent populations of North American mammals. American Midland Naturalist 37:223-249.
- Parker, P. G., and T. A. Waite. 1997. Mating systems, effective population size, and conservation of natural populations. Pp.243-261 in Behavioral approaches to conservation in the wild. (Clemmons, J. R. and R. Buchholz, eds.) Chapter 10. Cambridge University Press. Cambridge, United Kingdom. 380 pp.
- Pérez-García, E. A., J. Meave, and C. Gallardo. 2001. Vegetación y Flora de la Región de Nizanda, Istmo de Tehuatnepec, Oaxaca, México. Acta Botánica Mexicana 56:19-88.
- Péroux, R. 1995. Le liévre d'Europe. Bulletin Mensuel de l'Office National de la Chasse. No. 204. 96 pp.
- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65-110 in Research techniques in animal ecology, controversies and consequences (Boitani, L. and T. K. Fuller, eds.). Columbia University Press. New York. 442 pp.
- Seaman, D.E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.
- Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management 49:854-866.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Company. New York. 887 pp.
- Vargas, J. 2000. Distribución, abundancia y hábitat de la liebre endémica *Lepus flavigularis* (Mammalia: Lagomorpha) Tesis de Maestría en Biología Animal, Facultad de Ciencias, UNAM. México, D. F. 70 pp.
- Wolfe, A., and T. J. Hayden. 1996. Home range sizes of Irish mountain hares on coastal grassland. Biology and Environmental Proceedings of the Royal Academy 96B: 141-146.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.
- Zizumbo, D., and P. Colunga. 1982. Los Huaves. La apropiación de los recursos naturales. Universidad Autónoma Chapingo. México. 277 pp.

Adult Females	Number of	Fixed I	Kernel	Minimum Convex Polygon			
	Locations	Home Range 95 % isopleth	Core Area 50% isopleth	Home Range 95%	Core Area 50%		
AF45	70	37.78	3.80	31.76	5.99		
AF55	70	27.63	6.01	27.70	3.41		
AF56	70	60.75	11.75	51.13	10.36		
AF71	48	60.98	9.51	37.44	8.54		
AF73	40	36.21	7.69	21.17	3.63		
Mean <u>+</u> SE	60 <u>+</u> 7	44.7 <u>+</u> 6.9	7.8 <u>+</u> 1.4	33.8 <u>+</u> 5.1	6.4 <u>+</u> 1.4		

Table 1.1. Annual home range and core area sizes (ha) of adult tropical hares (*Lepus flavigularis*) in Llano Contreras, Oaxaca, Mexico, from May 2002 thru April 2003.

Adult	Number of	Fixed	Kernel	Minimum Convex Polygon			
Males	Locations	Home Range 95 % isopleth	Core Area 50% isopleth	Home Range 95%	Core Area 50%		
AM06	77	72.04	12.03	48.51	11.87		
AM22	68	46.95	6.18	48.28	5.45		
AM36	63	99.68	13.33	78.56	15.36		
AM41	46	78.60	12.42	70.16	9.32		
AM61	58	34.04	2.05	26.19	5.57		
Mean <u>+</u> SE	62 <u>+</u> 5	66.3 <u>+</u> 11.7	9.2 <u>+</u> 2.2	54.4 <u>+</u> 9.2	9.5 <u>+</u> 1.9		

			Fixed I	Kernel	Minimum Convex Polygon		
	Hare	n	Home Range Core Area		Home Range	Core Area	
Season	ID		95 % isopleth	50% isopleth	95%	50%	
Wet 2001	AF08	31	107.63	14.75	58.20	10.92	
	AF43	32	111.08	16.91	61.73	16.69	
	AF45	34	74.97	12.74	45.36	12.22	
Dry	AF48	23	63.68	6.75	41.85	4.64	
2002	Mean <u>+</u> SE		83.2 <u>+</u> 14.3	12.1 <u>+</u> 3.0	49.7 <u>+</u> 6.1	11.2 <u>+</u> 3.5	
	AF43	31	61.45	7.61	38.28	5.80	
	AF45	32	39.85	5.50	26.72	5.30	
	AF48	32	84.54	19.16	44.26	11.11	
Wet 2002	AF55	35	24.61	3.54	19.68	2.53	
	AF56	38	63.70	10.39	43.03	5.09	
	Mean <u>+</u> SE		54.8 <u>+</u> 10.4	9.2 <u>+</u> 2.7	34.4 <u>+</u> 4.8	6.0 <u>+</u> 1.4	
Dry 2003	AF45	38	32.60	5.49	22.21	3.95	
	AF55	35	21.62	4.89	12.38	3.49	
	AF56	32	52.68	6.87	35.01	3.94	
	AF71	34	67.26	6.13	39.48	10.00	
	AF73	33	33.20	7.91	18.29	3.34	
	AF75	31	25.36	3.33	20.78	1.88	
	Mean <u>+</u> SE		38.8 <u>+</u> 7.2	5.8 <u>+</u> 0.7	24.7 <u>+</u> 4.2	4.4 <u>+</u> 1.2	

Table 1.2. Seasonal home range and core area sizes (ha) of adult female tropical hares (*Lepus flavigularis*) in Llano Contreras, Oaxaca, Mexico, from May 2001 to April 2003.

			Fixed	Kernel	Minimum Convex Polygon		
Season	Hare ID	n	Home Range 95 % isopleth	Core Area 50% isopleth	Home Range 95%	Core Area 50%	
	AM06	35	73.30	12.87	61.53	7.18	
Wet 2001	AM24	22	101.57	19.77	45.30	16.60	
	Mean <u>+</u> SE		87.4 <u>+</u> 14.1	16.3 <u>+</u> 3.5	53.4 <u>+</u> 8.1	11.9 <u>+</u> 4.7	
	AM06	31	40.91	7.51	41.63	4.83	
	AM22	30	37.40	2.10	24.16	6.86	
Dry	AM39	31	93.31	16.01	46.52	19.65	
2002	AM41	31	165.90	15.12	94.02	20.98	
	Mean <u>+</u> SE		84.4 <u>+</u> 30.0	10.2 <u>+</u> 3.3	51.6 <u>+</u> 14.9	13.1 <u>+</u> 4.2	
Wet 2002	AM06	42	49.79	14.33	23.32	9.12	
	AM22	34	30.60	7.78	18.61	3.61	
	AM36	30	75.10	7.76	47.34	10.60	
	AM41	35	98.13	18.05	59.41	11.44	
	AM61	28	23.78	2.00	21.76	0.96	
	AM67	23	31.51	2.67	16.09	3.29	
	Mean <u>+</u> SE		51.5 <u>+</u> 12.3	8.8 <u>+</u> 2.6	31.1 <u>+</u> 7.3	6.5 <u>+</u> 1.8	
Dry	AM06	35	69.84	12.83	40.46	10.80	
2003	AM22	34	65.46	9.03	49.03	5.32	
	AM36	33	74.60	14.07	43.20	12.35	
	AM61	30	31.56	7.35	19.35	4.86	
	Mean <u>+</u> SE		60.4 <u>+</u> 9.8	10.8 <u>+</u> 1.6	38.0 <u>+</u> 6.5	8.3 <u>+</u> 1.9	

Table 1.3. Seasonal home range and core area sizes (ha) of adult male tropical hares (*Lepus flavigularis*) in Llano Contreras, Oaxaca, Mexico, from May 2001 to April 2003.



Figure 1.1 Location of the study area and the three populations of tropical hare. The study area was located at Llano Contreras in Oaxaca, Mexico. Numbers and circled areas in white show the distribution of three surviving populations of tropical hares (*Lepus flavigularis*). White arrows show areas of urbanization, overgrazed grasslands, and agricultural sites where tropical hares are no longer present.



Figure 1.2 Home range overlap between pairs of adult tropical hares. Mean home range overlap between adult tropical hare (*Lepus flavigularis*) dyads at Llano Contreras, Oaxaca, Mexico, for year 2002 – 2003 (black), wet 2001 (white), dry 2002 (dashed), wet 2003 (light gray), and dry 2003 (dark gray) seasons. The values over the bars indicate the number of overlapping dyads. Results indicate minimum degree of overlap because not all of the hares in the study area were monitored.



Figure 1.3 Home ranges of adult female and male tropical hares. Home ranges of adult female (a) and male (b) tropical hares (*Lepus flavigularis*) on Llano Contreras, Oaxaca, Mexico, during the wet season 2002. Home ranges were plotted using the 95% fixed kernel isopleth. ID number of hare is shown for each home range. Study area is represented by a polygon.



Figure 1.4 Core areas of adult female and male tropical hares. Core areas of adult female (blank) and male (dotted) tropical hares (*Lepus flavigularis*) on Llano Contreras, Mexico, during the wet season 2002. Core areas were plotted using the 50% fixed kernel isopleth. ID number of hare is shown for each core area. Study area is represented by a polygon.

CHAPTER 2

HABITAT SELECTION OF THE TROPICAL HARE

Abstract

The habitat selection of radio-marked tropical hares living in a savanna of the Isthmus of Tehuantepec in Oaxaca, Mexico, was studied between May 2001 and April 2003 to identify vegetation that should be target of conservation efforts. As indicated by compositional analysis, hares selected home ranges with relatively more grassy and sparse shrubby habitats and less dense vegetation. Within home ranges, hares used grassy habitats with sparse shrub or tree cover significantly more than grassy habitats with no cover. For resting, hares favored savanna with bushes of Byrsonima crassifolia that probably provide cover from predators, and for foraging, they favored savanna with scattered trees of *Crescentia* that may allow visual detection of predators. Tropical hares were most active during crepuscular and nocturnal hours and rested during the diurnal hours. No effects of sex and season on habitat selection were detected for adult tropical hares. Grassy habitats with no woody cover may pose higher predation risk for tropical hares than grassy habitats with scattered shrubs and trees. Preservation of savannas of native grasses with sparse woody cover is urgently needed for the conservation of remnant populations of tropical hares.

Key words: compositional analysis, conservation, habitat selection, *Lepus flavigularis*, Mexico, radio-telemetry, tropical hare.

Introduction

The tropical hare (*Lepus flavigularis*) is a rare Mexican endemic lagomorph of tropical coastal vegetation critically endangered by habitat loss and fragmentation (Anderson and Gaunt, 1962; Flux and Angermann, 1990). The former distribution of the tropical hare is not documented in detail, but Nelson (1909) estimated the leporid's historic range along the Mexican Pacific coast on the Isthmus of Tehuantepec from Salina Cruz in Oaxaca to Tonala in Chiapas, an area of perhaps 5,000 km² (Fig. 2.1). Vegetation inhabited by tropical hares has been destroyed and altered by urbanization, agriculture, and livestock (Flux and Angermann, 1990; Cervantes, 1993), thus the leporid remaining habitat exists where anthropogenic disturbances have been low (Lomolino and Channell, 1995). Three populations of tropical hare persist along savannas and grassy dunes on the shores of salt-water lagoons connected to the Gulf of Tehuantepec (Anderson and Gaunt, 1962; Flux and Angermann, 1990; Lorenzo et al., 2000). Plant diversity of savannas inhabited by the endangered lagomorph is high yet poorly studied (Perez-Garcia et al., 2001), and the leporid's extant range is not included within protected natural areas in Mexico. The need for investigation of habitat requirements and resource selection from tropical hare populations is urgent and essential for the management and conservation of the species and its remnant habitat (Garshelis, 2000; Marzluff et al., 2001).

Previous surveys indicate that tropical hares occur in grasslands with scattered shrubs and trees, open grassy shrublands, and coastal grassy dunes, but not in agriculture lands, deteriorated grasslands, or scrub (Lorenzo et al., 2000; Vargas, 2000; Lorenzo, 2001). Tropical hares are negatively affected by the degradation of savannas and are no

longer present in overgrazed grasslands for livestock or in continuous dense vegetation (Vargas, 2000; Lorenzo, 2001) (Fig. 1.1). Like most hare species, tropical hares seek shelter and concealment under shrubs and tall grasses during diurnal hours, feed mainly on grasses and forbs during crepuscular and nocturnal hours, and use open areas as runaways to escape from predator attacks (Flux and Angermann, 1990). Grassy habitats with scattered shrubs provide hares with both the visibility to detect predators, and the protective cover to reduce chances of being detected by a predator (Lechleitner, 1958; Longland, 1991).

I conducted radio-tracking research aimed to determine habitat selection of the tropical hare population on the northeast rim of the Inferior Lagoon, Isthmus of Tehuantepec, Oaxaca, Mexico. Radio-tracking of individual tropical hares allowed defining the total area used by each animal, and thus to investigate habitat selection (Garshelis, 2000; Marzluff et al., 2001) at different scales by employing compositional analyses (Aebischer et al., 1993). My predictions were that tropical hares would non-randomly select vegetation types to establish their home ranges. I expected that tropical hares would select grassy vegetation with sparse woody cover.

<u>Methods</u>

Study Area

Habitat use by tropical hares was assessed in the 9-km² study area of Llano Contreras located 2 km northwest from the locality of Montecillo Santa Cruz, Municipality of San Francisco del Mar Pueblo Nuevo, Oaxaca, Mexico, on the northeast rim of the Inferior Lagoon connected to the Gulf of Tehuantepec (Fig. 1.1). I distinguished four habitat types in the study area (Fig. 2.2): (1) Nanchal – savanna with sparse cover of shrubs of Byrsonima crassifolia and grass and forb understory (2) Morro savanna with the woody component dominated by the tree Crescentia spp and various species of shrubs, and grass and forb understory (3) Grassland – savanna plains dominated by grasses and forbs from the Poaceae Family (e.g., grama, Bouteloua spp., and paspalum, *Paspalum spp.*) with no woody cover, and (4) Scrub – dense vegetation along intermittent streambeds or as small patches within other vegetation types, characterized by a nearly continuous cover of shrubs and trees (Perez-Garcia et al., 2001). Nanchal has higher density of woody plant cover than Morro. Local people practice subsistence hunting and raise free-ranging cattle, horses, sheep, and goats in the study area. Climate is tropical with mean annual temperature of 25°C, mean annual rainfall of 800 mm (Garcia, 1964), and marked seasons. The rainy season is from May to October with an intra-estival drought in August, and the dry season is from November to April and is severe during late winter and early spring (Zizumbo and Colunga, 1982). Lowlands may flood during the rains after prolonged or heavy precipitation. Native terrestrial mammals associated with the tropical hare and observed during the study were cottontail rabbits (Sylvilagus floridanus), armadillos (Dasypus novemcinctus), skunks (Mephitis macroura), opossums (Didelphis marsupialis), mouse opossums (Marmosa canescens), gray foxes (Urocyon cinereoargenteus), racoons (Procyon lotor), and coyotes (Canis latrans) (Cervantes and Yepez, 1995; Lorenzo, 2000). Gray foxes and covotes are native predators of tropical hares.

Capture of Animals

I captured and radio-marked 51 tropical hares in Llano Contreras from February 2001 through November 2002. I recorded sex, age (juvenile or adult), weight, and

standard measurements (total length, tail length, foot length, and ear length), and attached 20-g, 30-g, or 40-g VHF radio collar transmitters (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA). Females (F) were identified by a thin longitudinal canal at the base of the clitoris that extends to the vulva. Adult females were palpated for embryos, and their fur around nipples was examined for suckling (Peroux, 1995). Males (M) were identified by the presence of a cylindrically shaped penis having a conic tip (Peroux, 1995). Individuals with external genitalia development and body weight ≥ 2500 g were considered adults. Six circular (2-mm diameter) clippings of skin from the ear were collected from captured hares and stored for subsequent genetic analysis. Capture and research activities were conducted in accordance with the approval of the Mexican Secretariat of Environment and Natural Resources (SEMARNAT) and from the Institutional Animal Care and Use Committee (IACUC) at The University of Massachusetts, Amherst, USA. (IACUC protocol number 22-02-07).

Radio-Tracking and Home Range Estimation

I radio-tracked tropical hares from February 2001 through July 2003 with a portable receiver (Telonics TR-4) equipped with a three element Yagi antenna. Hares were located by direct observation or, if hidden in vegetation, by homing on radio-signals to within an area with a diameter of ≤ 5 m. (White and Garrot, 1990). At these locations, I recorded the position (Universal Transverse Mercator coordinates; UTM), hare behavior (active or inactive), time (hour and minutes), and habitat type (Nanchal, Morro, Grassland, or Scrub).

Transmitters were mortality sensitive and thus allowed for location of carcasses or remains of radio-marked hares killed by predators. At these locations, I recorded the

position (Universal Transverse Mercator coordinates; UTM), carcass condition, time when found (hour and minutes), and habitat type (Nanchal, Morro, Grassland, or Scrub).

I used a portable Global Positioning System (GPS) unit (Garmin eTrex) with a precision of 3 to 15 m (Garmin eTrex Manual) to obtain the UTM coordinates, and locations were recorded when 6 to 12 satellites were available to improve precision. Locations were taken at random times throughout the 24-hour cycle. Every month, I located collared animals daily for one week, and the rest of the month I located the animals one to three times per week.

I determined activity or inactivity of tracked hares by listening to the individual's radio-signal, and corroborated different behaviors (i.e. resting or foraging) by direct observation. Radio-transmitters 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-second interval the radio-signal heard was stable, and active if the signal was chaotic. I collected one location per animal, per telemetry session, and consecutive telemetry sessions were separated by periods of at least one activity shift.

I partitioned data into four seasons: wet 2001 (May 2001 thru Oct 2001), dry 2002 (Nov 2001 thru Apr 2002), wet 2002 (May 2002 thru Oct 2002), and dry 2003 (Nov 2002 thru Apr 2003) to estimate seasonal home ranges for hares. Mean number of locations used to estimate seasonal home ranges was 32 ± 4 (SD) for adult hares (n = 31 ranges) and 22 ± 9 (SD) for juvenile hares (n = 19 ranges).

I calculated home ranges as the 95%-fixed-kernel isopleths with least-squares cross-validation (Worton, 1989; Seaman and Powell, 1996; Powell, 2000) using the

computer software ArcView 3.2 (Environmental Systems Research Institute Inc. (ESRI), Redlands, CA) with the Spatial Analyst (ESRI) and the Animal Movement Analysis (Hooge and Eichenlaub, 1997) ArcView extensions. The fixed kernel is a robust estimator that satisfies requirements for analysis of my data because it is a nonparametric estimator that computes home range boundaries based on an utilization distribution (Powell, 2000; Kernohan et al., 2001). Therefore, point locations can be accurately transformed into the area used by an animal with the fixed kernel (Seaman and Powell, 1996; Seaman et al., 1999).

Habitat Use Analysis

I delineated the boundaries of habitat types in Llano Contreras by walking around vegetation patches and logging UTM coordinates with a portable GPS unit (Garmin eTrex). To create the habitat type map, point data were converted into polygon data using software ArcView 3.1 (ESRI) with the Spatial Analyst (ESRI) extension (Fig. 2.3). Home range estimates of tropical hares were overlaid on the habitat type map. The total area for each habitat type within home ranges of individual hares, as well as the habitat type for every telemetry location, were determined using software ArcView 3.1 (ESRI) with the Spatial Analyst (ESRI) and GeoProcessing Wizard (ESRI) extensions.

Compositional analysis (Aebischer et al., 1993) was conducted using multivariate analysis of variance (MANOVA) with SPSS 8.0 multivariate general linear model (GLM) to investigate habitat selection at two scales. First, I determined if tropical hares selected or avoided certain habitats in establishing a home range by comparing habitat composition in home ranges with habitat composition in the study area (Aebischer et al.,

1993). Second, I determined if tropical hares had differential use of habitat types within their home range by comparing habitat composition of telemetry locations with available habitat types within each individual's home range (Aebischer and Robertson, 1992; Aebischer et al., 1993), and distinguished habitat selection during the periods of resting and foraging (Revilla et al, 2000). Wilk's lambda statistic tested for overall selection, and was compared with the F distribution and p value calculated by SPSS. When selection was indicated, contrasts comparing individual habitat types were conducted using Student's t tests (Erickson et al., 2001). I treated data for adult and juvenile hares separately in compositional analyses.

The proportion of a missing habitat within a hare's home range was set to 0.001, one order of magnitude less than the detectable minimum in my data (Aebischer et al., 1993).

I ranked habitat types in order of use by calculating the log-ratio differences for all possible pairs of habitat types and displayed them in a matrix (Aebischer and Robertson, 1992). Grassland was not always represented in a hare's home range, so for a given pair of habitat types the mean log-ratio difference in the matrix was based only on the home ranges containing both types (Aebischer and Robertson, 1992).

Habitat Selection for the Establishment of Home Ranges

First, I analyzed both years of data with MANOVA to test for the effects of sex and season on habitat composition of home ranges vs. the study area. I treated as units of analysis the 31 seasonal home ranges from 17 adult hares present during the wet 2001 (1 F, 2 M), dry 2002 (3 F, 4 M), wet 2002 (5 F, 6 M), and dry 2003 (6 F, 4 M) seasons (Table 2.1). Ten adult hares had more than one seasonal home range, and I treated them

as independent in this first MANOVA. No effects of sex and season on habitat use were detected, therefore I conducted a second MANOVA using individual hares as experimental units and reported these results. The 17 adult hares (9 F, 8 M) were the experimental units, because I averaged log-ratio differences across seasons for the 10 individuals (5 F, 5 M) with more than one seasonal home range.

To determine if juvenile hares showed no habitat selection in the establishment of home ranges, I conducted a MANOVA using 18 juvenile hares (11 F, 7 M) as experimental units and averaged log-ratio differences across seasons for a juvenile male that had two seasonal home ranges (Table 2.2).

I determined available habitat (Erickson et al., 2001) as a 9.09 km² concave polygon delineated to include the merging of 31 seasonal home ranges (95% fixed kernel, Chapter 1) from the 17 adult hares and 19 seasonal home ranges from the 18 juvenile hares (Fig. 2.3). I defined habitat use of each radio-marked animal as the habitat composition of its home range (Johnson, 1980). I classified habitat types in four categories: Nanchal, Morro, Grassland, and Scrub (Fig. 2.3).

Habitat Selection within Home Ranges

I analyzed both years of data with MANOVA to test for the effects of sex and season on habitat use within home ranges, and used the 17 adult hares (9 F, 8 M) as experimental units. To determine if juvenile hares showed no habitat selection within home ranges, I conducted a MANOVA using 18 juvenile hares (11 F, 7 M) as experimental units (Table 2.2).

Available habitat was defined for each individual as the habitat composition within the seasonal home range. Habitat use was described for each individual by the distribution of locations within the seasonal home range (Aebischer and Robertson, 1992). In this analysis I included habitat type categories Nanchal, Morro, and Grassland, and excluded Scrub, because hares avoided Scrub in establishing a home range according to my previous data analysis, and Scrub was absent in the locations distribution of most hares.

Habitat Selection for Inactive and Active Periods

I analyzed data from the 17 radio-tracked adult hares (9 F, 8 M) to distinguish variation in habitat types they selected during inactive and active periods by conducting two MANOVA.

Available habitat was defined for every individual as the habitat composition within the seasonal home range. Habitat use was described for every individual by the distribution of locations within the seasonal home range during each period: inactive or active (Aebischer and Robertson, 1992; Revilla et al., 2000). I included Nanchal, Morro, and Grassland, and excluded Scrub, in this analysis.

Activity Patterns

I created graphs of activity patterns using both years of data (May 2001 to April 2003) from radio-signals of 26 adult hares (16 F, 10 M), and plotted mean proportion of active radio-signals vs. time of the day.

The length of active and inactive periods was assessed separately by sex and season, according to the onset and cessation of activity in the activity patterns graph (Fig 2.5). Then, I divided the telemetry locations data of every animal according to the length of the active and inactive periods.

Adult females' resting period was from the 6:00 to 16:59 hours during the wet season and from the 7:00 to 17:59 hours during the dry season. The foraging period for adult females was from the 17:00 to 5:59 hours during the wet season, and from the 18:00 to 6:59 hours during the dry season. Adult males' resting period was from the 7:00 to 17:59 hours during the wet season and from the 8:00 to 18:59 hours during the dry season. The foraging period for adult males was from the 18:00 to 6:59 hours during the dry season and from the 8:00 to 18:59 hours during the dry season. The foraging period for adult males was from the 18:00 to 6:59 hours during the wet season and from the 18:00 to 6:59 hours during the dry season.

Habitat Type of Mortality Sites

Habitat type was determined for 25 sites where I located the remains of radiocollared hares killed by predators. I assumed that the hare was killed where the transmitter was found. I assumed predation as the cause of death when the carcass was partially or totally eaten, and the radio-collar had blood stains, hare hair, tooth marks, and signs of being chewed (twisted antenna, eaten elastic). The site was examined for signs from potential predators (gray foxes, coyotes) as tracks and scats, but with no results.

I compared the proportion of predator-caused mortality sites that fell in each habitat type, to the proportion of habitat use by radio-marked tropical hares, and to the proportion of habitat availability in the 9.09 km² study area polygon. The proportion of habitat used by hares was estimated as the average percentage of telemetry locations of individual hares in each habitat type.

Results

Home Range Estimates

Seasonal home range size for adult tropical hares ranged from 0.22 to 1.11 km^2 for females (n = 15) and from 0.24 to 1.66 km^2 for males (n = 16), with repeated measures of 10 individuals across seasons, over the two years of radio-tracking (Table 2.1). I determined habitat compositions of 31 seasonal home ranges from 17 adult tropical hares (9 F, 8 M).

Female juveniles had seasonal home ranges from 0.07 to 0.49 km² (n = 11), and male juveniles from 0.11 to 2.64 km² (n = 8) (Table 2.2). I determined habitat compositions of 19 seasonal home ranges from 18 juvenile tropical hares (11 F, 7 M).

Habitat Use Analysis

The most common habitat types at the study area were Nanchal and Morro, and represented 43% and 36% of the available area in the study area polygon (Fig. 2.5). Nanchal was present in the seasonal home ranges of all adult and juvenile hares. Morro was present in the seasonal home ranges of all adult and juvenile hares except in one seasonal home range of an adult male. Nanchal was present in the locations distributions of all hares, with a mean percentage of 49% for the 17 adult hares (Fig. 2.6) and 49% for the 18 juvenile hares (Fig. 2.7). Morro was present in the locations distributions of all adult females and all juvenile males, but was absent in the locations distributions of two adult males and one juvenile female. The mean percentage of locations in Morro was 43% for adult hares and 45% for juvenile hares.

Grassland was the least common habitat type and represented 6% of the available area. Grassland was absent in 53% (10 of 19) of seasonal home ranges of juvenile hares.

The mean percentage of locations in Grassland was 7% for adult hares and 5% for juvenile hares.

Scrub represented 16% of the available area and was absent in most of the seasonal locations distributions of adult and juvenile hares. Results show that the mean percentage of locations found in Scrub was 1% for adult and juvenile hares. Scrub was absent in 47% (9 of 19) of seasonal home ranges of juvenile hares.

Habitat Selection for the Establishment of Home Ranges

The proportions of habitat types used for home range establishment of adult and juvenile hares differed from available habitat types in the study area (Fig. 2.5). Wilk's lambda was $\lambda = 0.373$ (exact F _[3, 14] = 7.860, p = 0.003) indicating significant habitat selection for home range establishment of adult hares (Table 2.3). Morro was the most used habitat followed by Nanchal and Grassland, but relative to one another the utilization of Nanchal, Morro, and Grassland did not differ (p > 0.1). Scrub was the least used habitat type and was significantly underused relative to Nanchal (t = 4.623, df = 16, p = 0.000), Morro (t = 4.329, df = 16, p = 0.001), and Grassland (t = 2.161, df = 16, p = 0.019).

Wilk's lambda $\lambda = 0.279$ (exact F _[3, 15] = 12.948, p = 0.000) indicated significant habitat selection for the establishment of juvenile home ranges (Table 2.3). Morro was the most used habitat followed by Nanchal, but the utilization of Nanchal relative to Morro did not differ significantly (p > 0.1). Scrub and Grassland were the least used habitat types and the utilization of Grassland relative to Scrub did not differ significantly (p > 0.1). Scrub was significantly underused relative to Nanchal (t = 5.848, df = 17, p =

0.000) and Morro (t = 6.265, df = 17, p = 0.000), as was Grassland relative to Nanchal (paired t = 3.568, df = 17, p = 0.002) and Morro (paired t = 3.532, df = 17, p = 0.003). Habitat Selection within Home Ranges

The proportions of habitat types of telemetry locations were different from available habitat types in home ranges of adult (Fig. 2.6) and juvenile (Fig. 2.7) hares, particularly for Nanchal and Scrub for adult hares and Nanchal, Morro, and Scrub for juvenile hares. Wilk's lambda $\lambda = 0.484$ (exact F _[2, 15] = 8.011, *p* = 0.004) indicated significant overall selection for habitat use within home range of adult hares. According to compositional analysis, Nanchal was more used than Morro but the utilization of Nanchal relative to Morro did not differ significantly (paired *t* = 1.999, df = 16, *p* = 0.063) (Table 2.3). Grassland was the least used habitat, and was less used relative to Nanchal (*t* = 3.682, df = 16, *p* = 0.002) than to Morro (*t* = 2.869, df = 16, *p* = 0.011).

Wilk's lambda was $\lambda = 0.675$ (exact F _[2, 16] = 3.847, p = 0.043) and indicated significant overall selection within habitat use of juvenile hares (Table 2.3). Nanchal was the most used habitat followed by Morro, but the utilization of Nanchal relative to Morro did not differ significantly from random (p > 0.1). Grassland was less used relative to Nanchal (t = 2.133, df = 17, p = 0.048), but the utilization of Grassland relative to Morro did not differ (p > 0.1).

Habitat Selection for Inactive and Active Periods

Habitat use within home ranges of adult tropical hares was linked to their activity patterns (Table 2.3). Adult hares showed habitat selection in their home ranges during both inactive ($\lambda = 0.162$, exact F _[2, 15] = 38.670, *p* = 0.000) and active ($\lambda = 0.528$, exact F _[2, 15] = 6.709, *p* = 0.008) periods. Nanchal was the most used habitat type during the

inactive period (Fig. 2.8). Inactive hares significantly favored Nanchal relative to Morro (paired t = 3.945, df = 16, p = 0.001) and Grassland (t = 8.913, df = 16, p = 0.000). Morro was significantly more used relative to Grassland (t = 3.967, df = 16, p = 0.001) during the inactive period. In contrast, Morro was the most used habitat type during the active period (Fig. 2.9). Active hares made significantly more use of Morro relative to Nanchal (paired t = -3.015, df = 16, p = 0.008) and Grassland (t = 2.903, df = 16, p = 0.010) (Fig. 2.9). The utilization of Nanchal relative to Grassland was not different form random (t = 2.034, df = 16, p = 0.059) for active hares. Thus, grassland was less used during the inactive period when compared to the active period.

Activity Patterns

From May 2001 through April 2003, activity pattern monitoring was performed on 26 adult hares (16 F, 10 M) yielding a total of 1698 recordings of activity. Tropical hares were clearly crepuscular and nocturnal, and daily activity patterns were similar for both sexes (Fig. 2.4). Tropical hares began activity at dusk and ceased at dawn. Daily activity of males tended to start and end approximately 1 hour later than that of females. Activity during the dry season tended to start and end approximately 1 hour later than activity during the wet season. Tropical hares spent the diurnal hours resting, although radio-signals during this period indicated that animals did not sit motionless in their forms. The average percentages of diurnal activity for adult females were of 48% and 47% during the wet and dry seasons respectively, and that of adult males were of 56% and 57%.

Habitat Type of Mortality Sites

Grassland was the least common habitat type in the study area polygon, but 30% of mortality sites of 10 radio-marked adult hares that were killed by predators fell in Grassland (Table 2.4). Nanchal was the most common habitat type and had the highest proportion of mortality sites of tropical hares with 50 - 53%. Morro and Nanchal were habitat types favored by tropical hares, but the proportion of mortality sites of predator-killed hares was lower in Morro when compared to Nanchal, particularly for adult hares (20%). From fifteen juvenile tropical hares killed by predators, six were killed in Morro, eight in Nanchal, and one in Scrub.

Discussion

Home Range Establishment

Study results supported expectations that tropical hares would select habitat types with grass and shrubs when establishing a home range. The fact that Nanchal and Morro were present in the home ranges of all study animals may indicate that these vegetation types were most important to satisfy habitat requirements of the studied tropical hare population.

Adult hares respond with flexibility in their utilization of the available vegetation communities in the study area for home range establishment (Hulbert et al., 1996a,b). Home ranges that encompass areas of Nanchal, Morro, and Grassland benefit adult tropical hares with a mix of habitats types where hares may search for required forage and protection (Lechleitner, 1958; Longland, 1991; Marin et al., 2003).

Juvenile hares selected grassy and shrubby habitats, and avoided grassy habitats with no woody cover probably because they rely on concealment as behavior to avoid

predation when too young to outrun predators (Lechleitner, 1958; Aanes and Andersen, 1996).

Hares avoid Scrub when establishing their home ranges probably because continuous dense vegetation conceals ambushing predators such as gray foxes (Lechleitner, 1958; Trapp and Hallberg, 1975), and high density of vegetation impedes fleeing as escape strategy for hares (Lechleitner, 1958). It is most probable that Scrub patches within home ranges of tropical hares were inevitably included when individuals selected adjacent habitat types (Garshelis, 2000). However, I could observe that tropical hares sometimes used Scrub when it was next to sparse vegetation types (Lechleitner, 1958; Daniel et al., 1993). Some individuals were occasionally found hiding on Scrub edges adjacent to Nanchal, Morro, or Grassland, and flushed hares ran to sparse vegetation but not toward the inside of Scrub patches.

Habitat Selection within Home Ranges

Tropical hares may select Nanchal and Morro because these sparse vegetation types allow hares to feed, rest, hide, detect predators, and escape from attacks (Lechleitner, 1958). Nanchal and Morro have grass and forbs for food and shrubs and trees for cover from predation risk. But Grassland with no woody cover may pose higher predation risk for hares than Nanchal and Morro. Although Grassland was the least common habitat type in the study area, a high proportion of mortality sites of radiomarked adult hares that were killed by predators fell in this habitat type.

Grassland in the study area is left without the protection from woody cover because grassy habitats are constantly suffering fires induced by local people during the dry season. Burned Grassland turns into a bare habitat with little food and almost no

cover, and growing Grassland provides green biomass but very little cover for tropical hares (Fig. 2.2d). In contrast, shrubs and trees persist as protective cover for hares after fires in Nanchal and Morro.

I excluded Scrub from the compositional analyses of habitat selection within home ranges because results indicated that hares avoided Scrub in establishing a home range, and scrub was absent in the locations distribution of most adult and juvenile hares with Scrub in their home ranges.

Habitat Selection for Inactive and Active Periods

Habitat use by inactive or active periods showed that adult tropical hares favor Nanchal for resting and Morro for foraging. Tropical hares rest during diurnal hours and probably select Nanchal for its shrubby cover that allows hares that lie in forms not readily noticeable to predators (Lechleitner, 1958; Sievert and Keith, 1985). During daylight hours, flushed hares evade pursuing predators between shrubs in short distances inside Nanchal. In contrast, tropical hares forage during crepuscular and nocturnal hours and probably select Morro for having lower shrub density than Nanchal, thus allowing better visibility for detecting predators from the distance (Lechleitner, 1958, Daniel et al., 1993).

Foraging in Morro may be a behavior to diminish or avoid predation risk when hares are active (Rohner and Krebs, 1996). Predation risk was assumed to be lower in grasslands with scattered large shrubs than in shrublands for foraging black-tailed jackrabbits (*Lepus californicus*; Marin et al., 2003). In this study, the proportion of mortality sites of radio-marked adult tropical hares that were killed by predators was

lower in Morro when compared to Nanchal and Grassland, and more juvenile tropical hares were killed by predators in Nanchal vs. Morro.

Activity Patterns

Tropical hares were most active during crepuscular and nocturnal hours and rested during the diurnal hours, probably to minimize daytime predation as most hare species do (Cowan and Bell, 1986). Onset and cessation of activity of hares were related to sunset and sunrise, respectively. Thus, daily activity patterns of hares were related to photoperiod length. Photoperiod differences between the wet and dry seasons were not very marked in the study area. Sunrise and sunset differences between dry and wet seasons were less than 1 hour. Ambient temperatures are hotter and drier in the dry season compared to the wet season in the study area. Tropical hares may start activity later in the dry season to avoid hotter temperatures. Tropical hares spent the diurnal hours sitting in their forms, and most diurnal activity probably resulted from grooming and reingestion behaviors (Flux, 1981).

Conservation Implications

The present research on habitat selection by radio-marked tropical hares showed that savannas with a native structure of grass understory and scattered overstory of bushes and trees (i. e. *Byrsonima crassifolia* and *Crescentia*) are vegetation communities that need to be preserved for the survival of tropical hare populations. The extant range of the tropical hare is jeopardized by habitat alteration and degradation, and savanna protection is urgently needed for the conservation of remnant populations of tropical hares.

The number of native grass and forb species found in savannas from the Isthmus of Tehuantepec is very rich (Perez-Garcia, 2001), but introduction of exotic grasses and human induced fires are reducing this diversity (G. Davidse and M. Sousa, personal communication). Plant diversity found in the study area is important yet poorly studied, and native vegetation structure may be degraded by ongoing cattle-raising activities (Perez-Garcia, 2001). Grassland with little woody cover for protection may pose higher predation risk for tropical hares than grassy habitats with scattered shrub and tree cover. Coyotes and gray foxes, native predators of hares, may be favored by human-altered and deteriorated habitats (Fritzell and Haroldson, 1982).

Fire is a major factor in the maintenance of savannas (McPherson, 1997), but in the Isthmus of Tehuantepec fire frequencies have been accelerated by cattle-raising activities and savannas are deteriorating as a result. Savanna grasses are well adapted to periodic fires and may rapidly recolonize burned areas, but native grasses may compete and be excluded by exotic grasses during germination, emergence, and growth (McPherson, 1997). Few juvenile woody plants can survive even low intensity fires although most savanna woody plants are resistant to surface fires when they are mature (McPherson, 1997). Subjecting savannas in the Isthmus of Tehuantepec to accelerated fire frequencies (more than once per year) may strongly reduce woody plant cover. In North American savannas, mesquite (*Prosopis*) bushes are inconspicuous in areas burned five times per decade, in contrast to scattered mesquite bushes in areas burned twice per decade (McPherson, 1997).

The preservation of native vegetation is essential for conservation of endangered populations of lagomorphs, because leporid species may exclude each other when habitat

alteration favors the species better adapted to changed conditions (Flux and Angermann, 1990). For example, black-tailed jackrabbits (*Lepus californicus*) and white-sided jackrabbits (*Lepus callotis*) may coexist in open grassy plains with mesquite, cacti, and shrubs in arid regions, whereas in agricultural lands and deteriorated grasslands black-tailed jackrabbits exclude white-sided jackrabbits (Dunn et al., 1982; Daniel et al., 1993; Best, 1996).

Tropical hares are relatively more abundant than rabbits in savannas that had not been severely altered (Lorenzo et al., 2000; Lorenzo, 2001). In contrast, tropical hares were absent in disturbed savannas converted into lands for raising cattle, agriculture lands, and human settlements, whereas rabbits were present although in relatively low densities (Lorenzo et al., 2000; Vargas, 2000; Lorenzo, 2001; Santis, 2002) (Fig. 1.1). This study showed that savannas with native grasses and bushes of *Byrsonima crassifolia* and trees of *Crescentia spp*. are key habitats required for the conservation of the tropical hare. Further research is needed to investigate if rabbits establish on deteriorated savannas that tropical hares are unable to inhabit, or if rabbits exclude tropical hares from altered savannas.

The tropical hare population in this study persists in a native savanna where disturbance induced by humans was relatively low in the past, but unfortunately, low disturbance trends in the region are vanishing and certainly jeopardizing future survival of tropical hares if conservation strategies are not implemented soon.

During the two years of the study, the savanna suffered a rapid increase in disturbance induced by local people. The number of corrals for cows and horses gradually increased and covered the totality of the study area and beyond, and ranchers

caused fires that covered great extensions of the savanna every dry season in order to induce growth of green forage for cattle.

Interestingly, local people with low economic income obtain resources from the savanna such as meat from wild mammals and reptiles, wild fruits (i. e. from *Byrsonima crassifolia*), dry wood for fuel, and plant materials for houses and fence posts. Local people do recognize and appreciate the savanna's environmental services and may benefit from educational campaigns oriented toward conservation management of the tropical hare's remnant habitat.

Literature Cited

- Aanes, R., and R. Andersen. 1996. The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. Canadian Journal of Zoology 74: 1857-1865.
- Aebischer, N. J., and P. A. Robertson. 1992. Practical aspects of compositional analysis as applied to pheasant habitat utilization. Pp. 285-293 in Telemetry: remote monitoring and tracking of animals (I. G. Priede and S. M. Swift, eds.). Wildlife Ellis Horwood. Chichister; England.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.
- Anderson, S., and A. B. Gaunt. 1962. A classification of the white-sided jackrabbits of Mexico. American Museum Novitates 2088: 1-16.
- Best, T. L. 1996. Lepus californicus. Mammalian Species 530: 1-10.

Cervantes, F. A. 1993. Lepus flavigularis. Mammalian Species 423:1-3.

- Cervantes, F. A., and L. Yépez. 1995. Species richness of mammals from the vicinity of Salina Cruz, coastal Oaxaca, Mexico. Anales del Instituto de Biología Universidad Nacional Autónoma de México, Serie Zoología 66: 113-122.
- Chapman, J. A., J. E. C. Flux, A. T. Smith, D. J. Bell, G. G. Ceballos, K. R. Dixon, F. C. Dobler, N. A. Formozov, R. K. Ghose, W. L. R. Oliver, T. Robinson, E. Schneider, S. S. Stuart, K. Sugimurua, and Z. Changlin. 1990. Conservation action needed for rabbits, hares, and pikas. Pp. 154-168 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.). Chapter 14. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Cowan, D. P., and D. J. Bell. 1986. Leporid social behaviour and social organization. Mammalian Review 16:169-179.
- Daniel, A., J. Holechek, R. Valdez, A. Tembo, L. Saiwana, M. Fusco, and M. Cardenas. 1993. Jackrabbit densities on fair and good condition Chihuahuan desert range. Journal of Range Management 46:524-528.

- Dunn, J. P., J. A. Chapman, and R. E. Marsh. 1982. Jackrabbits: *Lepus californicus* and allies. Pp. 124-145 in Wild mammals of North America: biology, management, and economics (Chapman, J. A. and G. A. Feldhamer, eds). The Johns Hopkins University Press. Baltimore, Maryland. 1147 pp.
- Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001.
 Statistical issues in resource selection studies with radio-marked animals. Pp. 209-242 in: Radio tracking and animal populations. (Millspaugh J. J. and J. M Marzluff eds.) Chapter 8. Academic Press. San Diego, California. 474 pp.
- Flux, J. E. C. 1981. Field observations of behavior in the genus *Lepus*. Pp. 377-394 in: Proceedings of the World Lagomorph Conference (Myers, K. and C. D. Mac Innes, eds.). August 12-16, 1979. University of Guelph, IUCN/SSC, World Wildlife Fund. Ontario, Canada. 983 pp.
- Flux, J. E. C., and R. Angermann. 1990. The hares and jackrabbits. Pp. 61-94 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.) Chapter 4. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Fritzell, E. K. and K. J. Haroldson. 1982. Urocyon cinereoargenteus. Mammalian Species 189:1-8.
- García, E. 1964. Modificaciones al sistema de clasificación climática de Kopen (para adaptarlo a las condiciones de la República Mexicana). Instituto de Geografía, UNAM. México, D. F.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pp. 111-164 in Research techniques in animal ecology, controversies and consequences (Boitani, L. and T. K. Fuller, eds.). Columbia University Press. New York. 442 pp.
- Hulbert, I. A. R., G. R. Iason, D. A. Elston, and P. A. Racey. 1996a. Home-range sizes in a stratified upland landscape of two lagomorphs with different feeding strategies. Journal of Applied Ecology 33:1479-1488.
- Hulbert, I. A. R., G. S. Iason, and P. A. Racey. 1996b. Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding stategies. Journal of Applied Ecology 33:315-324.
- Hooge, P. N. and Eichenlaub, B. 1997. Animal movement extension to arcview. Ver 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA.

- Kernohan, B. J, R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 125-166 in: Radio tracking and animal populations. (Millspaugh J. J. and J. M Marzluff eds.) Chapter 5. Academic Press. San Diego, California. 474 pp.
- Lechleitner, R. R. 1958. Certain aspects of behavior of the black-tailed jack rabbit. The American Midland Naturalist 60:145-154.
- Lomolino, M. V., and R. Channell. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. Journal of Mammalogy 76:335-347.
- Longland, W. S. 1991. Risk of predation and food consumption by black-tailed jackrabbits. Journal of Range Management 44:447-450.
- Lorenzo, C. 2001. Conservation of the critically endangered *Lepus flavigularis*. Final Report. Lincoln Park Zoo Neotropic Fund. 10 pp.
- Lorenzo, C., O. Guiascon, F. A. Cervantes, J. Vargas, and G. Portales. 2000. Status survey of the critically endangered *Lepus flavigularis*. Final Report. El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas. 5 pp.
- Marín, A. I., L. Hernández, and J. W. Laundré. Predation risk and food quantity in the selection of habitat by black-tailed jackrabbit (*Lepus californicus*); and optimal foraging apporach. Journal of Arid Environments 55: 101-110.
- Marzluff, J. M., S. T. Knick, and J. J. Millspaugh. 2001. High-tech behavioral ecology: modeling the distribution of animal activities to better understand wildlife space use and resource selection. Pp. 309-326 in: Radio tracking and animal populations. (Millspaugh J. J. and J. M Marzluff eds.) Chapter 12. Academic Press. San Diego, California. 474 pp.
- Mongahan, P., and N. B. Metcalfe. 1985. Group foraging in wild brown hares: effects of resource distribution and social status. Animal Behavior 33: 993-999.
- Nelson, E. W. 1909. The rabbits of North America. North American Fauna 29:9-287.
- Pérez-García, E. A., J. Meave, and C. Gallardo. 2001. Vegetación y Flora de la Región de Nizanda, Istmo de Tehuatnepec, Oaxaca, México. Acta Botánica Mexicana 56:19-88.
- Péroux, R. 1995. Le liévre d'Europe. Bulletin Mensuel de l'Office National de la Chasse. No. 204. 96 pp.

- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65-110 in Research techniques in animal ecology, controversies and consequences (Boitani, L. and T. K. Fuller, eds.). Columbia University Press, New York. 442 pp.
- Revilla, E., F. Palomares, and M. Delibes. 2000. Defining key habitats for low density populations of Eurasian badgers in Mediterranean environments. Biological Conservation 95: 269-277.
- Rohner, C., and C. J. Krebs. 1996. Owl predation on snowshoe hares: consequences of antipredator behavior. Oecologia 108:303-310.
- Sántis, E. C. 2002. Distribución y abundancia de la liebre endémica *Lepus flavigularis* y el conejo castellano *Sylvilagus floridanus* (Mammalia: Lagomorpha) en el Istmo de Tehuantepec, Oaxaca, México. Tesis de Licenciado en Biología. Universidad de Ciencias y Artes de Chiapas. Tuxtla Gutierrez, Chiapas, México. 70 pp.
- Seaman, D.E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.
- Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management 49:854-866.
- Trapp, G. R., and D. L. Hallberg. 1975. Ecology of the gray fox (*Urocyon cinereoargenteus*): a review. Pp. 164-178 in The wild canids, their systematics, behavioral ecology, and evolution (M. S. Fox, ed.). Van Nostrand-Reinhold Co., New York. 508 pp.
- Vargas, J. 2000. Distribución, abundancia y hábitat de la liebre endémica *Lepus flavigularis* (Mammalia: Lagomorpha) Tesis de Maestría en Biología Animal, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D. F., México. 70 pp.
- White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press. San Diego, California. 383 pp.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Zizumbo, D., and P. Colunga. 1982. Los Huaves. La apropiación de los recursos naturales. Universidad Autónoma Chapingo. México. 277 pp.

	г 1	Home	% in Home Range			%	% of Locations				
Saacon	Female	range	N	M	G	<u> </u>	<u>N</u>	M	G	Ś	
Season		1 09	20	57	2	1	40	50	0	0	
dmy 2002		1.08	39 47	21 20	10	1	42	28 25	0	0	
dry 2002	АГ40 ЛЕ45	0.04	47	20 57	10	2 2	01 56	55 41	4	0	
dry 2002	АГ4 <i>3</i> АЕ42	0.75	33 51	37 41	1	ン つ	50 62	41	5	0	
dry 2002	АГ43 ЛЕ 5 6	1.11	51	41	0	$\frac{2}{26}$	05	30 10	0	5	
wet 2002	AF30	0.04	51 45	19	4	20	/4	18	3	5	
wet 2002		0.25	45	20 20	16	0	43	57 41	10	0	
wet 2002	АГ48 А Г45	0.85	42	59	10	3 5	41	41	19	0	
wet 2002	AF45	0.40	44	51	10	2	4/	50	0	3	
wet 2002	AF43	0.61	57	29	12	2	/4	23		3	
dry 2003	AF/5	0.25	42	36	12	0	39 10	39	23	0	
dry 2003	AF/3	0.33	33	49	12	2	18	13	9	0	
dry 2003	AF/I	0.67	29	66	1	3	24	/6	0	0	
dry 2003	AF56	0.53	45	30	2	23	69	31	0	0	
dry 2003	AF55	0.64	59	35	6	0	57	37	6	0	
dry 2003	AF45	0.22	46	51	0	3	47	53	0	0	
	Male	Home	%	% in Home Range.			%	% of Locations .			
Season	hares	size	Ν	Μ	G	S	N	М	G	S	
wet 2001	$\Delta M06$	0.73	78	5	16	2	86	0	14	0	
wet 2001	$\Delta M24$	1.02	33	56	10	7	50	45 	0	0 Д	
dry 2002	$\Delta M 41$	1.02	39	50 54	2	5			0	т 3	
dry 2002	$\Delta M39$	0.93	37 45	/3	27	5	-+0 /18	-10 /18	3	0	
dry 2002	$\Delta M22$	0.37	89	-15	8	3	90	-0	7	3	
dry 2002	AM06	0.37	65	13	22	0	74	6	20	0	
wet 2002	AM67	0.11	15	84	0	1	35	65	20	0	
wet 2002	AM61	0.32 0.24	12	59	19	0	82	7	11	0	
wet 2002	AM41	0.21	48	34	5	2	54	40	6	0	
wet 2002	AM36	0.75	45	44	2	17	40	60	0	0	
wet 2002	AM22	0.75	10	40	19	17 4	40 74	6	21	0	
wet 2002	AM06	0.00	15	90	23	10	43	19	38	0	
dry 2002	AM61	0.30	33	20 47	13	0	47	23	30	0	
dry 2003	AM36	0.52	59	3	0	17	33	58	0	9	
dry 2003	AM22	0.75	12	10	18	8	59	6	35	Ó	
dry 2003	AM06	0.70	18	26	16	18	37	37	17	9	

Table 2.1 Proportion (%) of habitat types (N = Nanchal, M = Morro, G = Grassland, S = Scrub) in seasonal home ranges (95% fixed kernel in km^2) and telemetry locations of 17 adult tropical hares in Llano Contreras, Oaxaca, Mexico.

Available habitat in study area polygon was 43% of Nanchal, 36% of Morro, 6% of Grassland and 16% of Scrub.
	Home % in Home Banga					fIcco	tions			
	Female	range	<u> </u>		<u>e Kalige</u>	<u> </u>	<u>%</u> C	<u>n Loca</u>		<u>.</u>
Season	hares	size	Ν	Μ	G	S	Ν	Μ	G	S
wet2001	JF12	0.39	63	32	0	5	83	17	0	0
wet2001	JF28	0.49	47	43	2	8	64	36	0	0
dry 2002	JF38	0.35	31	61	6	2	13	79	4	4
dry 2002	JF44	0.36	67	15	15	4	73	0	23	4
wet 2002	JF51	0.12	51	16	33	0	69	6	25	0
wet 2002	JF66	0.23	13	79	0	8	17	79	0	3
wet 2002	JF69	0.16	27	73	0	0	50	50	0	0
wet 2002	JF70	0.07	26	68	0	6	27	73	0	0
wet 2002	JF71	0.27	36	64	0	0	43	57	0	0
dry2003	JF77	0.16	34	50	16	0	31	46	23	0
dry2003	JF79	0.08	26	74	00	0	35	65	0	0
		Home								
	Male	range	<u>% in Home Range</u> .			<u> </u>	% of Locations .			•
Season	hares	size	Ν	Μ	G	S	Ν	Μ	G	S
wet 2001	JM09	2.64	49	38	5	8	61	34	3	3
wet 2001	JM22	1.14	55	33	5	7	48	44	4	4
dry 2002	JM35	0.26	25	75	0	0	15	85	0	0
dry 2002	JM36	0.59	44	54	0	3	44	56	0	0
dry 2002	JM46	0.11	38	62	0	0	50	50	0	0
dry 2002	JM47	0.28	67	33	0	0	73	27	0	0
wet 2002	JM35	0.84	52	40	8	0	59	41	0	0
dry2003	JM74	0.52	39	47	10	3	57	43	0	0

Table 2.2 Proportion (%) of habitat types (N = Nanchal, M = Morro, G = Grassland, S = Scrub) in seasonal home ranges (95% fixed kernel in km^2) and telemetry locations of 18 juvenile tropical hares in Llano Contreras, Oaxaca, Mexico.

Available habitat in study area polygon was 43% of Nanchal, 36% of Morro, 6% of Grassland and 16% of Scrub.

Habitat Use	Age	n 17	Compositional preference order ^{a,b}						
Home range	Adult		М	>	N	>	G	>>>	S
establishment	Juvenile	18	М	>	N	>>>	G	>	S
Within home	Adult	17	N	>	М	>>	G		
range	Juvenile	18	N	>	М	>	G		
Within home range during inactive peroid	Adult	17	N	>>>	М	>>>	G		
Within home range during active period	Adult	17	М	>>>	N	>	G		

Table 2.3 Compositional analysis of relative use of habitat types (N = Nanchal, M = Morro, G = Grassland, S = Scrub) by radio-marked tropical hares (*Lepus flavigularis*) in Llano Contreras, Oaxaca, Mexico, from May 2001 to April 2003.

^a > indicate no significant difference between groups with $p \ge 0.1$

>> indicate significant difference between groups with p < 0.05

>>> indicate significant difference between groups with p < 0.01

^b Scrub was excluded from the within home range analysis, because hares avoided Scrub in the analysis for home range establishment.

Table 2.4 Proportion of habitat types for predator-caused mortality sites compared to the proportion of habitat use by radio-marked tropical hares, relative to the proportion of available habitat types in the 9.09-km² study area polygon.

		Proportion (%) in habitat type						
Age	n ^a	Nanchal	Morro	Grassland	Scrub			
Adult	10	50	20	30	0			
Juvenile	15	53	40	0	7			
Adult	17	49	43	7	1			
Juvenile	18	48	45	5	1			
		43	36	6	16			
	Age Adult Juvenile Adult Juvenile	AgenaAdult10Juvenile15Adult17Juvenile18	AgenaNanchalAdult1050Juvenile1553Adult1749Juvenile1848	AgenªNanchalMorroAdult105020Juvenile155340Adult174943Juvenile184845	Proportion (%) in habitat typeAgenªNanchalMorroGrasslandAdult10502030Juvenile1553400Adult1749437Juvenile1848455433666			

^an = number of individuals

^bAverage percentage of telemetry locations of individual hares in each habitat type



Figure 2.1 Historic distribution of the tropical hare. The tropical hare's (*Lepus flavigualris*) historic distribution (dotted area) ranged along the Mexican Pacific coast on the Isthmus of Tehuantepec from Salina Cruz in Oaxaca to Tonala in Chiapas. Stars show the location of remnant populations of tropical hares.





Figure 2.2 Tropical hare, Nanchal, Morro, Grassland, and Scrub. Tropical hares (*Lepus flavigularis*) (a) in this study inhabited a savanna, where habitat types were classified as: (b) Nanchal (*Byrsonima crassifolia*), (c) Morro (*Crescentia spp.*), (d) Grassland, and (e) and Scrub.



Figure 2.3 Study area polygon with available habitat types. Llano Contreras, Oaxaca, Mexico, from May 2001 to April 2003.



Figure 2.4 Seasonal activity patterns from adult tropical hares. Twenty-six adult (16 F, 10 M) tropical hares (*Lepus flavigularis*) were monitored in Llano Contreras, Oaxaca, Mexico, from May 2001 to April 2003.



Figure 2.5 Habitat use in home ranges of adult and juvenile tropical hares compared to habitat availability in study polygon. Proportions of habitat types available in the study polygon (black bars) were compared to proportions of habitat types within home ranges of adult (light gray bars) and juvenile (dark gray bars) tropical hares (*Lepus flavigularis*). Values are percentage means with standard error from 17 adult hares and 18 juvenile hares.



Figure 2.6 Habitat use in telemetry locations of adult hares compared to habitat availability in home ranges. Proportions of habitat types within home ranges (black bars) of adult tropical hares (*Lepus flavigularis*) were compared to proportions of locations in habitat types (gray bars). Values are percentage means with standard error from 17 adult hares.



Figure 2.7 Habitat use in telemetry locations of juvenile hares compared to habitat availability in home ranges. Proportions of habitat types within home ranges (black bars) of juvenile tropical hares (*Lepus flavigularis*) were compared to proportions of locations in habitat types (gray bars). Values are percentage means with standard error from 18 juvenile hares.



Figure 2.8 Habitat use in telemetry locations of adult tropical hares during the inactive period compared to availability in home ranges. Proportions of habitat types within home ranges (black bars) of adult tropical hares (*Lepus flavigularis*) were compared to proportions of locations during the inactive period (gray bars) in habitat types. Values are percentage means with standard error from 17 adult hares.



Figure 2.9 Habitat use in telemetry locations of adult tropical hares during the active period compared to availability in home ranges. Proportions of habitat types within home ranges (black bars) of juvenile tropical hares (*Lepus flavigularis*) were compared to proportions of locations during the active period (gray bars) in habitat types. Values are percentage means with standard error from 17 adult hares.

CHAPTER 3

POPULATION ECOLOGY OF THE TROPICAL HARE

<u>Abstract</u>

The survival and cause of death of 51 tropical hares (Lepus flavigularis) in a savanna habitat on the Isthmus of Tehuantepec, Oaxaca, Mexico, were monitored by radiotelemetry from February 2001 to July 2003. Annual survival rate for adult hares was 0.43, and survival during the wet season (0.56) was lower than during the dry season (0.79), particularly for female hares. Survival of female juveniles was low during both the dry (0.06) and wet seasons (0.15), when compared to that of male juveniles (0.35 and0.48). Predation was the major cause of hare mortality with 67% of adult and 94% of juvenile deaths. Induced fires in the savanna and poaching accounted for 20% and 13% of adult deaths, respectively. Sex ratios for adult and juvenile hares did not differ from 1:1. Pregnant females were found from February to December, but the proportion of pregnant females was higher during the wet season. The mean number of embryos from six museum specimens was 2.0 (range 1 to 4). Simulations of possible population change are strongly influenced by the low survival of juvenile females. Estimation on demographic parameters should be improved to allow better prediction of population changes under potential management regimes for conservation.

Key words: conservation, demographic parameters, *Lepus flavigularis*, Mexico, mortality, radio-telemetry, survival, tropical hare.

Introduction

Three remnant populations of tropical hare (Lepus flavigularis) require urgent assessment of demographic parameters for conservation efforts. Populations of tropical hare are small (< 1,000 individuals; Lorenzo, personal communication) and isolated from each other along savannas on the Isthmus of Tehuantepec (Flux and Angermann, 1990; Lorenzo et al., 2000). The assessment and estimation of demographic parameters such as sex ratios, age structure, reproduction, and survival are basic to identifying factors that influence population dynamics of endangered wildlife (Krebs, 1985). Development of conservation strategies has been hindered by the absence of information on survival and cause-specific mortality of tropical hares. Knowledge of demographic parameters of tropical hares is important because declines resulting from habitat loss and fragmentation (Flux and Angermann, 1990) may lead to subsequent declines as a result of demographic and genetic stochasticity (Frankham et al., 2002). Small isolated populations are more likely to vary randomly in birth and death rates, and in sex ratio, increasing extinction risks (Frankham et al., 2002). Also, models that lead to the understanding of the possible mechanisms involved in regulating tropical hare populations are in need of robust estimates of demographic parameters (Krebs, 1985).

Parameters of maintenance and recruitment are basic demographic variables and critical components for population dynamics of the genus *Lepus*, therefore it is desirable to obtain estimates of adult and juvenile survival (Marboutin and Perox, 1995; Marboutin and Hansen, 1998). Population growth rate is determined by age-specific rates of survival and reproduction (Caughley, 1977; Marboutin and Peroux, 1995). Growth rates of hare populations with low juvenile survival are very sensitive to increases in adult mortality

(Marboutin and Peroux, 1995). Also, hare populations may fluctuate in numbers, decline to extinction, or recover due to changing survival, particularly of young hares (Keith et al., 1993; Marboutin and Hansen, 1998).

Changes in population dynamics of hares result mainly from the interaction of food availability, hares, and predators (Krebs et al., 1995). Predation is the main source of mortality for non-harvested populations of hares (Sievert and Keith, 1985; Keith et al., 1993; Krebs et al., 1995), and young hares are more vulnerable to predation than older hares (Rohner and Krebs, 1996). Hares may respond to predation by using areas of low risk but poor food quality, receiving poor nutrition that reduces survival and reproduction (Krebs et al., 1995; Hodges, 1999; Marin et al., 2002). Presumably, hares suffering from food stress are more susceptible to death from predation (Krebs et al., 1995).

I conducted radio-tracking research to estimate demographic parameters from one population of tropical hares, and use these parameters to obtain some idea of the factors most influencing population change. I monitored radio-marked tropical hares to estimate survival and cause-specific mortality rates from the population on the northeast rim of the Inferior Lagoon, Isthmus of Tehuantepec, Oaxaca, Mexico. My objective was to identify mortality factors that threaten the survival of the tropical hare population in the study area.

<u>Methods</u>

Study Area

The 16-km² study area of Llano Contreras is a savanna located 2 km northwest from Montecillo Santa Cruz, Municipality of San Francisco del Mar Pueblo Nuevo, Oaxaca, Mexico, on the northeast rim of the Inferior Lagoon connected to the Gulf of

Tehuantepec (Fig. 1.1). The savanna encompassed native grasses dominated by grama (Bouteloua spp.) and paspalum (Paspalum spp.), scattered trees dominated by morro (*Crescentia spp.*), sparse shrublands of nanche (*Byrsonima crassifolia*), and dense heterogeneous vegetation along streambeds (Perez-Garcia et al., 2001). Local people practice subsistence hunting and raise free-ranging cattle, horses, sheep, and goats in the study area. Climate is tropical with mean annual temperature of 25° C, mean annual rainfall of 800 mm (Garcia, 1964), and marked seasons. The rainy season is from May to October with an intra-estival drought in August, and the dry season is from November to April and is severe during late winter and early spring (Zizumbo and Colunga, 1982). Lowlands may flood during the rains after prolonged or heavy precipitation. Native terrestrial mammals associated with the tropical hare and observed during the study were cottontail rabbits (Sylvilagus floridanus), armadillos (Dasypus novemcinctus), skunks (Mephitis macroura), opossums (Didelphis marsupialis), mouse opossums (Marmosa canescens), gray foxes (Urocyon cinereoargenteus), racoons (Procyon lotor), and coyotes (Canis latrans) (Cervantes and Yepez, 1995; Lorenzo, 2000). Gray foxes and covotes are native predators of tropical hares.

Capture of Animals

From February 2001 through November 2002, 79 tropical hares were captured and 51 radio-tracked in Llano Contreras. I recorded sex, age (juvenile or adult), weight, and standard measurements (total length, tail length, foot length, and ear length), and attached 20-g, 30-g, or 40-g VHF radio-collar transmitters (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA). Females (F) were identified by a thin longitudinal canal at the base of the clitoris that extends to the vulva, and adult females were palpated for embryos and their fur around nipples was examined for suckling (Peroux, 1995). Males (M) were identified by the presence of a cylindrically shaped penis having a conic tip (Peroux, 1995). Young hares weighing less than 500 g were not collared because they were too small to comfortably wear one of the smallest radio-collars. Young hares weighting > 500 and < 2500 g were sexually immature and I identified them as juveniles. Captured individuals with external genitalia development were identified as adults, and most of them had body weight \geq 2500 g, except for one young adult male that weighted 2100 g.

Six circular (2-mm diameter) clippings of skin from the ear were collected from captured hares and stored for subsequent genetic analysis. Capture and research activities were conducted in accordance with the approval of the Mexican Secretariat of Environment and Natural Resources (SEMARNAT), and the Institutional Animal Care and Use Committee (IACUC) at The University of Massachusetts, Amherst, USA. (IACUC protocol number 22-02-07).

Age Assessment of Young Hares

To estimate approximate age in months of young hares and approximate age when juveniles reached adulthood, I used body weight data from six young tropical hares that were captured and then recaptured an average of 47 days later (range 35 to 69 days) to replace radio-collars. Calculations indicated that hares weighting between 520 and 2500 g gained an average of 497 g per month (Table 3.1). I assumed that young hares with body weight of approximately 500 g were probably between one to two months old, and that juvenile hares would gain approximately 497 g per month and probably would reach

adulthood at about six or seven months of age. However, growth is not linear but logistic, and a straight-line assumption would underestimate time to adulthood.

My assumptions are consistent with literature on closely related hares and with collected data in this study. One month after birth, body weight of young black-tailed jackrabbits (*Lepus californicus*) is only 13% of adult mass (Goodwin and Currie, 1965). Mean body weight from 42 records of adult tropical hares (26 F, 16 M) in my study was 3066 ± 401 g (range 2500 to 4000 g), therefore the body weight for a 1-month old tropical hare would be approximately 399 g (13% of 3066 g). Also, a leveret of *Lepus flavigularis* that weighted 190 g was found on 8 April 2002 in this study. The leveret was probably less than a week old because it had uncoordinated hopping and its muzzle was broad and short (Best, 1996). Published records account for three neonates of antelope jackrabbit (*Lepus alleni*) that weighted 185, 133, and 138 g (Best and Henry, 1993a).

I captured a female hare as a 1600-g juvenile and recaptured it as a 3500-g pregnant female 205 days later. I estimated that the female was approximately 10 or 11 months old when recaptured; thus females of *Lepus flavigularis* may breed in their year of birth. Also, I captured a male as a 1950-g juvenile and recaptured it as a 3000-g adult 128 days later; thereby I estimated that the male was about 8 or 9 months old when recaptured. The age of maturity for *Lepus flavigularis* may be similar to closely related species. Females of *Lepus alleni* (Flux and Angermann, 1990; Best and Henry, 1993a) and of *Lepus californicus* may breed in their year of birth (Gross et al., 1974).

Radio-Tracking

Tropical hares of both sexes and different ages were radio-tracked from February 2001 through July 2003 with a portable receiver (Telonics TR-4) equipped with a three-

element Yagi antenna. Mortality-sensitive transmitters with a life span of 6 to 12 months had whip antennas and thus were motion-sensitive, as well. Transmitters 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. The signal rate doubled if the transmitter had not moved in 8 hours. Scavengers and strong wind could inactivate a mortality signal by moving the transmitter. If a radio-signal indicated inactivity for more than 30 minutes, the animal was tracked until visually located. Radio-signals were monitored one to three times per week to check for mortalities.

Carcasses or remains of deceased radio-marked hares were recovered approximately within 12 hours of death, and carcass condition, position, and location was recorded. After 12 hours of death I only recovered the transmitter, because carcasses or remains were consumed by predators and scavengers, or decomposed by tropical weather in the study area.

I determined predation as the cause of death when the carcass was partially or totally eaten, and the radio-collar had blood stains, hare hair, tooth marks, and signs of being chewed (twisted antenna, eaten elastic). The site was examined for signs from potential predators (gray foxes, coyotes) as tracks and scats, but with no results.

I was able to recover two transmitters from hares killed by local poachers: the first was found in the hunter's house, and the second was found in the savanna with blood stains and the collar cut with a knife. When a radio-signal disappeared from the study area and fresh (1 or 2 days old) vehicle-tracks were observed in the home range of the missing hare, I assumed that poachers killed the hare and took the transmitter with them.

I recovered the partially burned carcass of a pregnant hare with one fetus a few hours after the savanna was burned by local ranchers. When a radio-signal disappeared from the study area following a fire in the savanna, I assumed that fire killed the hare and destroyed the transmitter.

When a radio-signal disappeared from the study area but no signs of poaching or fire were observed in the savanna, I assumed that I had lost contact because the transmitter had failed and that the hare was alive to the date when the radio-signal was last heard. It is not likely that predators destroyed the transmitter while taking a radiomarked hare, but it is possible that missing hares had emigrated from the study area. After their disappearance, radio-signals from missing hares were scanned every telemetry session until the expiration date for the transmitter's battery was reached. Deceased hares were visually located no more than seven days before its death.

Survival Rates and Mortality Causes

I calculated rates of survival and cause-specific mortality and their confidence intervals using the software MICROMORT (Heisey and Fuller, 1985). I first partitioned data into three years: year 2001 (Feb 2001 thru Oct 2001), year 2001-2002 (Nov 2001 thru Oct 2002), and year 2002-2003 (Nov 2002 thru July 2003). I assumed daily rates within a month were similar, but when differences between rates for consecutive months were not statistically significant according to z tests (Heisey and Fuller, 1985), I pooled survival data into wet (May to October) and dry (November to April) seasons. I similarly pooled data among years. I analyzed survival and cause-specific mortality rates separately for each sex, but pooled them, as well. However, I treated data for adult and juvenile hares

separately. I computed mortality rates of hares for three specific causes of death: predation, poaching, and fire.

Density

Density of the studied tropical hare population could not be estimated using markresighting surveys during this study because assumptions for the NOREMARK estimator were not satisfied (White, 1996). Although I had a sample of individuals marked with radio-collars and marked individuals could be examined by surveys, sighting probability was not the same for marked and unmarked tropical hares (White, 1996; Hale and Fuller, 1999). In fact, the only way to see a radio-collared hare was to follow the animal with the telemetry equipment; thus I could not obtain sighting frequencies of marked individuals.

I estimated density of tropical hares in the study area by analyzing the size of the core area of tropical hare's home range (Fuller et al., 2001) estimated in Chapter 1. Overlap with more than one individual suggests that tropical hares are polygamous (Chapter 1). However, tropical hares showed negligible core area overlap suggesting that at least some portion of the home range is preferentially not shared with other hares (Chapter 1). I assumed that tropical hares had exclusive use of core areas in their home ranges, that the size of annual core area of adult hares was in average 0.085 km², and that tropical hares selected prime hare habitat for core area establishment (Chapter 2). Prime hare habitat consisted of nanchal, morro, and grassland, and accounted for 85% (43%, 36%, and 6%, respectively) of available habitat in 9.09 km² of the study area.

Population Characteristics

Sex ratio was assessed from the 79 tropical hares captured. Binomial probability tests with SPSS 8.0 determined if the sex ratio differed from unity for adult and juvenile hares (Hale and Fuller, 1996).

From 24 records of adult females, I detected that seven females were pregnant and two females were lactating females when captured. I was not able to estimate litter size by palpation. I calculated for each month the proportion of adult females captured that were pregnant or had recently given birth. I was not able to detect when radio-tracked females had newborn leverets, much less their numbers at birth, for the following reasons: 1) hares give birth to their young on flat depressions on the ground and newborn leverets may separate from each other a few hours after birth, 2) female hares do not stay with their young during resting hours and spend only a few minutes per day feeding the leverets, and 3) newborn litters are secretive and sit motionless when in potential danger (Lechleitner, 1958; Stoddart, 1984; Flux and Angermann, 1990).

Litter size was derived from six museum specimens of tropical hare at the Mammalogy Collection of The National University of Mexico (UNAM), and from one fresh carcass of a pregnant female recovered during my study. Litter size was taken as the mean number of embryos per female, and compared to published litter size on closely related species.

Length of the reproductive season and number of litters per season were derived from literature on related *Lepus* species, data on six museum specimens from UNAM, and from data collected on 9 tropical hares that were pregnant or lactating when captured in this study.

Results

I monitored 51 tropical hares (30 F, 21 M) from February 2001 through July 2003, and individual hares were monitored for 1 to 827 days (mean \pm SD = 165 \pm 185 days). Individual adult females (n = 13) were monitored for 94 to 515 days, and individual adult males (n =12) for 31 to 827 days. Individual female juveniles (n = 21) were monitored from 1 (due to collar failure) to 129 days, and individual male juveniles (n = 14) were monitored from 5 (due to collar failure) to 162 days. Four female and five male juveniles that survived to adulthood were monitored as juveniles and as adults.

Ten adult hares (5 F, 5 M) were killed by predators, two adult males were taken by poachers, and the burned carcass of an adult female was recovered and two adult males were missing after a fire in the savanna. Five adults (4 F, 1 M) were alive at the end of the study and five other adults (3 F, 2 M) could not be recaptured to replace the transmitter before the battery was expended.

Fifteen juvenile hares (11 F, 4 M) were killed by predators, and one juvenile female disappeared after poachers entered the savanna. Nine juveniles (4 F, 5 M) survived to adulthood, and one juvenile female was still alive at the end of the study. I lost contact with nine juvenile hares (4 F, 5 M) during the study.

Survival Rates and Mortality Causes

The survival rate of adult females during the dry season (1.00) was higher than during the wet season (0.53; two-tailed *z* test, p = 0.001; Table 3.2). Survival rates of adult males did not differ between seasons (0.61 vs. 0.59). Survival rates during the dry season were higher for adult females (1.00) than for adult males (0.61; two-tailed *z* test, p = 0.010;

Table 3.2). The pooled survival rates for adult hares did not differ by season (0.79 vs. 0.56), and on an annual basis, averaged 0.43 (females = 0.51; males = 0.36; Table 3.2).

Predation mortality of adult females was higher during the wet season (0.39 vs. 0.00; two-tailed *z* test, p = 0.004; Table 3.3). For adult males, predation mortality was 0.33 during the wet season vs. 0.10 during the dry season with no statistical differences. The pooled predation rate of adult hares was higher during the wet season (0.36 vs. 0.05; two-tailed *z* test, p = 0.004; Table 3.3).

Overall, the survival rate for juvenile hares during the dry season was 0.15 and during the wet season was 0.25 (Table 3.4) with no statistical differences. Survival was lower for juvenile females than males during the wet (0.15 vs. 0.48) and dry seasons (0.06 vs. 0.35). No significant statistical differences between sexes for juvenile survival were found.

Predation mortality of juveniles was higher during the dry season (females = 0.94; males = 0.65) than during the wet season (females = 0.73; males = 0.52) but no statistical differences were detected (Table 3.3).

Predation was the major cause of hare mortality, causing 67% of adult and 94% of juvenile deaths. Human-induced fires in the savanna, and poaching, accounted for 20% and 13% of adult deaths, respectively. Annual predation mortality of adult hares was statistically higher (0.38) than fire mortality (0.11) (one-tailed *z* test, p = 0.005) and poaching mortality (0.08) (one-tailed *z* test, p = 0.001). Annual poaching mortality of adult hares did not differ from annual fire mortality (two-tailed *z* test, p = 0.615).

Density

Assuming that tropical hares do not overlap core areas in their home ranges, that core area size is similar between sexes for adult hares, and that average core area size is 0.085 km^2 , then density of adult tropical hares would be 11.8 hares per km² for the studied population. This density estimate assumes a maximum density with no unfilled spaces.

Lorenzo (personal communication) estimated the area of occupancy for the tropical hare population on the northeastern rim of Inferior Lagoon to be of 47 km². Assuming that tropical hares selected prime hare habitat for core area establishment, and that prime hare habitat types (Nanchal, Morro, and Grassland) accounted for 85% of available habitat in the 47 km²-occupancy area, then the studied population could have a maximum of 471.4 adult hares [(11.8 hares/km²) x (47 km² x 0.85)].

Population Characteristics

Of 79 tropical hares I captured, 16 were adult females, 12 adult males, 28 juvenile females and 22 juvenile males. I could not assess sex of one leveret that weighted 190 g and was a few days old. The sex ratios of adult (1.3F:1M) and juvenile hares (1.3F:1M) did not differ statistically from 1:1 (p = 0.571 and p = 0.480, respectively).

From 24 capture and recapture records, seven adult females were pregnant and two were lactating (Table 3.5). The proportion of adult females pregnant or lactating in a given month varied from 0% in June, September, and December to 100% in May and October. The proportion of adult females pregnant or lactating during the dry season was 33% and during the wet season was 50%. However, my estimates are likely to underestimate the proportion of pregnant females because I was able to detect only late pregnancy. Also, during the wet season and only six females were captured and two of them weighted 2500g and most likely just reached adulthood when captured in June. I was not able to estimate litter size by palpation. A newborn (< 1-week-old) leveret was found on 8 April.

If adult females are pregnant $\geq 33\%$ and $\geq 50\%$ of the time during the dry and wet seasons, respectively, and gestation period is approximately 6 weeks (Best and Henry, 1993a), then probably adult females are pregnant for 2 months during the dry season (2/6 = 0.33), and for 3 months during the wet season (3/6 = 0.50). Thus one litter per female may be produced during the dry season and two litters per female during the wet season.

Population Effects

To explore the effects of survival and cause-specific mortality rates on hare numbers, I combined rate estimates from this study with demographic parameters from the literature and from museum specimens of *Lepus flavigualris* into hypothetical calculations of potential population change. For simplification, I modeled only the female half of the population. The simulation model was programmed in an Excel spreadsheet, and ran until a stable age distribution was achieved.

To estimate length of the birthing season and litter size, I used data from seven museum specimens of females that were pregnant or lactating when collected. Females were collected on 7 February (2 embryos and lactating), 25 April (1 embryo), 28 May (3 embryos), 23 June (1 embryo), 6 August (0 embryos and lactating), 8 October (4 embryos and lactating), and 3 December (1 embryo). Therefore, when combined with my own field data, I assumed that pregnant females of tropical hares could be found any month of the year. The average number of embryos from the six museum specimens of tropical

hares was 2.0 (range 1 to 4); 1.3 for the dry season and 2.7 for the wet season. If I include the carcass of a pregnant female recovered in my study with the six museum specimens, then the average number of embryos was 1.8; 1.3 for the dry season and 2.3 for the wet season. The estimates seem reasonable when compared with literature on closely related species of hares: *Lepus alleni* has an average litter size of 2.1 (range 1 to 5), and *Lepus callotis* of 2.2 (range 1 to 4).

In general, fecundity in the genus *Lepus* is variable, but mean annual fecundity averages about ten young per female for most species (Flux, 1981). In California, the breeding season for *Lepus californicus* extends from January to August when apparently all adult females are pregnant, but sporadic pregnant females can be found any month of the year (Lechleitner, 1959). Females of black-tailed jackrabbits are capable of breeding at eight months of age, and litter size changes in numbers from one in January, then rise gradually to reach four in April, and diminish to one in August (Lechleitner, 1959). Gestation period is 41 to 47 days in *Lepus californicus* (Lechleitner, 1959).

Lepus alleni breeds year-round (Flux and Angermann, 1990; Best and Henry, 1993a) but the percentage of pregnant females peaks with rainfall, as does litter size which varied from 1.5 to 3.1 (mean 2.1, range 1 to 5) in Arizona, where a female may have three to four litters per year (Vorhies and Taylor, 1933). The gestation period for *Lepus alleni* is about 6 weeks (Best and Henry, 1993a).

The breeding season for the white-sided jackrabbit (*Lepus callotis*) extends at least from April to August (Best and Henry, 1993b) allowing at least two litters per year with a mean litter size of 2.2 (range 1 to 4) in New Mexico (Bednarz, 1977).

For the hypothetical calculations on population change, I assumed that if litter size of tropical hares changes in numbers between seasons, and if 33% and 50% of females are pregnant during the dry and wet seasons, respectively, then probably one litter with 1.3 young per female are born during the dry season (Nov to Apr), and two litters with 2.7 young per female are born during the wet season (May to Oct), like the seasonal variation in litter size of the antelope jackrabbit (Vorhies and Taylor, 1933), the blacktailed jackrabbit (Lechleitner, 1959), and the white-sided jackrabbit (Bednarz, 1977).

Also, I assumed that 100% of adult females reproduce (Lechleitner, 1959) and that average age of first reproduction could be between 9 and 12 months (Lechleitner, 1959). I captured a female of tropical hare as a juvenile on April and 205 days later recaptured it on October as an adult in late pregnancy, and estimated that the female was approximately 10 or 11 months old when recaptured. Sex ratios at birth and for juvenile and adult hares were assumed to be 1:1 (Lechleitner, 1959).

The hypothetical calculations started at the first day of the wet season (1 May). Juveniles that survived one 6-month period entered the following 6-month period as adults. Adults produced an average of two litters with 1.35 newborn females each during the wet season, and an average of one litter with 0.65 newborn female during the dry season. Survival rates during the wet season were 0.56 for adult and 0.25 for juvenile hares, and during the dry season were 0.79 for adult and 0.15 for juvenile hares. I ran the model until it reached a stable age distribution (Caughley, 1977).

The hypothetical calculations suggested that the tropical hare population was changing at a rate of about 1.10, or + 10% per year, with 27% and 61% adults during the wet and dry seasons, respectively (Table 3.6). But if instead of pooled seasonal survival

rates, I used the survival estimates for female adults (0.53 wet, 1.00 dry) and female juveniles (0.15 wet, 0.06 dry), then the hypothetical calculations suggested that the tropical hare population was changing at a rate of about 0.97 or -3% per year.

Overall, survival during the first year of life would be $0.20 (0.25 \times 0.79)$ for tropical hares born during the wet season, and of $0.08 (0.15 \times 0.56)$ for hares born during the dry season.

Discussion

Adult and Juvenile Survival

Annual survival for adult tropical hares (0.43) in this study may be compared with survival estimates for other species of hares. The proportion of adults present in the population prior to the breeding season was used by Swihart (1984) as an index of annual adult survivorship for populations of snowshoe hare, *Lepus americanus* (0.23, 0.30, and 0.45), black-tailed jackrabbit, *Lepus californicus* (0.19 and 0.23), European hare, *Lepus europaeus* (0.68), brown hare, *Lepus timidus* (0.45), and white-tailed jackrabbit, *Lepus timidus* (0.35).

Lower survival of juvenile tropical hares relative to adult survival is consistent with studies on population dynamics of hares where predation is the main mortality cause, but reduced juvenile survival is also correlated with declines in hare numbers (Boutin, 1984; Marboutin and Peroux, 1995). A decreasing population of European hares had adult survival (0.51) and mean life span (2.50 years) higher than estimated values for non declining European hare populations, but unsuccessful recruitment lead to a

declining trend in numbers of hares as annual juvenile survival (0.07) was lower than that of yearlings (0.39) and adults (Marboutin and Peroux, 1995).

Survival of female juveniles was the lowest for tropical hares in this study. Although differences between female and male juveniles were not statistically significant, survival of males more than doubled that of females in both the dry (0.06 vs. 0.35) and wet (0.48 vs. 0.15) seasons.

Marboutin and Peroux (1995) found that survival of European hare male yearlings was higher (0.47) than for female yearlings (0.24), and attributed the sex-dependent survival to high maternal investment by females. But female juveniles of tropical hares in this study are sexually immature and their survival is not constrained by reproductive investments. Studies on young snowshoe hares have failed to find significant survival differences between sexes (O'Donoghue, 1994; Gillis, 1998).

However, juvenile survival increased when Boutin (1984) removed most adults from a snowshoe hare population, suggesting that adults may exclude juveniles from home ranges and thus limit juvenile survival. But it might be speculative to think that survival of juvenile females of tropical hare may be limited by the presence of adult females.

Seasonal Survival and Predation

Seasonal age- and sex- specific survival in hares has been explained mainly by differential mortality determined primarily by predation (Keith et al., 1993). Snowshoe hare survival in a fragmented habitat was lower during spring-summer than during fall-winter (0.34 vs. 0.43) and reflected seasonal predation differences from increased activity

and movement accompanying breeding behavior (Keith et al., 1993). Decreased survival of snowshoe hares has been strongly associated with hare movements and factors tending to increase movements (Sievert and Keith, 1985).

Female adults of tropical to survived better than adult males, particularly during the dry season, and predation mortality was higher during the wet season for adult hares, particularly for females. During the wet season, a relatively high proportion of females were pregnant and litter size was bigger than during the dry season in this study. Pregnant females may be more sensitive to predation than adult males, and thus sex-specific differences in survival of adult hares may be linked to reproduction (Keith et al., 1993; Marboutin and Peroux, 1995; Marboutin and Hansen, 1998).

Juvenile hares survived better during the wet season, and predation mortality was higher during the dry season, particularly for females. I would have expected juvenile survival to be lower during the wet season as happened with adults, because juveniles are more vulnerable to predation than adults (Rohner and Krebs, 1996), and coyotes and gray foxes probably produce their young production at the beginning of the wet season (Fritzell and Haroldson, 1982). Also, during the wet season the savanna remains wet after heavy or continuous rains and would not impede gray fox or coyote movement, but young hares may sink in the substrate, decreasing their speed while running (Cox et al., 1997). However, during the dry season juvenile hares may be forced to increase movement in search of food, leading to increased predation mortality (Sievert and Keith, 1985; Rohner and Krebs, 1996).

Predation Mortality

Predation was the main cause of mortality for adult and juvenile tropical hares in this study. Radio-telemetry studies on hare survival and population dynamics show that different predators are responsible for the majority of hare deaths across age classes. Mammalian and raptor predators accounted for 83% of adult and juvenile deaths for snowshoe hares in boreal forests during four years of radio-tracking (Krebs et al., 1995). Predation, chiefly by coyotes, was the proximate cause of death among 96% of adult and juvenile snowshoe hares in fragmented habitat (Keith et al., 1993). Coyotes, lynx, goshawks, and owls killed 86% of weaned juveniles of snowshoe hare (Gillis, 1998), and squirrels killed 82% of preweaned leverets of snowshoe hare (O'Donoghue, 1994).

Coyotes and gray foxes are the main native predators of adult and juvenile tropical hares. I was unable to distinguish whether a radio-marked hare was killed by a coyote or a gray fox, and I have no quantitative indices of coyote or gray fox trends in the study area, but my impression from sightings and coyote-howling is that gray foxes are relatively more abundant than coyotes. Potential predators of newborn leverets in the study area are native snakes (*Boa spp*.; Villa and Cervantes, 2003), and domestic dogs are capable of killing young tropical hares (Vargas, 2000).

Poaching and Induced-Fire Mortality

Human-induced fires in the savanna accounted for 20% of adult deaths of radiocollared tropical hares. If adult hares are killed by human-induced fires, then it is evident that young hares may die during fires in the savanna, particularly leverets under parental care, and most likely at higher rates than adults. Induced fires for cattle-raising activities are common in the study area, but are an increasingly frequent practice (more than once per season) that jeopardizes the natural vegetation structure and diversity in the savannas of the Isthmus of Tehuantepec (Perez-Garcia et al., 2001).

Poaching mortality of tropical hares accounted for 13% of adult and 6% of juvenile deaths of radio-collared tropical hares. The study area is relatively inaccessible to non-local hunters and poaching rates reflect only occasional subsistence and leisure hunting by local residents. Tropical hares are not preferred game in the study area, but local hunters would kill a tropical hare if the opportunity arises. Poaching rates are likely to increase in future years because roads are being improved in the study area, thus opening easy access to non-local poachers who may come from nearby cities and decimate tropical hare populations in a few nights of sport hunting (Flux and Angermann, 1990; Lorenzo et al., 2000).

The tropical hare population under study has low juvenile survival, particularly of female juveniles, and its growth rate may be sensitive to any kind of additional mortality imposed on adults (Marboutin and Peroux, 1995), as fire and poaching mortality add to predation mortality.

Conservation Implications

Age- and sex-specific survival rates need to be combined with reproductive rates and age distribution data when assessing population dynamics of hares (Caughley, 1977), as well as with information on density, available habitat, isolation, immigration, and dispersal when species are of conservation concern (Caughley and Gunn, 1996). Populations of hares may have good adult survival, but low juvenile survival or reduced reproduction may produce a decrease in hare numbers (Marboutin and Peroux, 1995). Hare populations may have good reproduction and density, but low survival due to heavy predation and habitat fragmentation may stop increase in hare numbers (Keith et al., 1993).

The tropical hare population in this study faces habitat fragmentation and alteration, small population size, isolation from other populations, high predation rates, and low juvenile survival. Radio-telemetry research on demographic parameters should continue for estimation and monitoring of birth ratios, sex ratios, age structure, age- and sex- specific reproduction and survival rates, and to identify specific-predator mortality rates.

Predation was the main mortality cause for tropical hares in the study area. Because coyotes and gray foxes, native predators of hares, may be favored by humanaltered and deteriorated habitats (Fritzell and Haroldson, 1982), savannas need to be preserved to prevent further increase in coyote and gray fox densities. Savanna protection should include management of human-induced fires and eradication of poaching, which were mortality causes for a considerable proportion of radio-marked adult hares. Because juvenile survival was low, additional mortality imposed on adults by induced fires and poaching may negatively affect the growth rate of the tropical hare population (Marboutin and Peroux, 1995). Also, leverets of tropical hares may die during induced fires, and the number of grass and forb species found in savannas from the Isthmus of Tehuantepec are decreasing due to human-induced fires and cattle raising activities.

Survival estimates for juvenile and adult tropical hares were produced during this study, but demographic studies should continue. Besides age- and sex- specific survival rates, robust estimates of demographic parameters needed to develop models on population dynamics of tropical hare for conservation efforts are: age of first

reproduction, pregnancy rates, litter size, and number of litters produced per female per year. How to obtain these estimates from endangered and small populations that are very secretive in their nature becomes a challenge, which could probably be partially overcome through captive or semi-captive breeding of tropical hares.

Literature Cited

- Bednarz, J. 1977. The white-sided jackrabbit in New Mexico: distribution, numbers, and biology in the grasslands of Hidalgo County. Unpublished manuscript. New Mexico Department of Game and Fish, USA. 33 pp.
- Best, T. L. 1996. Lepus californicus. Mammalian Species 530: 1-10.
- Best, T. L., and T. H. Henry. 1993a. Lepus alleni. Mammalian Species 424: 1-8.
- Best, T. L., and T. H. Henry. 1993b. Lepus callotis. Mammalian Species 442: 1-6.
- Boutin, S. A. 1984. The effect of conspecifics on juvenile survival and recruitment of snowshoe hares. Journal of Animal Ecology 53: 623-637.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons. New York. 232 pp.
- Caughley G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science. Cambridge, Massachusetts. 459 pp.
- Cervantes, F. A., and L. Yépez. 1995. Species richness of mammals from the vicinity of Salina Cruz, coastal Oaxaca, Mexico. Anales del Instituto de Biología Universidad Nacional Autónoma de México, Serie Zoología 66: 113-122.
- Cox, E. W., R. A. Garrott, and J. R. Cary. 1997. Effects of supplemental cover on survival of snowshoe hares and cottontail rabbits in patchy habitat. Canadian Journal of Zoology 75:1357-1363.
- Flux, J. E. C. 1981. Reproductive strategies in the genus *Lepus*. Pp. 377-394 in: Proceedings of the World Lagomorph Conference (Myers, K. and C. D. Mac Innes, eds.). August 12-16, 1979. University of Guelph, IUCN/SSC, World Wildlife Fund. Ontario, Canada. 983 pp.
- Flux, J. E. C., and R. Angermann. 1990. The hares and jackrabbits. Pp. 61-94 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.) Chapter 4. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Frankham, R., J. D. Ballow, and D. A. Briscoe. 2002. The broader context: population viability analysis (PVA). Pp. 504 – 529 in: Introduction to Conservation Genetics. Cambridge University Press. 617 pp.
- Fritzell, E. K. and K. J. Haroldson. 1982. Urocyon cinereoargenteus. Mammalian Species 189:1-8.
- Fuller, T. K., E. C. York, S. M. Powell, T. A. Decker, and R. M. DeGraaf. 2001. An evaluation of territory mapping to estimate fisher density. Canadian Journal of Zoology 79:1691-1696.
- García, E. 1964. Modificaciones al sistema de clasificación climática de Kopen (para adaptarlo a las condiciones de la República Mexicana). Instituto de Geografía, UNAM. México, D. F.
- Gillis, E. A. 1998. Survival of juvenile hares during a cyclic population increase. Canadian Journal of Zoology 76: 1949-1956.
- Goodwin, D. L., and P. O. Currie. 1965. Growth and development of black-tailed jackrabbits. Journal of Mammalogy 46:96-98.
- Gross, J. E., L. C. Stoddart, and F. H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. Wildlife Monographs 40, 68 pp.
- Hale, M. B, and T. K. Fuller. 1996. Porcupine (Erethizon dorsatum) demography in central Massachusetts. Canadian Journal of Zoology 74:480.484.
- Hale, M. O., and T. K. Fuller. 1999. Estimating porcupine (*Erethizon dorsatum* Linnaeus, 1759) density using radiotelemetry and replicated mark-resight techniques. Z. Saugetierkunde 64:85-90.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668-674.
- Hodges, K. E. 1999. Proximate factors affecting snowshoe hare movements during a cyclic population low phase. Ecoscience 6:487-496.
- Keith, L. B., S. E. M. Bloomer, and T. Willebrand. 1993. Dynamics of a snowshoe hare population in fragmented habitat. Canadian Journal of Zoology 71: 1385-1392.
- Krebs, C. J. 1985. Ecology: The Experimental Analysis of Distribution and Abundance. 3rd Edition. Harper and Row. New York, USA.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science 269: 1112-1115.
- Lechleitner, R. R. 1958. Certain aspects of behavior of the black-tailed jack rabbit. The American Midland Naturalist 60:145-155
- Lechleitner, R. R. 1959. Sex ratio, age classes and reproduction of the black-tailed jack rabbit. Journal of Mammalogy 40:63-81.

- Lorenzo, C., O. Guiascon, F. A. Cervantes, J. Vargas, and G. Portales. 2000. Status survey of the critically endangered *Lepus flavigularis*. Final Report. El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, 5 pp.
- Marboutin E., and K. Hansen. 1998. Survival rates in a nonharvested brown hare population. Journal of Wildlife Management 62:772-779.
- Marboutin, E., and R. Peroux. 1995. Survival pattern of European hare in a decreasing population. Journal of Applied Ecology 32:809-816.
- Marín, A. I., L. Hernández, and J. W. Laundré. Predation risk and food quantity in the selection of habitat by black-tailed jackrabbit (*Lepus californicus*); and optimal foraging apporach. Journal of Arid Environments 55: 101-110.
- O'Donoghue, M. 1994. Early survival of juvenile snowshoe hares. Ecology 75:1582-1592.
- Pérez-García, E. A., J. Meave, and C. Gallardo. 2001. Vegetación y Flora de la Región de Nizanda, Istmo de Tehuatnepec, Oaxaca, México. Acta Botánica Mexicana 56:19-88.
- Péroux, R. 1995. Le liévre d'Europe. Bulletin Mensuel de l'Office National de la Chasse. No. 204. 96 pp.
- Rohner, C., and C. J. Krebs. 1996. Owl predation on snowshoe hares: consequences of antipredator behavior. Oecologia 108:303-310.
- Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management 49:854-866.
- Stoddart, L. C. 1984. Site fidelity and grouping of neonatal jack rabbits, *Lepus californicus*. Journal of Mammalogy 65: 136-137.
- Swihart, R. K. 1984. Body size, breeding season length,, and life history tactics of lagomorphs. Oikos 43:282-290.
- Vargas, J. 2000. Distribución, abundancia y hábitat de la liebre endémica *Lepus flavigularis* (Mammalia: Lagomorpha) Tesis de Maestría en Biología Animal, Facultad de Ciencias, UNAM. México, D. F. 70 pp.

- Villa, B., and F. A. Cervantes. 2003. Los mamíferos de México. Iberoamericana. Instituto de Biología, UNAM. México, D. F. 140 pp. and CD-rom.
- Vorhies, C. T., and W. P. Taylor. 1933. Life histories and ecology of jackrabbits *Lepus alleni*, and *Lepus californicus ssp.*, in relation to grazing in Arizona. University of Arizona Agricultural Experimental Station Technical Bulletin 49: 471-587.
- White, G. C. 1996. NOREMARK: population estimation from mark-resighting surveys. Wildlife Society Bulletin 24:50-52.
- White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pp. 288-331 in Research techniques in animal ecology, controversies and consequences (Boitani, L. and T. K. Fuller, eds.). Columbia University Press. New York. 442 pp.
- Zizumbo, D., and P. Colunga. 1982. Los Huaves. La apropiación de los recursos naturales. Universidad Autónoma Chapingo. México. 277 pp.

Hare ID	Dates	Days	Weight (g)	Gain per day (g)	Gain per 30 days (g)
JM35	06 Feb 02		520		
	16 Mar 02	38	1200	17.90	536.84
JM36	06 Feb 02		1140		
	13 Mar 02	35	1950	23.14	694.29
JM38	06 Feb 02		640		
	13 Mar 02	35	1000	10.29	308.57
JF51	08 Apr 02		900		
	05 Jun 02	57	1800	15.79	473.68
JF55	08 Apr 02		1700		
	17 Jun 02	69	2500	11.60	347.83
JF66	30 Apr 02		1050		
	16 Oct 02	46	2000	20.65	619.57
Mean		46.67			496.80
SD		13.81			150.89

Table 3.1. Gain in body weight of six young tropical hares (*Lepus flavigularis*) captured and recaptured in Llano Contreras, Oaxaca, Mexico.

Interv	al				
Length			No. of		vival
Season	(Days)	Sex	radio days	Rate	95% CI
Dry (Nov-Apr)	181	Female	1,602	1.00	1.00-1.00
		Male	1,476	0.61	0.38-1.00 ^a
		Both	3,078	0.79	0.63-0.96
Wet (May-Oct)	184	Female	1,716	0.53	0.31-0.88
		Male	1,734	0.59	0.37-0.94
		Both	3,450	0.56	0.39-0.79
Annual		Female	3,318	0.51	0.30-0.88
		Male	3,210	0.36	0.18-0.70
		Both	6,528	0.43	0.28-0.66

Table 3.2. Interval and annual survival rates for 25 adult (13 F, 12 M) radio-marked tropical hares (*Lepus flavigularis*) monitored at Llano Contreras, Oaxaca, Mexico, from February 2001 to July 2003.

^aTruncated at 1.00.

			Predation		Poaching		Fire	
Season	Sex	Age	Rate	95% CI ^a	Rate	95% CI	Rate	95% CI
Dry	female	adult	0.00		0.00		0.00	
		juvenile	0.94	0.79-1.00	0.00		0.00	
	male	adult	0.10	0.00-0.28	0.10	0.00-0.28	0.19	0.00-0.43
		juvenile	0.65	0.15-1.00	0.00		0.00	
Wet	female	adult	0.39	0.13-0.66	0.00		0.08	0.00-0.23
		juvenile	0.73	0.45-1.00	0.12	0.00-0.34	0.00	
	male	adult	0.33	0.07-0.59	0.08	0.00-0.24	0.00	
		juvenile	0.52	0.03-1.00	0.00		0.00	
Annual	female	adult	0.40	0.13-0.67	0.00		0.08	0.00-0.23
	male	adult	0.36	0.11-0.60	0.14	0.00-0.32	0.14	0.00-0.32

Table 3.3. Cause-specific mortality rates of 51 radio-marked tropical hares (*Lepus flavigularis*) monitored at Llano Contreras, Oaxaca, Mexico, from February 2001 to July 2003 (n = 31 mortalities).

^aTruncated at 0.00 or 1.00

Interv	al					
Length			No. of		Survival	
Season	(Days)	Sex	radio days	Rate	95% CI	
Dry (Nov-Apr)	181	Female	317	0.06	0.01-0.69	
		Male	340	0.35	0.08-1.00 ^a	
		Both	657	0.15	0.04-0.60	
Wet (May-Oct)	184	Female	672	0.15	0.04-0.61	
		Male	501	0.48	0.17-1.00 ^a	
		Both	1,173	0.25	0.10-0.61	

Table 3.4. Interval survival rates for 35 juvenile (21 F, 14 M) radio-marked tropical hares (*Lepus flavigularis*) monitored at Llano Contreras, Oaxaca, Mexico, from February 2001 to July 2003.

^aTruncated at 1.00.

Season	Month	Total no. of females captured	Number pregnant	Number lactating	Total	Percent
Dry	November	2	1	0	1	0.50
	December	1	0	0	0	0.00
	January	0				
	February	11	2	0	2	0.18
	March	0				
	April	4	2	1	3	0.75
Wet	May	1	0	1	1	1.00
	June	2	0	0	0	0.00
	July	0				
	August	0				
	September	1	0	0	0	0.00
	October	2	2	0	2	1.00

Table 3.5. Proportion of adult female tropical hares (*Lepus flavigularis*) that were pregnant or lactating when captured at Llano Contreras, Oaxaca, Mexico.

Season	Parameter	Adult	Juvenile	Total
Wet	Beginning number	27.03		
	Reproduction rate ^a	2.7F/adult =	72.97	100
	Survival rate ^b	0.56	0.25	
	Ending number	15.13	18.24	
Dry	Beginning number	33.38		
	Reproduction rate ^a	0.65F/adult =	=21.70	55.07
	Survival rate	0.79	0.15	
	Ending number	26.37	3.25	
Wet	Beginning number	29.62		
	Reproduction rate ^a	2.7F/adult =	79.78	109.60

Table 3.6. Hypothetical change for a population of 100 adult and juvenile female tropical hares (*Lepus flavigularis*). Average annual rate of change (?) equals 1.10 (i.e., 109.6/100), with a stable age distribution of 27% and 61% adults (i.e., 27/[27+73] and 33/[33+21]) during the wet and dry season, respectively.

^aReproduction was calculated as: (no. of adult females) x (1.00 = proportion pregnant) x (1.35 female young per female x 2 litters) for the wet season (01 May to 31 Oct), and as: (no. of adult females) x (1.00) x (0.65 female young per female x 1 litter) for the dry season (01 Nov to 30 Apr).

^bSurvival rates are pooled estimates for adults during the wet and dry seasons, and for juveniles during the wet and dry seasons.

CHAPTER 4

CONSERVATION OF TROPICAL HARE POPULATIONS

Abstract

The tropical hare (*Lepus flavigularis*) is an endangered leporid endemic of Oaxaca, Mexico, where only three small and isolated populations survive in vanishing savannas and grassy dunes. The present work summarizes available information on tropical hare biology, and generates guidelines relevant for developing potential conservation strategies. Main recommendations are to inform local people about the endangerment of tropical hares, to propose a natural area for hare conservation, and to continue research on hare populations. Public education programs on wildlife conservation for local people and authorities are urgently needed to enforce conservation laws that protect tropical hares and to integrate local people into further conservation strategies. Savannas need to be legally protected for the conservation of tropical hares, and cattle-raising activities, agriculture, and human settlements should be avoided in prime hare habitat. Research should continue on determining demographic parameters needed to develop models of tropical hare population dynamics, and to identify mortality rates caused by specific predators.

Key words: conservation, habitat, *Lepus flavigularis*, Mexico, radio-telemetry, savanna, Tehuantepec jackrabbit, tropical hare.

Introduction

The tropical hare (*Lepus flavigularis*) is an endangered leporid endemic of Oaxaca, Mexico, where three populations survive in vanishing savannas and grassy dunes (Flux and Angermann, 1990; Lorenzo et al., 2000). Habitat loss and fragmentation, small population size, genetic isolation, and poaching threaten tropical hare populations (Chapman et al., 1990). Savannas are prime habitat that needs to be preserved for the conservation of tropical hares, but instead remnant savannas are being altered by cattleraising activities, agriculture, and human settlements (Flux and Angermann, 1990; Cervantes, 1993). Tropical hares are protected by Mexican and international legislation, but local authorities do not enforce conservation laws and hares are hunted for sport by non-local poachers, or are killed occasionally for subsistence by resident people (Flux and Angermann, 1990; Lorenzo et al., 2000, Vargas, 2001).

Lack of scientific knowledge on the biology of tropical hares hampered past efforts to develop conservation strategies or management plans (CSBG, 1996). Ecological research on tropical hares, begun in 2002, produced sound information on home range, habitat selection, activity patterns, survival and mortality causes, and preliminary data on reproduction and density. Conservation efforts may now be guided by recent information on ecology and population dynamics of tropical hares.

The present work summarizes available information on tropical hare biology, and generates guidelines and recommendations relevant for developing conservation strategies.

Results

Geographic Range, Extent of Occurrence, and Area of Occupancy

The former range of the tropical hare is not documented in detail, but the geographic distribution of *Lepus flavigularis* is entirely tropical and represents the southernmost limit of the genus in North America (Hall, 1981). The leporid was named Tehauntepec jackrabbit (or hare) after its geographic range estimated along the Mexican

Pacific coast on the Isthmus of Tehuantepec from Salina Cruz in Oaxaca to Tonala in Chiapas (Nelson, 1909; Hall, 1981), an area of perhaps only 5,000 km² (Fig. 2.1). The tropical hare was a rare species even before recent habitat changes.

Recently, the extent of occurrence for three remnant populations of tropical hare was estimated in about 520 km² (Lorenzo, personal communication). One population is found near Santa Maria del Mar on the sand bar separating the southern rim of Inferior Lagoon from the Gulf of Tehuantepec, along a distance of 5 km. The second population is located on an approximately continuous savanna between San Dionisio del Mar and Montecillo Santa Cruz on the northern rim of Inferior Lagoon. San Dionisio del Mar and Montecillo Santa Cruz are separated by 21 km of road. The third population inhabits grassy dunes on the sand bar of San Francisco del Mar Puerto Viejo on the southeast rim of Inferior Lagoon, along a distance of 13 km (Fig. 1.1). Tropical hares have not been found in Chiapas (Retana and Lorenzo, 2002).

Based on direct observations and surveys since the year 2000, the area of occupancy was estimated in as few as 5 km² for the tropical hare population in Santa Maria del Mar (Vargas, 2000), 47 km² for the population between San Dionisio del Mar and Montecillo Santa Cruz (Lorenzo, pers. comm.), and maybe 15 km² for the population in San Francisco del Mar Pueblo Viejo (Lorenzo, pers. comm.).

Habitat Use

In previous studies, tropical hares were observed in grassy habitats with scattered shrubs and trees, open grassy shrublands, and coastal grassy dunes, but not in agricultural lands, deteriorated and overgrazed grasslands, or in continuous dense vegetation (Lorenzo et al., 2000; Vargas, 2000; Lorenzo, 2001). Tropical dry savannas of native

grasses (grama, *Bouteloua spp.*, and paspalum, *Paspalum spp.*) with sparse bushes and trees (i. e. nanche, *Byrsonima crassifolia*, and morro, *Crescentia spp.*) were selected by radio-marked tropical hares for home range establishment (Chapter 2). Grassy habitats with scattered shrubs provide other hare species with both the visibility to detect predators from some distance, and the protective cover to reduce chances of being detected or tracked by a predator (Lechleitner, 1958; Longland, 1991). Habitat use within home range of radio-marked tropical hares favored savanna with bushes of *Byrsonima crassifolia* for resting and savanna with scattered trees of *Crescentia* for foraging, avoided dense vegetation, and underused grassy habitats with no vegetation cover (Chapter 2).

Home Range and Temporal Ecology

Home range overlap with more than one individual suggest that tropical hares are polygamous in their mating behavior, and non-territorial in their social organization. Annual home range and core area sizes of 10 radio-marked tropical hares averaged 0.56 km² (range = $0.28 - 1.00 \text{ km}^2$) and 0.09 km^2 (range = $0.02 - 0.13 \text{ km}^2$) for adults of both sexes using the 95% and 50% fixed kernel isopleths, respectively (Chapter 1). Seasonality seemed not to influence range size for radio-marked hares, and seasonal home ranges varied from 0.22 to 1.11 km² for 15 home ranges of adult females, and from 0.24 to 1.66 km² for 16 home ranges of adult males.

Radio-marked tropical hares were most active during crepuscular and nocturnal hours and rested during diurnal hours (Chapter 2).

Survival and Cause-Specific Mortality

Annual survival was higher for adult females (0.51) than for adult males (0.36), and the pooled estimate was 0.43 for 25 radio-marked adult tropical hares (Chapter 3). Adult survival during the wet season (0.56) was lower than during the dry season (0.79), particularly for female hares. Survival of 21 juvenile females was low during both dry (0.06) and wet (0.15) seasons when compared with survival of 14 juvenile males (0.35 and 0.48, respectively; Chapter 3).

Predation was the major cause of 31 mortalities of radio-marked tropical hares and accounted for 67% of adult and 94% of juvenile deaths (Chapter 3). Gray foxes (*Urocyon cinereoargenteus*) and coyotes (*Canis latrans*) are the main native predators of tropical hares. Human-induced fires in the savanna and poaching accounted for 20% and 13% of adult deaths, respectively (Chapter 3).

Preliminary Data on Reproduction, Sex Ratios, and Density

Pregnant females were found from February to December, but the proportion of pregnant females was higher during the wet season. The mean number of embryos from six museum specimens was 2.0 (range 1 to 4). Sex ratios for 79 captured tropical hares did not differ from 1:1 (Chapter 3).

Density of tropical hares was estimated based on direct observation and surveys of the three known populations (Vargas, 2000; Santis, 2002). In Santa Maria del Mar, density was estimated to be a maximum of 11.5 and a minimum of 0.8 hares per km² (Vargas, 2000). A mean density of 6.0 hares per km² was estimated for the population near Montecillo Santa Cruz, and a mean density of 6.5 hares per km² for the population near San Francisco del Mar Pueblo Viejo (Santis, 2002). Densities of tropical hares are

higher during the wet season when compared to the dry season (Lorenzo et al., 2000; Vargas, 2000; Santis, 2002).

I estimated a potential maximum density of 11.8 adult hares per km^2 for the tropical hare population near Montecillo Santa Cruz by analyzing the size of the core area of home ranges (Fuller et al., 2001). I assumed that tropical hares do not overlap core areas in their home ranges, that core area size is similar between sexes for adult hares, and that average core area size is 0.085 km² (Chapter 3).

Threats for Tropical Hare Populations

Degradation of savannas threatens the survival of tropical hare populations. Savanna vegetation appears to provide the most important habitat for tropical hares, and savanna is the natural vegetation structure in the region. The number of native grass and forb species found in savannas from the Isthmus of Tehuantepec is very rich (Perez-Garcia, 2001), but introduction of exotic grasses and human-induced fires are reducing this plant diversity (G. Davidse and M. Sousa, pers. comm.). Plant diversity found in the study area is important yet poorly studied, and may be degraded by ongoing cattle-raising activities (Perez-Garcia, 2001).

Telemetry research indicated high predation rates and low juvenile survival due to predation in the studied population of tropical hares (Chapter 3). Savannas inhabited by hares need to be preserved because coyotes and gray foxes, native predators of hares, may be favored by human-altered and deteriorated habitats (Fritzell and Haroldson, 1982). Human-induced fires turn savannas into open habitats devoid of vegetation cover for protection from predators, and grassy habitats with no cover may pose higher predation risk for tropical hares than grassy habitats with scattered vegetation cover

(Chapter 2). Radio-marked adult tropical hares died during induced fires in the savanna, so it is clear that newborn and young hares may be killed by fire as well (Chapter 3).

Poachers may come from nearby cities and decimate tropical hare populations in a few nights of sport hunting (Flux and Angermann, 1990; Lorenzo et al., 2000) because conservation laws to protect the tropical hare are not enforced by local authorities. Poaching accounted for 13% of adult and 6% of juvenile deaths of radio-marked tropical hares, but these numbers reflect only occasional subsistence and sport hunting by resident people on the studied population because the study area was relatively inaccessible to non-local hunters.

Conservation Actions in Place

The only conservation action in place is the protection of tropical hares by Mexican and international conservation laws, but this legal protection is failing because local authorities in Mexico do not enforce conservation laws. The tropical hare is listed as critically endangered in the Mexican official norm NOM-059-ECOL-2001 on endangered wildlife. The current Red List of endangered species of the International Union for the Conservation of Nature (IUCN) lists the tropical hare as endangered, and the assessment may be changed to list the tropical hare as critically endangered because of the genuine change in status of the species generated by new and better information available (Andrew Smith, pers. comm.). The distribution range of tropical hares is not included within protected natural areas in Mexico.

Discussion

Guidelines for Conservation of Tropical Hares

Public education programs on wildlife conservation are urgently needed to integrate local people and authorities into conservation actions for the tropical hare and its habitat. Local people and authorities are unaware of the uniqueness and endangerment of tropical hares and savannas in the Isthmus of Tehuantepec, and do not enforce conservation laws to protect endangered wildlife. People in rural areas in the Isthmus of Tehuantepec, particularly in Oaxaca, are among the most marginalized people in Mexico. People living near tropical hare populations obtain food, building materials, and fuel from savannas, and may greatly benefit from educational programs oriented for conservation management of hare prime habitat. Local people need to be informed and aware of wildlife conservation issues in their homelands to accept and integrate conservation efforts into strategies implemented in the region.

Savanna vegetation needs to be legally protected for the conservation of tropical hares, and cattle-raising activities, agriculture, and human settlements should be avoided. Savannas inhabited by tropical hares are not legally protected natural areas in Mexico, and thus are used as private livestock corrals by ranchers who pay annual rents to local authorities. A conservation area needs to be proposed based on information on habitat selection by tropical hares and using a geographic information system to connect hare populations by corridors of restored vegetation. Until the designation of a natural protected area for tropical hares is achieved, hare habitat may be protected by Mexican government agencies and/or national and international non-government organizations (NGO) paying the rent or rights of use of savannas inhabited by hares.

However, cattle-raising activities give tropical hares protection from poaching. Wire-fences built by ranchers tend to discourage non-local poachers from introducing vehicles into savannas inhabited by hares. Poachers do not trespass or cut wire-fences to avoid confrontation with ranchers and local people, but they would not respect fenced savannas without cattle. Thus, until conservation laws protecting tropical hares from poaching are enforced, cattle density may need to be gradually reduced to a minimum that would guarantee poaching inhibition.

Further Research to Enhance Conservation Actions

Research on demographic parameters should continue for estimation and monitoring of birth ratios, sex ratios, age structure, age- and sex- specific reproduction and survival rates, dispersal, and density of tropical hare populations.

Reliable estimates of age of first reproduction, pregnancy rates, litter size, and number of litters produced per female per year are needed to develop models on population dynamics of tropical hare for conservation efforts.

Research on mortality causes of tropical hares should continue and be targeted to identify mortality rates caused by specific predators, for potential predator management plans and hare mortality reduction.

Research on food habits of tropical hares and its relation to plant biodiversity in savannas should be pursued in order to enhance knowledge of tropical hare biology for conservation efforts.

Literature Cited

Cervantes, F. A. 1993. Lepus flavigularis. Mammalian Species 423:1-3.

- Chapman, J. A., J. E. C. Flux, A. T. Smith, D. J. Bell, G. G. Ceballos, K. R. Dixon, F. C. Dobler, N. A. Formozov, R. K. Ghose, W. L. R. Oliver, T. Robinson, E. Schneider, S. S. Stuart, K. Sugimurua, and Z. Changlin. 1990. Conservation action needed for rabbits, hares, and pikas. Pp. 154-168 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.). Chapter 14. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- CBSG, 1996. International Workshop for the Conservation of Mexican Lagomorphs in Danger of Extinction. Inform. Apple Valley, MN 55124 USA: IUCN/SSC Conservation Breeding Specialist Group.
- Flux, J. E. C., and R. Angermann. 1990. The hares and jackrabbits. Pp. 61-94 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.) Chapter 4. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Fuller, T. K., E. C. York, S. M. Powell, T. A. Decker, and R. M. DeGraaf. 2001. An evaluation of territory mapping to estimate fisher density. Canadian Journal of Zoology 79:1691-1696.
- Hall, E. R. 1981. The mammals of North America. 2nd edition. John Wiley and Sons. New York. 1:1-609.
- Lechleitner, R. R. 1958. Certain aspects of behavior of the black-tailed jack rabbit. The American Midland Naturalist 60:145-154.
- Longland, W. S. 1991. Risk of predation and food consumption by black-tailed

jackrabbits. Journal of Range Management 44:447-450.

- Lorenzo, C. 2001. Conservation of the critically endangered *Lepus flavigularis*. Final Report. Lincoln Park Zoo Neotropic Fund. 10 pp.
- Lorenzo, C., O. Guiascon, F. A. Cervantes, J. Vargas, and G. Portales. 2000. Status survey of the critically endangered *Lepus flavigularis*. Final Report. El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, 5 pp.

Nelson, E. W. 1909. The rabbits of North America. North American Fauna 29:9-287.

- Pérez-García, E. A., J. Meave, and C. Gallardo. 2001. Vegetación y Flora de la Región de Nizanda, Istmo de Tehuatnepec, Oaxaca, México. Acta Botánica Mexicana 56:19-88.
- Retana, O. G., and C. Lorenzo. 2002. Lista de los mamíferos terrestres de Chiapas: endemismo y estado de conservación. Acta Zoológica Mexicana (Nueva serie) 85:25-49.
- Sántis, E. C. 2002. Distribución y abundancia de la liebre endémica Lepus flavigularis y el conejo castellano Sylvilagus floridanus (Mammalia: Lagomorpha) en el Istmo de Tehuantepec, Oaxaca, México. Tesis de Licenciado en Biología. Universidad de Ciencias y Artes de Chiapas. Tuxtla Gutierrez, Chiapas, México. 70 pp.
- Vargas, J. 2000. Distribución, abundancia y hábitat de la liebre endémica *Lepus flavigularis* (Mammalia: Lagomorpha) Tesis de Maestría en Biología Animal, Facultad de Ciencias, UNAM. México, D. F., 70 pp.
- Vargas, Z. 2001. Valoración de los vertebrados terrestres por los huaves y zapotecas de la zona lagunar del Istmo de Tehuantepec, Oaxaca. Tesis de Maestría. El Colegio de la Frontera Sur. Chiapas, México. 46 pp.

BIBLIOGRAPHY

- Aanes, R., and R. Andersen. 1996. The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. Canadian Journal of Zoology 74: 1857-1865.
- Aebischer, N. J., and P. A. Robertson. 1992. Practical aspects of compositional analysis as applied to pheasant habitat utilization. Pp. 285-293 in Telemetry: remote monitoring and tracking of animals (I. G. Priede and S. M. Swift, eds.). Wildlife Ellis Horwood. Chichister; England.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.
- Anderson, S., and A. B. Gaunt. 1962. A classification of the white-sided jackrabbits of Mexico. American Museum Novitates 2088: 1-16.
- Bednarz, J. 1977. The white-sided jackrabbit in New Mexico: distribution, numbers, and biology in the grasslands of Hidalgo County. Unpublished manuscript. New Mexico Department of Game and Fish, USA. 33 pp.
- Best, T. L. 1996. Lepus californicus. Mammalian Species 530: 1-10.
- Best, T. L., and T. H. Henry. 1993a. Lepus alleni. Mammalian Species 424: 1-8.
- Best, T. L., and T. H. Henry. 1993b. Lepus callotis. Mammalian Species 442: 1-6.
- Boutin, S. 1984. Effect of late winter food addition on numbers and movements of snowshoe hares. Oecologia 62:393-400.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons. New York. 232 pp.
- Caughley G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science. Cambridge, Massachusetts. 459 pp.
- CBSG, 1996. International Workshop for the Conservation of Mexican Lagomorphs in Danger of Extinction. Inform. Apple Valley, MN 55124 USA: IUCN/SSC Conservation Breeding Specialist Group.

Cervantes, F. A. 1993. Lepus flavigularis. Mammalian Species 423:1-3.

Cervantes, F. A., and C. Lorenzo. 1997. Morphometric differentiation of rabbits (*Sylvilagus* and *Romerolagus*) and jackrabbits (*Lepus*) of Mexico. Gibier Faune Sauvage 14:405-425.

- Cervantes, F. A., and L. Yépez. 1995. Species richness of mammals from the vicinity of Salina Cruz, coastal Oaxaca, Mexico. Anales del Instituto de Biología Universidad Nacional Autónoma de México, Serie Zoología 66: 113-122.
- Chapman, J. A., J. E. C. Flux, A. T. Smith, D. J. Bell, G. G. Ceballos, K. R. Dixon, F. C. Dobler, N. A. Formozov, R. K. Ghose, W. L. R. Oliver, T. Robinson, E. Schneider, S. S. Stuart, K. Sugimurua, and Z. Changlin. 1990. Conservation action needed for rabbits, hares, and pikas. Pp. 154-168 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.). Chapter 14. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Cotè, I. M. 2003. Knowledge of reproductive behavior contributes to conservation programs. Pp. 77-92 in Animal behavior and wildlife conservation (Festa-Bianchet, M. and M. Apollonio, eds.) Chapter 6. Island Press. Washington, D. C. 380 pp.
- Cowan, D. P., and D. J. Bell. 1986. Leporid social behaviour and social organization. Mammalian Review 16:169-179.
- Cox, E. W., R. A. Garrott, and J. R. Cary. 1997. Effects of supplemental cover on survival of snowshoe hares and cottontail rabbits in patchy habitat. Canadian Journal of Zoology 75:1357-1363.
- Crooks, K. R, and D. Van Vauren. 1996. Spatial organization of the island fox (*Urocyon littoralis*) on Santa Cruz Island, California. Journal of Mammalogy 77:801-806.
- Daniel, A., J. Holechek, R. Valdez, A. Tembo, L. Saiwana, M. Fusco, and M. Cardenas. 1993. Jackrabbit densities on fair and good condition Chihuahuan desert range. Journal of Range Management 46:524-528.
- Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.
- Dunn, J. P., J. A. Chapman, and R. E. Marsh. 1982. Jackrabbits: *Lepus californicus* and allies. Pp. 124-145 in Wild mammals of North America: biology, management, and economics (Chapman, J. A. and G. A. Feldhamer, eds). The Johns Hopkins University Press. Baltimore, Maryland. 1147 pp.

- Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. Pp. 209-242 in: Radio tracking and animal populations. (Millspaugh J. J. and J. M Marzluff eds.) Chapter 8. Academic Press. San Diego, California. 474 pp.
- Flux, J. E. C. 1981. Field observations of behavior in the genus *Lepus*. Pp. 377-394 in: Proceedings of the World Lagomorph Conference (Myers, K. and C. D. Mac Innes, eds.). August 12-16, 1979. University of Guelp, IUCN/SSC, World Wildlife Fund. Ontario, Canada. 983 pp.
- Flux, J. E. C. 1981. Reproductive strategies in the genus *Lepus*. Pp. 155-174 in: Proceedings of the World Lagomorph Conference (Myers, K. and C. D. Mac Innes, eds.). August 12-16, 1979. University of Guelp, IUCN/SSC, World Wildlife Fund. Ontario, Canada. 983 pp.
- Flux, J. E. C., and R. Angermann. 1990. The hares and jackrabbits. Pp. 61-94 in Rabbits, hares, and pikas. Status survey and conservation action plan (Chapman, J. A. and J. E. C. Flux, eds.) Chapter 4. International Union for Conservation of Nature and Natural Resources. Gland, Switzerland. 168 pp.
- Ford, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist 23:315-326.
- Forys, E. A., and S. R. Humphrey. 1996. Home range and movements of the Lower Keys Marsh Rabbit in a highly fragmented habitat. Journal of Mammalogy 77:1042-1048.
- Frankham, R., J. D. Ballow, and D. A. Briscoe. 2002. The broader context: population viability analysis (PVA). Pp. 504 529 in: Introduction to Conservation Genetics. Cambridge University Press. 617 pp.
- Fritzell, E. K. and K. J. Haroldson. 1982. Urocyon cinereoargenteus. Mammalian Species 189:1-8.
- Fuller, T. K., E. C. York, S. M. Powell, T. A. Decker, and R. M. DeGraaf. 2001. An evaluation of territory mapping to estimate fisher density. Canadian Journal of Zoology 79:1691-1696.
- García, E. 1964. Modificaciones al sistema de clasificación climática de Kopen (para adaptarlo a las condiciones de la República Mexicana). Instituto de Geografía, UNAM. México, D. F., México.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pp. 111-164 in Research techniques in animal ecology, controversies and consequences (Boitani, L. and T. K. Fuller, eds.). Columbia University Press. New York. 442 pp.

- Gillis, E. A. 1998. Survival of juvenile hares during a cyclic population increase. Canadian Journal of Zoology 76: 1949-1956.
- Goodwin, D. L., and P. O. Currie. 1965. Growth and development of black-tailed jackrabbits. Journal of Mammalogy 46:96-98.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140-1162.
- Griffith, R. E., and J. Evans. 1970. Capturing jackrabbits by night-lighting. Journal of Wildlife Management 34:637-639.
- Gross, J. E., L. C. Stoddart, and F. H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. Wildlife Monographs 40, 68 pp.
- Hale, M. B, and T. K. Fuller. 1996. Porcupine (Erethizon dorsatum) demography in central Massachusetts. Canadian Journal of Zoology 74:480.484.
- Hale, M. O., and T. K. Fuller. 1999. Estimating porcupine (*Erethizon dorsatum* Linnaeus, 1759) density using radiotelemetry and replicated mark-resight techniques. Z. Saugetierkunde 64:85-90.
- Hall, E. R. 1981. The mammals of North America. 2nd edition. John Wiley and Sons. New York. 1:1-609.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668-674.
- Hewson, R., and M. D. C. Hinge. 1990. Characteristics of the home range of mountain hares *Lepus timidus*. Journal of Applied Ecology 27:651-666.
- Hulbert, I. A. R., G. R. Iason, D. A. Elston, and P. A. Racey. 1996. Home-range sizes in a stratified upland landscape of two lagomorphs with different feeding strategies. Journal of Applied Ecology 33:1479-1488.
- Hulbert, I. A. R., G. S. Iason, and P. A. Racey. 1996. Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding stategies. Journal of Applied Ecology 33:315-324.
- Hodges, K. E. 1999. Proximate factors affecting snowshoe hare movements during a cyclic population low phase. Ecoscience 6:487-496.
- Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to arcview. Ver 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA.

- Keith, L. B., S. E. M. Bloomer, and T. Willebrand. 1993. Dynamics of a snowshoe hare population in fragmented habitat. Canadian Journal of Zoology 71: 1385-1392.
- Kernohan, B. J, R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 125-166 in: Radio tracking and animal populations. (Millspaugh J. J. and J. M Marzluff eds.) Chapter 5. Academic Press. San Diego, California. 474 pp.
- Komdeur, J., and C. Deerenberg. 1997. The importance of social behavior studies for conservation. Pp.262-276 in Behavioral approaches to conservation in the wild. (Clemmons, J. R. and R. Buchholz, eds.) Chapter 11. Cambridge University Press. Cambridge, United Kingdom. 380 pp.
- Krebs, C. J. 1985. Ecology: The Experimental Analysis of Distribution and Abundance. 3rd Edition. Harper and Row. New York, USA.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science 269: 1112-1115.
- Larivière, S., and F. Messier. 1998. Spatial organization of a prairie striped skunk population during the waterfowl nesting season. Journal of Wildlife Management 62: 199-204.
- Lechleitner, R. R. 1958. Certain aspects of behavior of the black-tailed jack rabbit. The American Midland Naturalist 60:145-154.
- Lechleitner, R. R. 1959. Sex ratio, age classes and reproduction of the black-tailed jack rabbit. Journal of Mammalogy 40:63-81.
- Lomolino, M. V., and R. Channell. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. Journal of Mammalogy 76:335-347.
- Longland, W. S. 1991. Risk of predation and food consumption by black-tailed jackrabbits. Journal of Range Management 44:447-450.
- Lorenzo, C. 2001. Conservation of the critically endangered *Lepus flavigularis*. Final Report. Lincoln Park Zoo Neotropic Fund. 10 pp.
- Lorenzo, C., O. Guiascon, F. A. Cervantes, J. Vargas, and G. Portales. 2000. Status survey of the critically endangered *Lepus flavigularis*. Final Report. El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas. 5 pp.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. Nature 301:379-384.

- Marboutin E., and K. Hansen. 1998. Survival rates in a nonharvested brown hare population. Journal of Wildlife Management 62:772-779.
- Marboutin, E., and R. Peroux. 1995. Survival pattern of European hare in a decreasing population. Journal of Applied Ecology 32:809-816.
- Marín, A. I., L. Hernández, and J. W. Laundré. Predation risk and food quantity in the selection of habitat by black-tailed jackrabbit (*Lepus californicus*); and optimal foraging apporach. Journal of Arid Environments 55: 101-110.
- Marzluff, J. M., S. T. Knick, and J. J. Millspaugh. 2001. High-tech behavioral ecology: modeling the distribution of animal activities to better understand wildlife space use and resource selection. Pp. 309-326 in: Radio tracking and animal populations. (Millspaugh J. J. and J. M Marzluff eds.) Chapter 12. Academic Press. San Diego, California. 474 pp.
- Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. Ecological Applications 2:178-188.
- Mongahan, P., and N. B. Metcalfe. 1985. Group foraging in wild brown hares: effects of resource distribution and social status. Animal Behavior 33: 993-999.
- Mohr, C. O. 1947. Table of equivalent populations of North American mammals. American Midland Naturalist 37:223-249.
- Nelson, E. W. 1909. The rabbits of North America. North American Fauna 29:9-287.
- O'Donoghue, M. 1994. Early survival of juvenile snowshoe hares. Ecology 75:1582-1592.
- Parker, P. G., and T. A. Waite. 1997. Mating systems, effective population size, and conservation of natural populations. Pp.243-261 in Behavioral approaches to conservation in the wild. (Clemmons, J. R. and R. Buchholz, eds.) Chapter 10. Cambridge University Press. Cambridge, United Kingdom. 380 pp.
- Pérez-García, E. A., J. Meave, and C. Gallardo. 2001. Vegetación y Flora de la Región de Nizanda, Istmo de Tehuatnepec, Oaxaca, México. Acta Botánica Mexicana 56:19-88.
- Péroux, R. 1995. Le liévre d'Europe. Bulletin Mensuel de l'Office National de la Chasse. No. 204. 96 pp.

- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65-110 in Research techniques in animal ecology, controversies and consequences (Boitani, L. and T. K. Fuller, eds.). Columbia University Press. New York. 442 pp.
- Revilla, E., F. Palomares, and M. Delibes. 2000. Defining key habitats for low density populations of Eurasian badgers in Mediterranean environments. Biological Conservation 95: 269-277.
- Retana, O. G., and C. Lorenzo. 2002. Lista de los mamíferos terrestres de Chiapas: endemismo y estado de conservación. Acta Zoológica Mexicana (Nueva serie) 85:25-49.
- Rohner, C., and C. J. Krebs. 1996. Owl predation on snowshoe hares: consequences of antipredator behavior. Oecologia 108:303-310.
- Sántis, E. C. 2002. Distribución y abundancia de la liebre endémica *Lepus flavigularis* y el conejo castellano *Sylvilagus floridanus* (Mammalia: Lagomorpha) en el Istmo de Tehuantepec, Oaxaca, México. Tesis de Licenciado en Biología. Universidad de Ciencias y Artes de Chiapas. Tuxtla Gutierrez, Chiapas, México. 70 pp.
- Seaman, D.E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.
- Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management 49:854-866.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Company. New York. 887 pp.
- Stoddart, L. C. 1984. Site fidelity and grouping of neonatal jack rabbits, *Lepus californicus*. Journal of Mammalogy 65: 136-137.
- Swihart, R. K. 1984. Body size, breeding season length,, and life history tactics of lagomorphs. Oikos 43:282-290.

- Trapp, G. R., and D. L. Hallberg. 1975. Ecology of the gray fox (*Urocyon cinereoargenteus*): a review. Pp. 164-178 in The wild canids, their systematics, behavioral ecology, and evolution (M. S. Fox, ed.). Van Nostrand-Reinhold Co., New York. 508 pp.
- Vargas, J. 2000. Distribución, abundancia y hábitat de la liebre endémica *Lepus flavigularis* (Mammalia: Lagomorpha) Tesis de Maestría en Biología Animal, Facultad de Ciencias, UNAM. México, D. F. 70 pp.
- Vargas, Z. 2001. Valoración de los vertebrados terrestres por los huaves y zapotecas de la zona lagunar del Istmo de Tehuantepec, Oaxaca. Tesis de Maestría. El Colegio de la Frontera Sur. Chiapas, México. 46 pp.
- Villa, B., and F. A. Cervantes. 2003. Los mamíferos de México. Iberoamericana. Instituto de Biología, UNAM. México, D. F. 140 pp. and CD-rom.
- Vorhies, C. T., and W. P. Taylor. 1933. Life histories and ecology of jackrabbits *Lepus alleni*, and *Lepus californicus ssp.*, in relation to grazing in Arizona. University of Arizona Agricultural Experimental Station Technical Bulletin 49: 471-587.
- White, G. C. 1996. NOREMARK: population estimation from mark-resighting surveys. Wildlife Society Bulletin 24:50-52.
- White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pp. 288-331 in Research techniques in animal ecology, controversies and consequences (Boitani, L. and T. K. Fuller, eds.). Columbia University Press. New York. 442 pp.
- White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press. San Diego, California. 383 pp.
- Wolfe, A., and T. J. Hayden. 1996. Home range sizes of Irish mountain hares on coastal grassland. Biology and Environmental Proceedings of the Royal Academy 96B: 141-146.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.
- Zizumbo, D., and P. Colunga. 1982. Los Huaves. La apropiación de los recursos naturales. Universidad Autónoma Chapingo. México. 277 pp.