

PORCUPINES, PINYON PINES, AND PINE  
ENGRAVER BEETLES: MULTITROPHIC  
INTERACTIONS IN PINYON-JUNIPER  
WOODLANDS OF TEXAS

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Submitted to the Faculty of the  
Graduate College of the  
Oklahoma State University  
in partial fulfillment of  
the requirements for  
the Degree of  
DOCTOR OF PHILOSOPHY  
May, 2001

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## PREFACE

All chapters of this dissertation were written as manuscripts that will be submitted to peer-reviewed journals. Chapter 1, “Demographic and Behavioral Characteristics of the North American Porcupine (*Erethizon dorsatum*) in the Pinyon-Juniper Woodlands of Texas” follows the style and guidelines of The American Midland Naturalist. Chapter 2, “Porcupines, Pinyon and Pine Engravers: What’s the Connection?” follows style and format for Ecology. Chapter 3, “Porcupine Expansion and Establishment in the Edwards Plateau of Texas: a Dendrochronological Exploration” follows the style and format for Southwestern Naturalist.

## ACKNOWLEDGMENTS

Effective research is dependent on the combined efforts of numerous individuals. Above all, I wish to express my sincere gratitude to my major advisor Dr. Eric Hellgren who encouraged me to pursue my passion for the porcupine and has exhibited patience, tolerance, and support above and beyond the call of duty. He intuitively knew when to push and when to praise. We have worked together in the past and his willingness to work with me once again is a sign that he is either a great fool or a great friend—I'll stick with the latter! I have benefitted immensely from his tutelage over the years and hope that our professional paths will continue to cross.

My committee members, Drs. David M.. (Chip) Leslie, Jr., Ronald Masters, and William Ross provided support in many ways. They offered wise counsel, accepted angst-ridden calls from the field, and exhibited an uncommon willingness to work within my all-too-narrow time limits for meeting deadlines.

Dave Stuart and Daniel Klepper, superintendent and park ranger at Kickapoo, were absolutely essential to the project. Dave's personal curiosity was the inspiration behind development of the primary hypothesis of this research. He arranged for me to live in the "lodge" during my lengthy field tenure, provided an ATV for transportation, and granted unfettered access to every nook and cranny of Kickapoo Caverns State Park. He and Daniel wore many hats including postman, trapper, mechanic, and field technician. Most importantly, Dave and Daniel became cherished friends. We shared an immeasurable appreciation for the fauna and flora of Kickapoo, lots of laughter, good

meals, and great coffee. Tragically, in November 1999, Dave lost his battle with lymphoma. I regret that he never saw the results of the research he made possible.

I am equally grateful to fellow students who truly understood the depths of despair and the heights of triumph associated with graduate endeavors. Phil and Laila Lienesch, Cara Shillington, Brain McEwen, Jodi Whittier, and Rich Kazmaier provided friendship, support, and lively discussions and musings. I would like to believe that we sustained each other through the journey and I suspect that our meeting was more than a chance encounter.

My parents, Dick and Marie, always encouraged me and long ago accepted the truth that I “step to the beat of a different drummer”. Both saw me start this endeavor; regrettably neither lived to see its completion. I think they would have been pleased with the final product.

My brother Kurt brought “the Mule” when the ATV was incapacitated. He and his son Keenan also helped in the re-capture and release of porcupines after the research was complete. My sisters, Sue, Gretchen, and Carolyn provided constant moral support. Gretchen and Carolyn shared laughter when it was most needed, tears when we were shaken by common loss and tragedy,----and some great dining experiences!

The Mark Lacy Family, Sid and Shirley Rucker and Mark and Janice Ross, “Kickapoo regulars”, brightened my stay in the field. They provided fellowship, field assistance, and fun. Long-time friends, Sharyn and Gary Reynolds, the James Broadway Family, Lynda Morgan, and Linda MacNeilage have been a constant source of support and strength. Together we have traveled many rugged trails and along the way they showed me that miracles are more than fantasy. Debbie Broadway provided a constant

stream of uplifting e-mails and humorous gifts and survival packages at particularly stressful times.

I would be remiss if I failed to offer gratitude to the “Spirits of Kickapoo.” First and foremost, of course are the porcupines who endured my daily intrusions. They were incredible subjects who never failed to fascinate me. I hope my work will dispel some of the myths surrounding these unique mammals. They were not alone in garnering my sense of amazement. I was awed by the bats of Stuart Cave and Devil’s Sinkhole. I saw my first endangered black-capped vireos and was witness to many a fledgling taking its first flight. I had numerous encounters with the abundant ringtails—perhaps the subject of future research. Cries of red-tailed hawks soaring through the canyons, meteor showers, barking frogs, elf owls, foxes, a million stars unobscured by city lights, and raccoons tapping on the windows of the “lodge” are but a few of the benefits that come with extensive field work. The knowledge I gained and the pleasure I derived from this endeavor were beyond words. I left the park with a sense of sadness for the times that would never be again—much has changed. But I took with me a lifetime of memories.

Finally, I wish to dedicate this dissertation to the memories of my parents, Dick and Marie Ilse, and to my friend and mentor, Dave Stuart. Although their dances on this great planet ended much too soon, their spirits will remain forever.

Funding for this research was provided by grants received from Rob and Bessie Welder Wildlife Foundation, Max McGraw Wildlife Foundation, Texas Parks and Wildlife Department, Oklahoma Cooperative Fish and Wildlife Research Unit (Okla. State Univ., Okla. Dep. of Wildl. Conserv., U.S.G.S. Biolo. Resour. Div., Wildl., Manage. Inst.

Inst. Cooperating), Theodore Roosevelt Memorial Fund of the American Museum of Natural History, American Society of Mammalogists, and Sigma Xi.

## TABLE OF CONTENTS

| Chapter   | Page |
|---|------|
| <b>I. DEMOGRAPHIC AND BEHAVIORAL CHARACTERISTICS OF<br/>NORTH AMERICAN PORCUPINES (ERETHIZON DORSATUM)<br/>IN PINYON JUNIPER WOODLANDS OF TEXAS</b> . . . . . 1 |      |
| Abstract  | 1    |
| Introduction  | 1    |
| Materials and Methods   | 3    |
| Study area  | 3    |
| Animal capture and handling   | 4    |
| Survival and reproduction   | 4    |
| Population modeling   | 5    |
| Results   | 6    |
| Capture and monitoring  | 6    |
| Survival and reproduction   | 6    |
| Population growth and density   | 8    |
| Discussion  | 8    |
| Literature Cited  | 13   |
| <br><b>II. PORCUPINES, PINYON PINES, AND PINE ENGRAVERS:<br/>WHAT'S THE CONNECTION?</b> . . . . . 23  |      |
| Abstract  | 23   |
| Introduction  | 24   |
| Methods and Materials   | 29   |
| Study area  | 29   |
| Animal capture and handling   | 30   |
| Tree selection  | 30   |
| Morphology of transect trees  | 30   |
| Physiology of transect trees  | 29   |
| Experimental manipulation   | 32   |
| Statistical analyses  | 33   |
| Results   | 34   |
| Selection of trees by porcupines  | 34   |
| Morphology of transect trees  | 34   |
| Physiology of transect trees  | 35   |
| Experimental-manipulation   | 37   |



| Chapter  | Page |
|--|------|
| Discussion .....   | 38   |
| Selection of trees by porcupines .....   | 38   |
| Selection of trees by beetles .....  | 40   |
| Experimental manipulation .....  | 43   |
| Ecological and Conservation Implications .....   | 45   |
| Literature Cited .....   | 49   |
|  |      |
| III. PORCUPINE EXPANSION AND ESTABLISHMENT IN THE<br>EDWARDS PLATEAU OF TEXAS: A DENDROECOLOGICAL<br>EXPLORATION ..... | 78   |
| Abstract .....   | 78   |
| Introduction .....   | 78   |
| Methods and Materials .....  | 80   |
| Results .....  | 82   |
| Discussion .....   | 83   |
| Literature cited .....   | 88   |
|  |      |
| APPENDIX. MORPHOMETRIC DATA FOR PORCUPINES .....   | 104  |

## LIST OF TABLES

| Table   | Page |
|---|------|
| I. 1. Causes of porcupine mortality .....   | 18   |
| II.1. Use and Availability of Dominant Tree Species .....   | 61   |
| II.2. Morphological Characteristics of Pinyon Pines Used by<br>Porcupines and Pine Engraver Beetles .....       | 62   |
| II.3. Percent Composition of Monoterpenes in Pinyon<br>Pines Used by Porcupines and Pine Engraver Beetles ..... | 63   |

## LIST OF FIGURES

| Figure  | Page |
|---|------|
| I. 1. Location of Kickapoo Caverns State Park . . . . .   | 20   |
| I. 2. Survival Rates of Adult/Yearling Porcupines . . . . .   | 22   |
| II.1. Study Site, Kickapoo Caverns State Park . . . . .   | 65   |
| II.2. Transects Established for Sampling of Porcupine-<br>and Bark Beetle-Damaged Trees . . . . .                                       | 67   |
| II.3. Association of Bark Beetle Activity on Porcupine-Damaged and<br>Non-damaged Pinyon Pines . . . . .                                | 69   |
| II.4. Comparison of Resin Flow on Control and Manipulated (bark removed)<br>Pinyon Pines . . . . .                                      | 71   |
| II.5. Comparison of Fructose and Glucose Concentrations on Control<br>and Manipulated (bark removed) Pinyon Pines . . . . .             | 73   |
| II.6. Comparison of Percent Composition of Seven Major Monoterpenes<br>on Control and Manipulated (bark removed) Pinyon Pines . . . . . | 75   |
| II.7. Monthly Precipitation Patterns . . . . .  | 77   |
| III.1. Cross-section of Porcupine Feeding Scar . . . . .  | 94   |
| III.2. Transects Established on Kickapoo Caverns State Park . . . . .   | 96   |
| III.3. Histogram of Oldest Porcupine Feeding Scars Collected from<br>Papershell Pinyon Pines . . . . .                                  | 98   |
| III. 4. Histogram of Random Porcupine Feeding Scars Collected from<br>Papershell Pinyon Pines . . . . .                                 | 100  |
| III.5. Relationship Among Porcupine Feeding Scars, Rainfall, and Year . . . . .   | 102  |

## CHAPTER I

### DEMOGRAPHIC AND BEHAVIORAL CHARACTERISTICS OF NORTH AMERICAN PORCUPINES (*ERETHIZON DORSATUM*) IN PINYON JUNIPER WOODLANDS OF TEXAS

**ABSTRACT**-----The North American porcupine (*Erethizon dorsatum*) has expanded its range into the Edwards Plateau of Texas, an area harboring a disjunct relict population of papershell pinyon pine (*Pinus remota*). I captured 39 porcupines and monitored 37 of these animals by radiotelemetry from 1997 to 1999 to assess their demographic characteristics and determine their potential impact in this unique wooded ecosystem. The adult population was biased toward females (3 females:1 male), and annual rates of survival were greater ( $P < 0.01$ ) for adult females ( $S = 0.90$ , 95% CI = 0.77-1.00) than for adult males ( $S = 0.42$ , 95% CI = 0.00-0.85). Birth rates of reproductively mature females averaged 0.82 annually during the 3-year study. I calculated a mean reproductive rate of 0.41 (female young/female) based on birth rates and juvenile sex ratio. The estimated growth rate of 0.034 indicated that the study population was growing. Direct and indirect ecological effects of porcupines in this woodland ecosystem warrant investigation.

### INTRODUCTION

The North American porcupine (*Erethizon dorsatum*) maintains an extensive geographic distribution, yet studies of its ecology and demography have been conducted primarily in the northeastern United States (Dodge, 1967; Roze, 1989; Hale and Fuller, 1996; Griesemer *et al.*, 1995). Recently, Sweitzer and Berger (1993, 1997, 1998), and Sweitzer *et al.*, 1996) examined ecology of the porcupine in the Great Basin Desert region of Nevada. Taylor (1935), in Arizona, conducted the only extensive research of this

species toward the southern limits of its distribution. The porcupine has expanded its range in Texas (Davis and Schmidly, 1994) and is now found in pinyon-juniper woodlands of the Edwards Plateau. It has been reported as far south as the western South Texas Plains (D. R. Synatzske, Texas Parks and Wildlife Department, pers. comm.) and as far east as the Gulf Coast Prairies (D. L. Drawe, Rob and Bessie Welder Wildlife Foundation, pers. comm.). The porcupines' potential negative impact on wooded ecosystems (Krefting *et al.*, 1962; Storm and Halvorson, 1967; Sullivan *et al.*, 1986) justifies attention to the ecological effects of changes in its distribution and abundance.

Occurrence of porcupines in the Edwards Plateau is of particular importance because of the presence of a disjunct, relict population of papershell pinyon pine (*Pinus remota*). This pine was prolific throughout the Chihuahuan Desert before the Pleistocene, but has experienced a dramatic reduction in range and, today, is found only in parts of northeastern Mexico, parts of Big Bend National Park, and an isolated area on the Balcones escarpment of the Edwards Plateau in Texas (Betancourt, 1987; Wells, 1987).

Vulnerability of this unique wooded ecosystem is exacerbated by presence of the pine engraver beetle (*Ips hoppingi*). Less aggressive than many bark beetles, *Ips* is often associated with stressed conditions. Outbreaks of this and other dendrophagic insects have been precipitated by lightning, fire, drought, and mechanical or physical injury (Anderson and Anderson, 1968; Mattson and Haack, 1987; Conner and Rudolph, 1995). Bark, particularly of softwoods, constitutes a major portion of the porcupine's winter diet (Dodge, 1967; Harder, 1979; Roze, 1984; Hendricks and Allard, 1988). Stress to pinyon pines from this activity may place trees at increased vulnerability to bark beetle infestation.

I examined porcupines in the Edwards Plateau region of Texas during 1996-1999 to assess population characteristics of this species and to verify reports that it was expanding into this area. I also estimated the population growth rate and density to assist in future studies evaluating the effects of porcupines on the woodland community.

## MATERIALS AND METHODS

*Study area.*--Research was conducted at the 2577 ha Kickapoo Caverns State Natural Area (KCSNA) located about 35 km north of Brackettville, Texas. The site straddles Kinney and Edwards counties in the southwestern region of the Edwards Plateau (Fig. I.1). Topography is predominantly steep limestone hills and deep canyons with elevations between 482-610 m. Average annual rainfall is about 45 cm (National Oceanic and Atmospheric Administration, 1999). No standing water or active springs are present on the site.

Shallow clay soils of east and north facing slopes supported pinyon-juniper-oak plant communities. In addition to the relict papershell pinyon pines, dominant tree species included Ashe juniper (*Juniperus ashei*), plateau live oak (*Quercus fusiformis*), Texas persimmon (*Diospyros texana*), and vasey oak (*Quercus pungens* var. *vaseyana*). Woody shrubs included evergreen sumac (*Rhus virens*), guajillo (*Acacia berlandieri*) prickly pear (*Opuntia* spp.), and Roemer acacia (*Acacia roemeriana*). Ground cover was represented by cedar panicgrass (*Dichanthelium pedicellatum*) and cedar sedge (*Carex planostachys*) in shaded areas, and sideoats grama (*Bouteloua curtipendula*) and hairy tridens (*Erioneuron pilosum*) in more open areas.

Shallow soils of the south and west facing slopes were dominated by guajillo plant communities and pinyon pines are restricted to lower slope regions. Shrub species

included guajillo, coyotillo (*Karwinskia humboldtiana*) and leatherstem (*Jatropha dioica*). Grasses included threeawn (*Aristida* spp.) and red grama (*Bouteloua trifida*).

Mottes of plateau live oak mixed with vasey oak and Ashe juniper were common in canyons and drainages where moisture was more abundant and soil was deeper. Pinyon pines and netleaf hackberry (*Celtis reticulata*) also occurred in these areas. Dominant grasses included threeawn and annual dropseed (*Sporobolus* spp.).

*Animal capture and handling.*--Porcupines were captured in cage-type live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) using apples and salt as bait (Hale and Fuller, 1996). An adjustable pole-mounted syringe facilitated capture of animals in trees or in dens. Animals were immobilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, A. H. Robbins, Richmond, Virginia) at 7 mg/kg body weight (Hale *et al.*, 1994). Individuals were weighed, sexed, and classified as adult, yearling or juvenile based on dentition patterns, pelage and weight (Dodge, 1982). All animals were marked with self-piercing ear tags (National Band and Tag Co., Newport, Kentucky) and individuals weighing  $\geq 1.5$  kg were outfitted with radio-transmitters (L&L Electronics, Manomet, Illinois) secured by nylon mesh collars. Reproductive status of adult females was determined by observation and evidence of lactation as indicated by manual expression of milk.

*Survival and reproduction.*--Radiotelemetry was used to monitor reproduction, survival and dispersal. Animals were located at least twice weekly from year to year and locations were assigned UTM (Universal Transverse Mercator) grid coordinates. I used the Kaplan-Meier product-limit method modified for staggered entry (Pollock *et al.*, 1989) to estimate annual survival (S) for all animals combined and for each sex-age class. I used

Z-tests to compare endpoint survival rates and log-rank tests to compare annual survival functions (Pollack *et al.*, 1989). All telemetry data were converted to a single year for analyses. Gross examination and field necropsies were performed on all dead porcupines to ascertain cause of death. Date of death was assumed to be the median date of the interval between last live observation and date animal was found dead.

Reproductive data, including litter size, were augmented by observation.

Extensive searches for juveniles were conducted in the vicinity surrounding all reproductively mature females during April-August to determine birth rate and litter size.

*Population modeling.*--Population growth rate was determined using the program VORTEX (Lacy, 1993) with demographic parameters (age-specific survival, sex ratio and reproductive rates) estimated from telemetric monitoring and observation. One thousand iterations were completed using an initial population of 100 animals and a carrying capacity of 1000 animals.

I derived two density estimates using my observations of animals, known home ranges and ArcView version 3.2 (Environmental Systems Research Institute, Redlands CA, USA). One estimate was based on observations of all individual porcupines, marked and unmarked, divided by total area within Kickapoo Caverns State Natural Area.

Analysis of animal locations indicated that 77% (1102 of 1427) of all porcupine locations on the study site occurred within 125 m of the dry creek beds central to canyons; hence, I considered this to be preferred porcupine habitat. I created a 250-m buffer around creek beds (125 m on either side) and derived an estimate of ecological density within this preferred habitat by dividing number of telemetered animals by the area surrounding all known home ranges within this buffer.



## RESULTS

*Capture and monitoring.*--I captured 39 animals and outfitted 37 (24F:13M) with radio-collars. Thirty-three animals were tracked > 1 month and monitoring totaled 27.3 porcupine-years. Adult sex ratio was female-biased ( $\chi^2 = 5.5$ ,  $df = 1$ ,  $P < 0.02$ ;  $n=17F$ , 5M), but yearling ( $n = 4F$ , 5M) and juvenile ( $n= 3F$ , 3M) sex ratios did not differ significantly from 1:1. Age structure of captured animals favored adults; however, juveniles were particularly difficult to detect amid dense vegetation and were presumably under-represented. Adult body mass differed ( $P < 0.001$ ) between adult males ( $\bar{x} = 10.1$  kg) and females ( $\bar{x} = 6.5$  kg).

The limited sample of juveniles in this study precluded conclusions regarding dispersal patterns; however, two of the three captured juvenile females disappeared from the study site and the collar of one of these animals was located 5 km from the site of capture. The remaining juvenile female survived, remained in the range of her initial capture, survived to yearling status and was alive when her collar was removed at the conclusion of the study. Of the three male juveniles, one lost its collar within 400 m of capture, one died of disease-related causes after attaining yearling status and the remaining animal maintained his original home range until his collar was removed at the conclusion of the study.

*Survival and reproduction.*--Annual survival rates for adults ( $S_{\text{female}} = 0.91$ , 95% CI = 0.77-1.00;  $S_{\text{male}} = 0.42$ , 95% CI = 0.00-0.85,  $P < 0.01$ ) and yearlings ( $S_{\text{female}} = 1.0$ ,  $S_{\text{male}} = 0.5$ , 95% CI = 0.00-1.00,  $P < 0.01$ ) differed between sexes and mirrored the skewed adult sex ratio (Fig. I.2). Mortalities were most prevalent during the early breeding season (September-October) and late winter-early spring (February-April). There was no

difference in the annual pattern of mortality for adults by sex ( $\chi^2 = 1.39$ ,  $P = 0.23$ ) or for yearlings by sex ( $\chi^2 = 1.0$ ,  $P = 0.23$ ).

Mortalities of seven (5M, 2F) radio-collared animals and three unmarked porcupines (undetermined sex) were recorded during the study. One yearling male died of injuries sustained during a fall from a tree and one adult male was shot by a hunter on an adjoining ranch. Two males, one yearling and one adult, perished of disease-related causes. The adult suffered from an ear infection that had passed into the brain. The juvenile exhibited diminished body condition at the time of its initial capture. Cause of death for the remaining animals could not be authenticated. Predation did not appear to be a factor during that period; however, tooth marks were observed on one carcass indicating that it was fed upon.

The only marked adult male whose cause of death could not be ascertained was first observed in declining physical condition in November 1998 during the breeding season. At this time, his collar was replaced, his weight had dropped and numerous deep cuts and scratches were observed on his body suggesting that he had engaged in combative interactions. Although wounds were treated, his overall condition continued to decline and when his body was discovered in February, he had acquired more wounds. Two of the other four radio-collared adult males exhibited similar wounds during the breeding season. Agonistic behavior was not observed during other periods of the study.

Breeding activities, apparent by increased observations of male/female pairs, vocalizations, and scent, began in late August and continued throughout December and early January. Presence of juveniles was evident from April to August. An annual birth rate of 0.82 was calculated by averaging birth rates of reproductively aged females of 1.0

(n = 3 females), 0.67 (n = 12) , and 0.80 (n = 10) for 1997, 1998, and 1999, respectively. Thirteen sexually mature females were monitored during the study, and six of these were known to give birth in successive years. Three were monitored only during one season but reproduced in that year. One was never observed with young. The remaining three were observed with young during one of two years that they were monitored. Observed litter size was always one and no yearlings were observed with juveniles. A mean reproductive rate during the study was calculated as 0.41 female young/adult female/year by incorporating birth rate, litter size ( $\bar{x} = 1.0$ ) and the observed 1:1 juvenile sex ratio.

*Population growth and density.*--I incorporated my estimates of adult reproductive rate (0.41) and survival rates ( $S_{\text{female}} = 0.91$ ,  $S_{\text{male}} = 0.38$  for adults and yearlings combined) in the population model. The lower survival rates for yearlings and adults combined reflects the death of animals captured as yearlings, but died after reaching adulthood. The limited number of juveniles in my sample precluded estimation of survival rates for this age class; but, I adopted the 0.38 estimated by Hale and Fuller (1996) for use in my population model. Applying those demographic parameters to my model,  $r$  was 0.034 ( $\lambda = 1.03$ ), indicating that the study population was growing at 3.4% annually. My estimates of density ranged from 1.9 porcupines/km<sup>2</sup> using the entire study area (25.7 km<sup>2</sup>) and total animals observed (n = 50) to 3.3 porcupines/km<sup>2</sup> using telemetered animals only (n = 37) divided by preferred habitat area (11.2 km<sup>2</sup>).

## DISCUSSION

My report of female-biased sex ratios and survival rates is consistent with previous examinations of porcupine demography (Dodge 1967; Roze; 1989; Hale and Fuller, 1996). The higher incidence of male mortality may be attributed to increased activity and

competition for mating opportunities during the breeding period as suggested by Hale and Fuller (1996). Porcupines exhibit a female-defense polygyny whereby males, responding to the characteristic olfactory and auditory signals of pre-estrous females, engage in active defense and competition (Sweitzer and Berger 1997). Roze (1989) and Sweitzer and Berger (1997) reported intense battling between males resulting in injury and quill impalements during the breeding season, but only Dodge (1982) related this behavior directly to an incidence of mortality.

Mortalities occurring during late winter and early spring likely reflect diminished body condition resulting from the nutrient-poor winter diet of porcupines that is dominated by inner bark (Oveson, 1983; Roze, 1984; Stricklan, 1986). Sweitzer and Berger (1993) determined that depletion of energy reserves occurs early in winter. Late in the season, animals are more vulnerable to deleterious effects of nutritional stress. Males may be at even greater risk during this period if they have entered the winter in diminished health as a result of competing for mates.

Although predation represented the most significant cause of mortality reported by Sweitzer *et al.* (1997; Table 1), it was not pivotal in my research or in reports by Roze (1989) and Hale and Fuller (1996). Predator control in the counties surrounding my study site (D. Stuart and K. Bryan, Texas Parks and Wildlife Department, pers. comm.) has almost eliminated coyotes (*Canis latrans*), but bobcats (*Lynx rufus*) remain extant. Mountain lions (*Felis concolor*) also exist in the area, albeit in limited abundance. Alternative prey, including opossum (*Didelphus virginianus*), desert cottontail (*Sylvilagus auduboni*), black-tailed jackrabbit (*Lepus californicus*), rock squirrels (*Spermophilus variegatus*), mice (*Peromyscus* spp.) and cotton rats (*Sigmodon hispidus*) are abundant in

the area and may constitute more easily available prey for existing predators. Additionally, the recent expansion of porcupines into this area may indicate a lack of familiarity by predators with porcupines as prey.

Climatic conditions and starvation have been reported as significant factors in porcupine mortality in other regions (Table I.1), but the milder climatic regime typical of the Edwards Plateau region of Texas weakens their influence in this area. Although interactions with humans accounted for only one mortality in my study, the possible impact of anthropogenic interactions as the population increases and expands poses perhaps the greatest threat to porcupines in this area.

Dispersal has been described as a response of animals to avoid inbreeding and competition for mates, and Greenwood (1980) reports that the majority of mammalian species exhibit male-biased dispersal. My results were consistent with those of Roze (1989) and Sweitzer and Berger (1998), who provide compelling evidence for an atypical pattern of female-biased natal dispersal in porcupines. These results contradict Greenwood's (1980) contention that mating systems often predict dispersal patterns and that in taxa exhibiting polygamous mate-defense, the limited sex is most likely to disperse. Roze (1989) suggested the female-biased sex ratio and increased resource demand on females during gestation and lactation provide probable cause for this anomaly, whereas Sweitzer and Berger (1998) indicate that avoidance of inbreeding provides the strongest explanation. The limited data available on porcupine dispersal suggests that research into this aspect of their ecology warrants greater scrutiny.

My estimated birth rate of 0.82 for females  $\geq 2$  y old is greater than observed by Hale and Fuller (0.63; 1996) who reported a declining population. Sweitzer and

Holcombe (1993) used hormonal analyses and ultrasound to estimate a birth rate of 0.92 for this same age group. These latter techniques were likely more complete relative to my observation and palpation techniques, and may explain their higher reported birth rates. Juveniles in my study were difficult to find due to dense vegetative cover, cryptic coloration, and hiding behavior. Hence, my estimate may be biased low. The lack of observed pregnancies and births in the yearling age class may be attributed to limited visibility and a small sample of this group. However, my observations are consistent with the low rates of reproduction reported for this age class by Roze (1989), Sweitzer and Holcombe (1993) and Hale and Fuller (1996).

Reliable methods of determining density have not been established for the porcupine. The arboreal habits of this mammal obscure its presence, precluding most estimates dependent on visual observation. I attempted to circumvent this shortcoming by estimating density based on observation, known home ranges, and preferred habitat, but I acknowledge that my estimates are likely underestimates of the true population density. My estimates are lower than the estimates reported in a variety of habitats and geographic regions that range in extremes from 0.4-34 porcupines/km<sup>2</sup> in Arizona (Taylor, 1935) to 38 porcupines/km<sup>2</sup> in Wisconsin (Krefting *et al.*, 1962). The methods used in obtaining these estimates, number killed per area, and number shot over a 10-m period, respectively, represent relative indices only and preclude valid comparison. I include these estimates to establish extremes in density estimation. More accurate estimates using feeding trails in snow (Roze 1984) were not feasible in my study region. However, I assert that KCSNA can support a greater population of porcupines than is currently present on the site. My

assertion is validated by the gradual rate of increase in my study population and the apparent use of areas not within the preferred areas surrounding creeks and canyons.

My findings support observations that porcupines are expanding their range in southwestern Texas (Davis and Schmidly, 1994). The availability of suitable habitat and the current growth rate of the study population suggest that this trend will continue under current conditions. I speculate that expansion of porcupines into this region of Texas has been precipitated by land use changes and predator control. The role of predation, specifically by mountain lions and fishers, in limiting porcupine populations has been documented by Taylor (1935), Powell and Brander (1977) and Sweitzer *et al.* (1997); however, the effects of coyote predation on porcupine populations has not been addressed.

Payette (1987) used dendrochronological data to validate expansion of porcupines in Quebec and hypothesized that climatic change affecting availability of resources stimulated this response. The potential for continued expansion of porcupines in the Edwards Plateau is affected by these factors and is amplified by the preponderance of females, and by high survival and reproductive rates.

Use of feeding trees by porcupines varies with geographic distribution and forest composition. Direct tree mortality resulting from porcupine feeding activity is limited (Curtis and Kozicky, 1944; Curtis and Wilson, 1953; Roze, 1989) and often exaggerated (Curtis 1941). However, sublethal damage can negatively affect radial growth (Storm and Halvorson, 1967) and resultant physiological stress may lead to increased susceptibility to disease and insect infestation (Sullivan *et al.*, 1986). The limited height and multitemmed morphological characteristics of pinyon pines may cause them to be more vulnerable to

porcupine activity ( Taylor, 1935). I assert that the occurrence of the pine engraver beetle and the papershell pinyon pine in this region necessitates monitoring and evaluation of possible indirect effects of this unique mammal in Texas and other inclusive areas of its distribution.

*Acknowledgments.*--I am grateful to the Rob and Bessie Welder Wildlife Foundation, Sigma Xi, American Society of Mammalogists, the Theodore Roosevelt Memorial Fund of the American Museum of Natural History, Texas Parks and Wildlife Department, Max McGraw Wildlife Foundation, and the Oklahoma Cooperative Fish and Wildlife Research Unit (Okla.State Univ., Dep. of Wildlife Conserv., U.S.G.S. Biological Resource Division, Wildl. Manage. Inst. Cooperating) funding this research. D. Stuart and D. Klepper of Texas Parks and Wildlife provided a variety of technical and logistical support. I also thank T. Reeder, the M. Lacy Family, K. R. Ilse and K. J. Ilse, and for assistance in capture and monitoring of animals. R. T. Kazmaier assisted in discussion and analyses of data. D. M. Leslie, Jr. provided helpful comments on an earlier draft of this manuscript. This report is Welder Contribution Number 558.

#### **LITERATURE CITED**

- ANDERSON, N. H., AND D. B. ANDERSON. 1968. Ips bark beetle attacks and brood development on a lightning-struck pine in relation to its physiological decline. *Fla Ent.*, 51:23-30.
- BETANCOURT, J.L. 1987. Paleoecology of the pinyon-juniper woodlands. p. 129-139. *In: Proceedings of the pinyon-juniper conference, Reno, NV. U.S. Department of Agriculture, Forest Service, General Technical Report INT 215.*



- CONNER, R. N., AND D. C. Rudolph. 1995. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. *Wilson Bull*, 107:81-92.
- CURTIS, J.D. 1941. The silvicultural significance of the porcupine. *J. Forest.*, 39:583-594.
- \_\_\_\_\_, AND E. L. KOZICKY. 1944. Observations on the eastern porcupine. *J. Mammal.*, 25:137-146.
- \_\_\_\_\_, AND A. K. WILSON. 1953. Porcupine feeding on ponderosa pine in central Idaho. *J. Forest.*, 51:339-341.
- DAVIS, W. R., AND D. J. SCHMIDLY. 1994. Porcupine. p. 206-208. *In: The mammals of Texas.* Texas Parks and Wildlife Department, Austin.
- DODGE, W.E. 1967. The biology and life history of the porcupine (*Erethizon dorsatum*) in western Massachusetts. Ph.D. Dissertation, University of Massachusetts, Amherst.
- \_\_\_\_\_. 1982. Porcupine (*Erethizon dorsatum*). p. 355-366. *In: J. A. Chapman and G. A. Feldhamer, eds. Wild mammals of North America.* Johns Hopkins University Press, Baltimore MD.
- GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.*, 28:1140-1162.
- GRIESEMER, S. J., T. K. FULLER, AND R. M. DEGRAAF. 1998. Habitat use by porcupines (*Erethizon dorsatum*) in central Massachusetts: effects of topography and forest composition. *Am. Midl. Nat.*, 140:271-279.

- HALE, M. B., S. J. GRIESEMER, AND T. K. FULLER. 1994. Immobilization of porcupines with tiletamine hydrochloride and zolazepam hydrochloride (Telazol). *J. Wildl. Dis.*, 30:429-431.
- \_\_\_\_\_, AND T. K. FULLER. 1996. Porcupine (*Erethizon dorsatum*) demography in central Massachusetts. *Can. J. of Zool.*, 74:480-484.
- HARDER, L. D. 1979. Winter feeding by porcupines in montane forests of southwestern Alberta. *Can. Field Nat.*, 93:405-410.
- HENDRICKS, P., AND H. F. ALLARD. 1988. Winter food habits of porcupines in Montana. *Prairie Nat.*, 21:1-6.
- KREFTING, L. W., J. H. STOECKELER, B. J. BRADLE, AND W. D. FITZWATER. 1962. Porcupine-timber relationships in the lake states. *J. For.*, 60:325-330.
- LACY, R. C. 1993. Vortex: a computer simulation model for population viability analysis. *Wildl. Res.* 20:45-65.
- MATTSON, W. J., AND R. A. HAACK. 1987. The role of drought in plant-eating insects. *Bioscience*, 37:110-118.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1999. Texas Climatological. National Climatic Data Center, Asheville, North Carolina, USA.
- OVESON, M. C. 1983. Behavioral and metabolic adaptations of porcupines (*Erethizon dorsatum*) to winter stress. M.S. Thesis. Brigham Young University, Provo, Utah, 20 p.
- PAYETTE, S. 1987. Recent porcupine expansion at tree line: a dendroecological analysis. *Can. J. Zool.*, 65:551-557.

- POLLACK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: The staggered entry design. *J. Wildl. Manage.*, 53:7-15.
- POWELL, R. A., AND R. B. BRANDER. 1977. Adaptations of fishers and porcupines to their predator-prey systems. p 44-53 *In*: R. L. Phillips and C. Jonkel, eds. Proceedings of the 1975 predator symposium. Montana Forest and Conservation Experimental Station, University of Montana.
- ROZE, U. 1984. Winter foraging by individual porcupines. *Can. J. Zool.*, 62:2425-2428.
- \_\_\_\_\_. 1989. The North American porcupine. Smithsonian Institution Press, Washington, D.C.
- STORM, G. L., AND C. H. HALVORSON. 1967. Effect of injury by porcupines on radial growth of ponderosa pine. *J. For.*, 65:740-743.
- STRICKLAN, D. 1986. Factors affecting dietary selection and movement of porcupines in Utah. M.S. Thesis. Brigham Young University, Provo, Utah. 38 p.
- SULLIVAN, T. P., W. T. JACKSON, J. POJAR, AND A. BANNER. 1986. Impact of feeding damage by the porcupine on western-hemlock-Sitka spruce forests of north-coastal British Columbia. *Can. J. For. Res.*, 16:642-647.
- SWEITZER, R.A. AND J. BERGER. 1993. Seasonal dynamics of mass and body condition in Great Basin porcupines (*Erethizon dorsatum*). *J. Mammal.*, 74:198-203.
- \_\_\_\_\_, AND D. W. HOLCOMBE. 1993. Serum-progesterone and pregnancy rates in Great Basin porcupines (*Erethizon dorsatum*). *J. Mammal.*, 74:769-776.

- \_\_\_\_\_. AND J. BERGER. 1997. Sexual dimorphism and evidence for intrasexual selection from quill impalements, injuries, and mate guarding in porcupines (*Erethizon dorsatum*). *Can. J. Zool.*, 75:847-854.
- \_\_\_\_\_. S. H. JENKINS, AND J. BERGER. 1997. Near extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin Desert. *Conserv. Biol.*, 11:1407-1417.
- \_\_\_\_\_. AND J. BERGER. 1998. Evidence for female-biased dispersal in North American porcupines (*Erethizon dorsatum*). *J. Zool.*, 244:159-166.
- TAYLOR, W.P. 1935. Ecology and life history of the porcupine (*Erethizon epixanthum*) as related to the forests of Arizona in the southwestern United States. *Univ. of Arizona Bull.*, 6:1-177.
- WELLS, P. V. 1987. Systematics and distribution of pinyons in the late Quaternary. p. 104-108. *In: Proceedings of the pinyon-juniper conference, Reno, NV.*, Department of Agriculture, Forest Service, Gen. Tech. Rept.. INT-215.

Table I.1. Causes of porcupine mortality in 4 major studies.

| Cause              | Roze<br>1989 | Hale and Fuller<br>1996 | Sweitzer <i>et al</i> ,<br>1997 | This<br>study |
|--------------------|--------------|-------------------------|---------------------------------|---------------|
| Predation          | 0            | 0                       | 27                              | 0             |
| Injury             | 3            | 2                       | 0                               | 1             |
| Human              | 5            | 2                       | 4                               | 1             |
| Climate/Starvation | 6            | 4                       | 13                              | 0             |
| Disease            | 2            | 2                       | 0                               | 2             |
| Unknown            | 3            | 4                       | 2                               | 3             |
| <b>TOTAL</b>       | <b>19</b>    | <b>14</b>               | <b>46</b>                       | <b>7</b>      |

Fig. I.1. Location of Kickapoo Caverns State Natural Area.

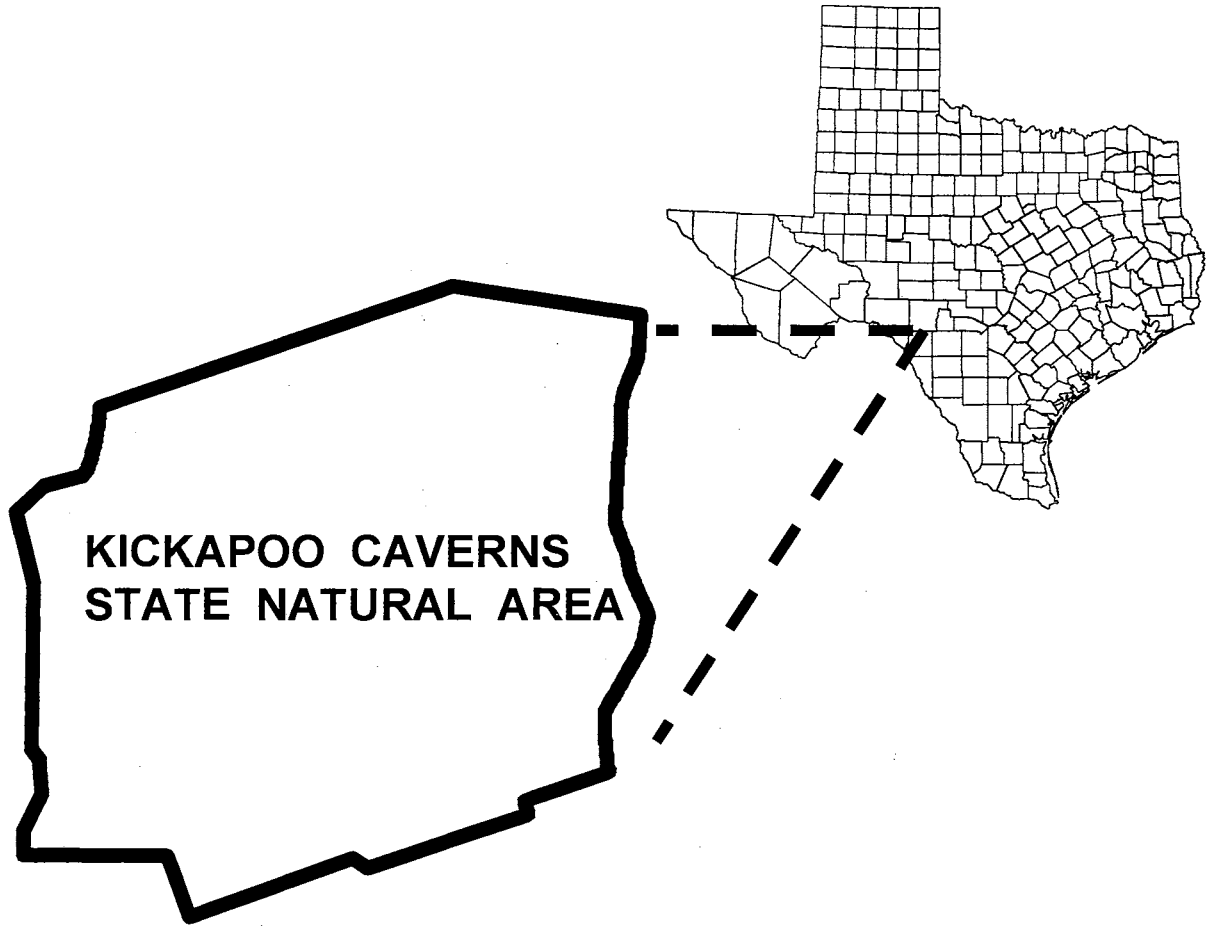
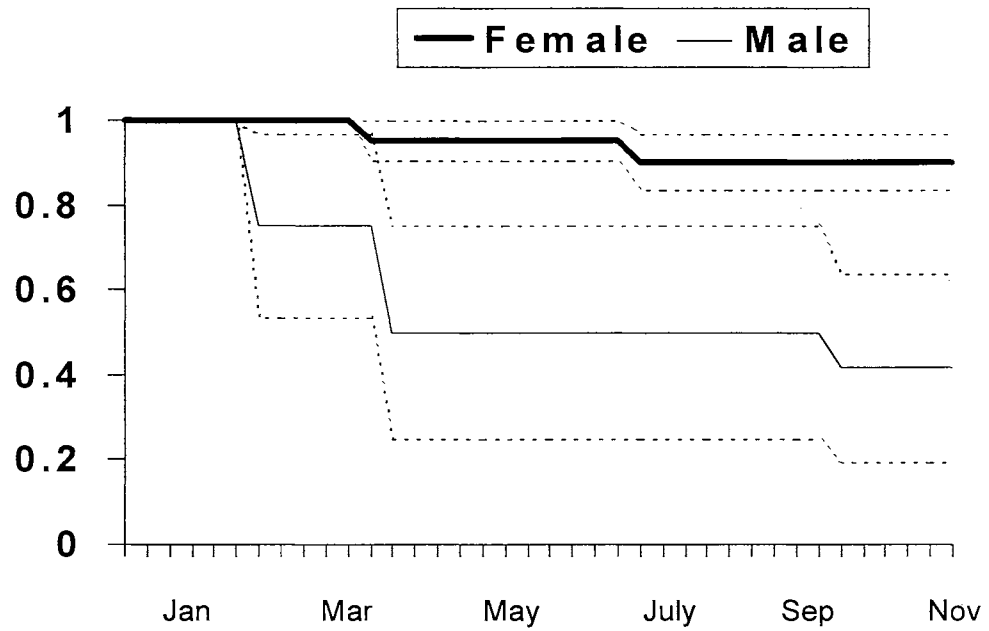


Fig. I.2. Survival rates of adult/yearling porcupines on Kickapoo Caverns State Natural Area, 1997-1999. Dashed lines represent  $\pm 1$  SE.





## CHAPTER II

### PORCUPINES, PINYON PINES, AND PINE ENGRAVERS: WHAT'S THE CONNECTION?

**Abstract.** Understanding linkages among different trophic levels is important to conservation and management of ecosystems. The goal of this research was to test the hypothesis that the North American porcupine (*Erethizon dorsatum*) predisposes the papershell pinyon pine (*Pinus remota*), a Pleistocene-relict species, to colonization by pine engraver beetles of the genus *Ips*. I examined porcupine ecology, pinyon pine physiology and physiognomy, and beetle-pine associations on a study area in the southwestern Edwards Plateau of Texas from June 1997 to August 1999 to elucidate relationships among 3 non-related taxa. Porcupines selected pinyon pines over more abundant species ( $P < 0.001$ ) and were selective at the level of morphology, whereas pine engraver beetles were selective of tree morphology and physiology. Trees colonized by beetles had higher concentrations of fructose and glucose and lower percent composition of limonene, sabinene, and terpinolene than uncolonized trees. Distribution of bark beetle infestation varied ( $\chi^2 = 75.3$ ,  $df = 3$ ,  $P < 0.01$ ) between damaged and undamaged trees. Although attacks by beetles were evident on both types of trees, successful colonization was greater on pines damaged by porcupines. Intensity of porcupine attack, indexed by number of feeding scars and area of bark removed, also was associated with colonization by beetles. I propose that release of volatile terpenes as a result of porcupine feeding and reallocation of carbon resources as a response to stress explains the association of beetle colonization with porcupine-damaged trees. These data on interspecific relationships are of regional

interest relative to conservation of this unique pinyon-juniper woodland. This study is of general value showing the role of distinct phyla that define community structure in woodland ecosystems. Although, current conditions in this particular system do not warrant active management, the population and recruitment of pinyon pines should be monitored for potential changes.

Key Words: *bark beetles*, *Erethizon dorsatum*, indirect effects, *Ips hoppingi*, multitrophic interaction, pine engraver, pinyon-juniper woodland, *Pinus remota*, porcupine

## INTRODUCTION

The role of direct interspecific interactions in structuring communities is evident in extensive examinations of competition (Connell 1983, Schoener 1983) and predator-prey relations (Sih et al. 1985, Martin 1988). The strength of indirect effects occurring among different trophic levels has received much less attention and is likely a result of the inherent difficulty in detecting these types of relationships (Wooton 1994). The role of a requisite third species in these events compromises the efficacy and timely detection of indirect interactions (Davidson et al. 1984).

Indirect ecological interactions among species in disparate taxa are essential to the functional roles of these individual species (Christiansen and Whitham 1993, Elkinton et al. 1996, Martinsen et al., 1998). Discounting or ignoring the role of indirect effects can lead to erroneous conclusions regarding community dynamics of a system (Davidson et al. 1984, Wooton 1992). Although Huntly (1991) reviewed effects of herbivores in structuring and altering plant communities, interactions among herbivores of different taxa have received minimal attention. Potential impacts of these interactions could be far-reaching given the effect of herbivory on competitive interactions (McNaughton 1976,

McInnes et al. 1992, Christensen and Whitham 1993) and subsequent alteration of landscapes by these disturbances (Reichman and Smith 1985, Johnston and Naiman 1990).

Insects and mammals constitute integral components of forests and woodlands. Their behavioral and biological activities influence species composition, organic decomposition, and soil properties within the ecosystem (Sharpe et al. 1995, Elkinton et al. 1996). The porcupine (*Erethizon dorsatum*) and bark beetles (Coleoptera: Scolytidae) are taxonomically distinct dendrophagous taxa. Both are phloem feeders, disrupting the physiological integrity of the host (Barbosa and Wagner 1989). At the level of individual trees, translocation of carbohydrates may be altered by wounding or girdling, resulting in increased activity of bark beetles (Dunn and Lorio 1992). Likewise, herbivory may induce qualitative changes in defensive chemistry (Tallamy and Raupp 1991, Loreto et al. 2000), resulting in increased occurrence of related and non-related herbivorous taxa (Martinsen et al. 1998, Redman and Scriber 2000, Tomlin et al. 2000).

Mechanisms of host attack exhibited by porcupines and bark beetles differ. The porcupine, with its widespread and expanding geographic distribution (Woods 1973, Davis and Schmidly 1994), exploits a variety of habitat types (Woods 1973) and can attack healthy, vigorous trees (Sharpe et al. 1995). Although trees may be girdled in the process, damage frequently is restricted to rectangular or ovate patches positioned within grasping distance of branches occupied by the porcupine (Spencer 1964). Conversely, scolytid species of the *Ips* genus, attack, feed, and oviposit in stressed or otherwise compromised conifers and exhibit greater host specificity at the species level (Cane et al. 1990, Wood 1963).

Pinyon pines of the southwestern United States are the primary hosts for allopatrically occurring *I. confusus* and *I. hoppingi* (Lanier 1970, Wood 1982, Cane et al. 1990). Additionally, these pine engraver beetles may inoculate the host with fungi, yeasts, and bacteria (Coulson and Wittwer 1983, Barbosa and Wagner 1989). Events known or presumed to precipitate pine engraver infestations include fire, severe drought, mechanical injury, lightning, and even cavity-nesting by the red-cockaded woodpecker (*Picoides borealis*) (Blanche et al. 1985, Nebeker and Hodges 1985, Conner and Rudolph 1995). As with porcupine damage, host mortality following infestation is contingent upon attack intensity and tree vigor.

The constitutive oleoresin system of healthy conifers acts as a primary defense response against attack by flushing out invaders. A secondary, or induced, response contains the infection when the primary response is insufficient to repel attack. The wound site is first saturated with resin. Cellular necrosis then occurs in surrounding tissues, accompanied by synthesis and release of secondary compounds. (Berryman 1972, Cates and Alexander 1982, Raffa 1991). Host resistance and defense responses are strongly related to physical properties of the resin such as flow rate, viscosity, crystallization rate, and chemical composition (Hodges et al. 1979). Factors that may ameliorate efficacy of the defense response include stand density and crown cover (Lorio 1993), flooding, fire, soil properties, moisture stress, fungal disease, air pollution and mechanical injury (Paine and Baker 1993). Mattson and Haack (1987) reported that during drought, host trees accumulated sugars, amino acids, and other organic acids, thereby lowering osmotic potential. Moisture stress was suggested as a primary cause of host susceptibility by Christiansen et al. (1987), who also hypothesized that carbon may be

a critical, albeit often overlooked, facet in beetle-insect dynamics. Trees struck by lightning that removed bark to the cambium exhibited decreased levels of moisture and non-reducing sugars (sucrose) with concomitant increases in reducing sugars (Hodges and Pickard 1971). Essentially, chemical and nutritional imbalances resulting from a variety of stressors diminish a host's ability to mount a defensive response and increases the potential for pathogenic response and increased susceptibility to bark beetle invasion.

Porcupines feed on a variety of vegetation, concentrating on herbaceous species in spring and summer. During autumn and winter, they become more arboreal, feeding primarily on phloem and cambium of coniferous species (Spencer 1964, Dodge 1967, Roze 1984). However, emergence of pine engravers, including *Ips* spp., occurs primarily in spring. Aggregation and development of multiple generations continues through summer (Stark 1982). Therefore trees in ecosystems occupied by porcupines and bark beetles, may be under attack for much of the year, jeopardizing their survival.

Porcupines and pine engravers feed upon the papershell pinyon pine (*Pinus remota*) in the pinyon-juniper woodlands of the Edwards Plateau region of Texas (pers. obs.). A paucity of information is available on this rare conifer because of its confusion with the closely related Mexican pinyon pine (*P. cembroides*) and its biogeographical history. *P. remota* was first described as a new variety of *P. cembroides* by Little (1966) based on its reduced number of needles per fascicle ( $n = 2$ ) and its thinner-shelled seeds. Bailey and Hawksworth (1979) elevated it to a separate species after determining that it also exhibits open fascicle sheaths, has  $> 2$  resin ducts per needle and occurs sympatrically with *P. cembroides* in west Texas. Examination of wood rat middens indicates this pine was prolific throughout the Chihuahuan Desert before the Pleistocene (Betancourt, 1987;

Wells, 1987). The warmer, drier conditions typical of post-Pleistocene climate caused a dramatic range reduction in this conifer, and today it is restricted to scattered populations in northeastern Mexico, Big Bend National Park, and an isolated area on the Balcones escarpment of the Edwards Plateau in Texas (Betancourt, 1987; Wells, 1987). The latter population represents the only living population of pinyon pines occurring in the United States at elevations of 460-600 m (Wells, 1987). The diminishing range of the papershell pinyon pine (Betancourt 1987, Wells, 1987) puts it at increased risk of extirpation.

Preliminary reconnaissance in the southwestern Edwards Plateau region of Texas revealed the presence of porcupines and pinyon pines. Close observation of these pines indicated extensive porcupine feeding scars on living trees. However, examination of dead and dying trees indicated additional presence of pine engraver beetles (*Ips hoppingi*). These observations led to development of my hypothesis that porcupine feeding activity predisposes these pinyon pines to subsequent colonization by bark beetles.

I investigated multitrophic interactions in a system involving porcupines and pine engraver beetles feeding on a relict population of papershell pinyon pines. I examined porcupine use of feeding trees, morphological and physiological differences between target (feeding) and non-target (non-feeding) trees, and beetle response on both types of trees. I predicted that if an important indirect interaction occurred among these taxa I would find that porcupines selected pinyon pines over more abundant species. I expected to discern differences in morphology and physiology of target and nontarget trees attributed to dendrophagous selection. Finally, I predicted that successful colonization of pine engraver beetles would be greater on those trees that had been previously damaged by porcupines.

## METHODS AND MATERIALS

### *Study area*

Research was conducted on the 2577-ha Kickapoo Caverns State Natural Area (KCSNA) located about 35 km north of Brackettville, Texas. The site straddles Kinney and Edwards counties in the southwestern region of the Edwards Plateau (Fig. II.1).

Topography is predominantly steep limestone hills and deep canyons with elevations of 482--610 m. Average annual rainfall is about 45 cm (National Oceanic and Atmospheric Administration, 1999). No standing water or active springs are present on the site.

Shallow clay soils of east and north facing slopes supported pinyon-juniper-oak plant communities. In addition to the relict papershell pinyon pines, dominant tree species included Ashe juniper (*Juniperus ashei*), plateau live oak (*Quercus fusiformis*), Texas persimmon (*Diospyros texana*), and vasey oak (*Quercus pungens* var. *vaseyana*). Woody shrubs included evergreen sumac (*Rhus virens*), guajillo (*Acacia berlandieri*) prickly pear (*Opuntia* spp.), and Roemer acacia (*Acacia roemeriana*). Ground cover was represented by cedar panicgrass (*Dichanthelium pedicellatum*) and cedar sedge (*Carex planostachys*) in shaded areas, and sideoats grama (*Bouteloua curtipendula*) and hairy tridens (*Erioneuron pilosum*) in more open areas.

Shallow soils of the south and west facing slopes were dominated by guajillo plant communities and pinyon pines were restricted to lower slope regions. Shrub species included guajillo, coyotillo (*Karwinskia humboldtiana*) and leatherstem (*Jatropha dioica*). Grasses included threeawn (*Aristida* spp.) and red grama (*Bouteloua trifida*).

Mottes of plateau live oak mixed with vasey oak and Ashe juniper were common in canyons and drainages where moisture was more abundant and soil was deeper. Pinyon



pinus and netleaf hackberry (*Celtis reticulata*) also occurred in these areas. Dominant grasses include threeawn and annual dropseed (*Sporobolus* spp.).

#### *Animal capture and handling*

Porcupines were captured in cage-type live traps (Tomahawk Live Trap Co., Tomahawk, WI) using apples and salt as bait (Hale and Fuller, 1996). An adjustable pole-mounted syringe facilitated capture of animals in trees or in dens. Tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, A.H. Robbins, Richmond, VA) was used at a rate of 7 mg/kg body weight (Hale et al. 1994) to immobilize porcupines. All animals were marked with self-piercing ear tags (National Band and Tag Co., Newport, KY), and individuals  $\geq 1.5$  kg body mass were outfitted with radio-transmitters (L&L Electronics, Mahomet, Illinois) secured by nylon mesh collars.

#### *Tree selection*

Radio-telemetry was used to locate and obtain visual observations on all animals at least twice weekly. Triangulation was used only when an animal left the study site and appropriate authorization or hunting seasons precluded my safe and/or lawful access. I recorded location and activity of each porcupine and the tree species for every animal located within a tree.

Three hundred, 0.04-ha fixed-radius plots were randomly established across the study site and sampled to assess relative availability of tree species. I tallied all trees  $\geq 1.5$  m in height because porcupines were rarely observed using trees below this height limit.

#### *Morphology of transect trees*

I randomly established 20, 500-m transects (Fig. II.2) in woodland habitat used by porcupines across the study area. Transects were not placed in open grassland or guajillo

habitats where porcupine activity was limited. At 25-m intervals on each transect, the nearest porcupine-damaged (target) tree was tagged. Target trees were paired with a non-damaged (nontarget) tree, and a variety of morphological measurements, including diameter at root collar (DRC; Cognac 1996), height, crown diameter, crown density and bark thickness, were recorded for each tree. Basal area was determined using a 10 factor prism at each tagged tree.

Overall limb structure was recorded for individual trees as vertical if lateral limbs extended upward and horizontal if lateral limbs extended outward. Total number of porcupine feeding scars was recorded and area of bark removed (cm<sup>2</sup>) was estimated for each target tree. Presence or absence of bark beetles was noted for all trees and placed into 1 of 3 levels of beetle activity: (1) no beetle activity (N); (2) attack only (A), evident by the presence of resin tubules but no successful colonization; and (3) colonization (C), evident by the presence of  $\geq 1$  dead stems or branches resulting from beetle engravings.

#### *Physiology of transect trees*

Physiological characteristics of pinyon pines were evaluated by measuring plant moisture stress, 24-hr resin flow, monoterpene content of resin, and carbohydrate content of phloem. Plant moisture stress was evaluated using the pressure-bomb technique (Waring and Cleary 1967, Ritchie and Hinckley 1975). Stems representing current year's growth were excised and sampled during pre-dawn hours to ensure trees were at equilibrium with regard to water potential.

Exudate from an arch punch wound (1.25 cm) was collected in plastic vials to determine 24-hr resin flow (Hodges et al. 1979) for all tagged trees. All trees were tapped between 0700 and 0900 h to alleviate photoperiod effects. Tissue removed from the arch

punch wound from 3 randomly selected pairs of trees from each transect was placed in plastic bags and frozen before processing for carbohydrate analyses. Phloem was separated from the outer bark and dried at 45° C to a constant weight. Samples were ground using a mortar and pestle. Sugar extraction was performed using a modification of the method described by McCready et al. (1950) and modified by Wood and McMeans (1981) for woody tissues. Three extractions were completed using 80% ethanol and then brought to volume using 80% ethanol for a 1:400 dilution. Glucose, fructose, and sucrose were identified using high pressure liquid chromatography (HPLC) and expressed in mole fractions (Russo et al. 1998).

Resin for monoterpene analyses was collected from the same 3 randomly selected pairs of trees used in carbohydrate analyses. Holes (12 mm) were drilled at an upward angle into the tree and 1-dram glass vials were screwed directly into the hole to alleviate evaporative loss of hydrocarbons. Vials were removed after 24 h and processed for subsequent gas chromatograph analysis of 7 monoterpenes ( $\alpha$ -pinene, camphene, sabinene,  $\beta$ -pinene, myrcene, limonene, and terpinolene). Equal volumes of chromatographic grade pentane were added to aliquots of each sample (Snyder 1992) to facilitate injection into a gas chromatograph (Smith 1977) .

#### *Experimental manipulation*

I conducted an experiment in 1999 to test my hypothesis and identify the mechanism responsible for mediation by porcupines of bark beetle invasion. Twenty-four trees exhibiting no prior porcupine or beetle damage were selected for experimental manipulation. A bark spoon (Forestry Suppliers, Jackson, MS) was used to remove bark from 12 trees to simulate feeding activity of porcupines. The number of artificial scars

ranged from 2 to 7, and the total area of bark removed ranged from 14 cm<sup>2</sup> to 80 cm<sup>2</sup>, reflecting means of these parameters from transect trees of similar diameter classes. All trees were sampled for resin-flow rate, resin chemical constituents, and phloem sugars on 10 April, 1 day before bark removal. Sampling was repeated at 2-, 6-, and 12-wk intervals (24 April, 22 May, 30 June) following manipulation.

#### *Statistical analyses*

Selection of trees species by porcupines was determined by comparing use with availability using Chi-square analysis and the Bonferonni z-statistic to define preference and avoidance of dominant tree species within the study site (Neu et al. 1974, Byers et al. 1984). A location of an individual porcupine served as the experimental unit, and data were pooled across season.

Morphological and physiological data for all trees were averaged across each transect ( $n = 20$ ); hence, transects were the experimental units. Target and nontarget trees were compared using paired *t*-tests and significance was set at  $P < 0.05$ . Association of bark beetle activity with morphological characteristics of target and nontarget trees was compared using 2-way ANOVA, with level of beetle activity and tree classification (target, nontarget) as main effects. Resin chemistry data were entered as percent composition of 8 dominant monoterpenes and subjected to angular transformation before comparison of target and nontarget trees using 2-way ANOVA. Levels of sucrose, glucose, and fructose were recorded as  $\mu\text{mol/mL}$  and compared for differences between target and non-target trees using 2-way ANOVA. Repeated-measures ANOVA were used to analyze data collected from experimental trees. Analysis of variance was used to compare physiological and morphological characteristics of transect trees with experimental trees.

Multiple regression and correlation analyses were performed to determine if percent composition of individual monoterpenes was associated with area of exposed xylem resulting from porcupine herbivory. Analysis of variance was performed to determine if extent of herbivory and bark removal by porcupines were associated with level of beetle activity.

## RESULTS

### *Selection of trees by porcupines*

Thirty-seven animals (24F;13M) were equipped with radio collars and were tracked > 1 month during the 3-year study period, yielding 1496 total locations. Visual observations comprised 1401 of the locations. Eighty percent of those locations ( $n = 1118$ ) were in trees, 14% ( $n = 197$ ) were on the ground, and only 6% ( $n = 86$ ) were located in dens.

I tallied 1,046 trees representing 10 distinct genera in the plot sampling. Ashe juniper, Texas persimmon, oaks, and pinyon pines accounted for 92% of all available tree species, and 97% of all porcupine observations occurred in these species. I therefore restricted use-availability analyses to these 4 taxa. Porcupines selected pinyon pines and oaks and avoided more abundant juniper and Texas persimmon ( $\chi^2 = 537.85$ ,  $df = 3$ ,  $P < 0.0001$ , Table 1).

### *Morphology of transect trees*

Data were collected on 366 trees (183 pairs) because of the limited availability of nontarget trees. Five morphological characteristics of trees varied by tree classification (Table 2). Porcupines used trees that were greater in girth ( $P < 0.001$ ), taller ( $P < 0.001$ ), greater in crown diameter ( $P < 0.001$ ), thicker barked ( $P < 0.001$ ), and greater in resin

flow ( $P < 0.006$ ) than nontarget trees. *Post hoc* analyses of those 5 characteristics revealed significant correlations between diameter at root collar with height ( $r = 0.79$ ,  $P < 0.0001$ ), bark thickness ( $r = 0.83$ ,  $P < 0.0001$ ), crown diameter ( $r = 0.89$ ,  $P < 0.0001$ ), and resin flow ( $r = 0.50$ ,  $P < 0.001$ ). Additionally, 72 % ( $n = 131$ ) of all trees damaged by porcupines ( $n = 183$ ) exhibited horizontal instead of vertical lateral limb structure, indicating disproportionate use of this structural characteristic ( $\chi^2 = 35.2$ ,  $df = 1$ ,  $P < 0.0001$ ). Similarly, beetle colonization was associated with horizontal limb structure ( $\chi^2 = 13.6$ ,  $df = 2$ ,  $P < 0.001$ ).

Trees damaged by porcupines were more likely to be colonized, and undamaged trees were more likely to be free from beetle attack ( $\chi^2 = 75.3$ ,  $df = 3$ ,  $P < 0.01$ , Fig. II.3). However, tree characteristics varying by level of beetle activity were not consistent with those associated with porcupine use of trees (Table 2). Although trees more likely to be fed upon by porcupines and colonized by beetles were larger than nontargeted trees, resin flow did not vary across levels of beetle activity, and colonization was associated with pines exhibiting less dense crowns. Pinyon pine basal area varied by the interacting effects of beetle activity and tree classification ( $F_{2,92} = 3.94$ ,  $P = 0.02$ ). Basal area of pinyon pines was greater on colonized, nontarget trees ( $\bar{x} \pm SE = 3.1 \pm 0.8 \text{ m}^2/\text{ha}$ ) than on any other combination of beetle activity and tree class ( $\bar{x} \pm SE = 1.4 \pm 0.3 \text{ m}^2/\text{ha}$ ).

#### *Transect trees--physiology*

Measurable amounts of sucrose were found in only 2 samples collected from transects. Glucose and fructose dominated all samples, but did not differ between target and nontarget trees (glucose  $\bar{x} \pm SE = 0.410 \text{ } \mu\text{mol/mL} \pm 0.020$ ; fructose  $\bar{x} \pm SE = 0.417 \text{ } \mu\text{mol/mL} \pm 0.023$ ). Trees that were colonized by beetles had higher levels of both these

sugars (glucose  $\bar{x} \pm SE = 0.451 \mu\text{mol/mL} \pm 0.021$ ,  $P < 0.01$ ; fructose  $\bar{x} \pm SE = 0.455 \mu\text{mol/mL} \pm 0.022$ ,  $P < 0.03$ ) than trees that had no beetle activity or had been attacked only (glucose  $\bar{x} \pm SE = 0.389 \mu\text{mol/mL} \pm 0.019$ ; fructose  $\bar{x} \pm SE = 0.395 \mu\text{mol/mL} \pm 0.022$ ). There tended to be an interaction ( $P < 0.08$ ) in fructose concentration across levels of beetle activity and by tree classification. Undamaged trees that were colonized by beetles had higher levels of fructose ( $\bar{x} \pm SE = 0.5438 \mu\text{mol/mL} \pm 0.04$ ) than undamaged trees with no beetle activity or attack only ( $\bar{x} \pm SE = 0.3860 \mu\text{mol/mL} \pm .02$ ). Fructose concentrations also were higher in undamaged colonized trees than all target trees ( $\bar{x} \pm SE = 0.4219 \mu\text{mol/mL} \pm 0.03$ ).

The most abundant monoterpenes in target and nontarget trees ( $n = 120$ ) were  $\alpha$ -pinene,  $\beta$ -pinene, and limonene (Table 3). Alpha-pinene was correlated negatively with sabinene ( $r = -0.36$ ,  $P < 0.0017$ ),  $\beta$ -pinene ( $r = -0.89$ ,  $P < 0.0001$ ), myrcene ( $r = -0.73$ ,  $P < 0.0001$ ), limonene ( $r < -0.88$ ,  $P < 0.001$ ), and terpinolene ( $r = -0.35$ ,  $P < 0.002$ ). Positive correlations were evident between sabinene and myrcene ( $r = 0.40$ ,  $P < 0.0005$ ),  $\beta$ -pinene and myrcene ( $r = 0.72$ ,  $P < 0.0001$ ),  $\beta$ -pinene and limonene ( $r = 0.67$ ,  $P < 0.0001$ ), myrcene and limonene ( $r = 0.48$ ,  $P < 0.001$ ), myrcene and terpinolene ( $r = 0.45$ ,  $P < 0.0001$ ) and terpinolene and sabinene ( $r = 0.97$ ,  $P < 0.0001$ ).

Myrcene occurred in lower proportions in target than in nontarget trees ( $P = 0.008$ ; Table 3). Negative associations were detected between area of bark removed and levels of sabinene ( $r = -0.48$ ,  $P = 0.03$ ), terpinolene ( $r = -0.47$ ,  $P = 0.03$ ), and myrcene ( $r = -0.16$ ,  $P = 0.08$ ). Sabinene, limonene, and terpinolene occurred in lower proportions in trees that had been colonized or attacked than in trees with no beetle activity (Table 3). The only monoterpene affected by the interaction of beetle activity and tree classification

was camphene ( $F_{2,63} = 5.16, P = 0.008$ ). Undamaged, colonized trees had higher proportions of this monoterpene ( $\bar{x} \pm SE = 2.4\% \pm 1.9$ ) than trees with other combinations of beetle activity and porcupine damage ( $\bar{x} \pm SE = 0.4\% \pm 0.1$ ).

Number of porcupine scars was correlated positively with area of bark that had been removed ( $r = 0.8986, P < 0.0001$ ). Area of bark removed was less ( $P < 0.001$ ) on trees that exhibited no beetle activity or attack only ( $\bar{x} \pm SE = 302.5 \text{ cm}^2 \pm 74.8$ ) than on trees that had been colonized ( $\bar{x} \pm SE = 988.9 \text{ cm}^2 \pm 152.1$ ).

### *Experimental manipulation*

Trees sampled in the experimental manipulation were smaller ( $P < 0.0001$ ) than damaged trees sampled on transects (DRC<sub>experimental</sub>  $\bar{x} \pm SE = 12.1 \text{ cm} \pm 0.5$ , height<sub>experimental</sub>  $\bar{x} \pm SE = 3.6 \text{ m} \pm 0.6$ ; DRC<sub>transect</sub>  $\bar{x} \pm SE = 22.4 \text{ cm} \pm 1.1$ , height<sub>transect</sub>  $\bar{x} \pm SE = 4.6 \text{ m} \pm 0.2$ ). Pre-manipulation percent composition of sabinene was lower for experimental than transect trees ( $\bar{x}_{\text{experimental}} = 0.02\%$ ,  $\bar{x}_{\text{transect}} = 0.2\%$ ,  $P < 0.03$ ).

Conversely, limonene composition was higher ( $P < 0.03$ ) on the experimental trees ( $\bar{x}_{\text{experimental}} = 1.6\%$ ,  $\bar{x}_{\text{transect}} = 0.7\%$ ). Glucose and fructose concentrations were higher ( $P < 0.0001$ ) for targeted transect trees (glucose  $\bar{x} \pm SE = 0.419 \text{ } \mu\text{mol/mL} \pm 0.02$ , fructose  $\bar{x} \pm SE = 0.427 \text{ } \mu\text{mol/mL} \pm 0.02$ ) than premanipulation concentrations for experimental trees (glucose  $\bar{x} \pm SE = 0.108 \text{ } \mu\text{mol/mL} \pm 0.02$ , fructose  $\bar{x} \pm SE = 0.158 \text{ } \mu\text{mol/mL} \pm 0.02$ ).

Likewise, resin flow was higher ( $P < 0.0001$ ) on target transect trees ( $\bar{x} \pm SE = 2.6 \text{ mL/24h} \pm 0.4$ ) than for premanipulation experimental trees ( $\bar{x} = 0.9 \text{ mL/24hr} \pm 0.2$ ).

Resin flow ( $P < 0.002$ ), carbohydrate concentrations ( $P < 0.0001$ ), and terpene compositions ( $P < 0.0001$ ), were affected by sampling period, but not affected by bark removal. Although there was no interactive effect, resin flow on manipulated trees



generally increased over time, whereas flow began to decline on control trees around week 12 (Fig. II.4). Unlike resin flow, glucose and fructose concentrations peaked at 2- and 6-wk sampling periods on both manipulated and control trees (Fig. II.5). Percent composition of several monoterpenes tended to increase over time, peaking around week 12 following manipulation (Fig. II.6). Conversely, composition of  $\alpha$ -pinene and camphene generally declined over time (Fig. II.6). Attack or colonization by beetles did not occur on either manipulated or control trees during the 12-wk monitoring.

## DISCUSSION

### *Selection of trees by porcupines*

Disproportionate use by porcupines of pinyon pines over more abundant species may be a response to nutrient acquisition and thermoregulation. Coniferous species provide thermal advantages over deciduous species (Clarke and Brander 1973, Roze 1984) and frequently constitute the preferred feeding and resting trees of porcupines (Dodge 1967, Griesemer 1995, Speer and Dilworth 1978). Feeding on oaks was restricted to the canopy and consumption of leaves and acorns, whereas consumption of bark was apparent only in pinyons. Pine bark and cambium is easier to remove than oak bark and is generally higher in fats and water content. Conversely, leaves and acorns are higher in proteins (Stricklan et al. 1995). Live oaks on site allowed porcupines to supplement and balance winter nutritional needs with foliage, precluding a diet restricted to bark. The higher water content of the pinyon pine cambium (Stricklan et al. 1995) also may help porcupines to satisfy water requirements in this arid region.

Paired sampling on transects allowed elimination of site favorability as a cause for tree selection by porcupines. Significant correlations of height, crown diameter, bark

thickness, and resin flow with DRC indicate that size-age is the dominant factor in intraspecific selection of trees. Similar findings of size-related selectivity by porcupines have been reported (Krefting et al. 1962, Sullivan et al. 1986, Tenneson and Oring, 1985). Preponderance of horizontal limb structure in target trees was indicative of the habit of porcupines to rest on branches and then feed and remove bark within comfortable reach (Spencer 1964). These data validate the contention that morphological selection of trees by porcupines reflects foraging and energetic optimization (Roze 1989).

Asymmetrical occurrence of branches on the papershell pinyon pine explains the patchy removal of bark evident in this study, because a foraging porcupine must move up or down the main stem to facilitate feeding and bark removal. Symmetrical branching might have resulted in greater girdling of trees because the animal could remain at the same height while circumnavigating the tree to facilitate easy grasp of bark.

My data indicate that biochemical variability may influence porcupine diet selection, but minimally. I found no correlation between feeding activity of porcupines and levels of limonene as observed by Snyder and Linhart (1997). Target trees had lower levels of myrcene than nontarget trees; however, area of bark removed was correlated only with composition of sabinene and terpinolene and not myrcene. These data suggest that porcupine foraging was intensified with low levels of these terpenes. The porcupine's range recently has expanded into the Edwards Plateau region (Davis and Schmidly 1994), and the relict population of papershell represents a new food resource. Although the pine is a preferred resource, it represented only 14% of the species available to the porcupine on the site. Therefore, strong intraspecific selectivity by porcupines may not have been possible in this system.

### *Selection of trees by beetles*

Beetles, in contrast to the porcupine, exhibited selection at the levels of morphology and physiology. Not surprisingly, trees colonized by beetles were larger than nontargeted trees. Lack of response to resin flow and plant moisture was surprising because susceptibility to bark beetle invasion commonly is affiliated with drought and decreased resin flow (Hodges et al. 1979, Paine et al. 1988). Despite the common occurrence of drought in the study region (Stahle and Cleaveland 1988), my results did not support this contention. My findings may be linked to higher than normal rainfall during the sampling period, August-September 1998 (Fig. II.7).

The pressure-bomb technique of evaluating plant water stress is simple, flexible, and compatible with thermodynamic principles (Waring and Cleary 1967, Ritchie and Hinckley 1975); however, assumptions associated with the technique are easily violated. Morphological and structural differences (e.g., overall tree height, crown density, leaf age-size, and microsite) will impact water potential, resulting in variation, even within the same tree. Meteorologic conditions, soil conditions, and genetics also may bias results. Applicability and validity of water potential data obtained by this technique may be more robust in controlled experimental conditions, but efficacy likely was compromised in my study because of numerous confounding variables associated with natural field conditions. Hence, I proffer the lack of significance in moisture stress be viewed with caution. Lajtha and Barnes (1991) and Gerdol et al. (2000) describe a method for measuring water use efficiency obtained by measuring leaf-needle carbon isotope ratio and leaf-needle intercellular CO<sub>2</sub> concentration. These indirect measurements of water relations may be

more useful and meaningful than traditional pressure-bomb measurements of plant moisture stress, particularly in uncontrolled field studies.

Association of increased beetle colonization on trees with higher levels of glucose and fructose is not surprising given nutritional requirements of the pine engraver (Haack and Slansky 1987). However, it also may reflect seasonality in growth patterns of the tree. Spring is the period of greatest beetle activity and coincides with earlywood formation in most pine species (Blanche et al. 1992). Carbohydrate partitioning is limited to growth processes instead of increased resin production and defense responses; thus, the tree is less resistant to beetle invasion at this time (Lorio 1993).

High levels of limonene are toxic to many bark beetles (Harborne 1993) and explain increased beetle activity on trees exhibiting low proportions of this monoterpene. Loreto et al. (2000) reported increased emissions of limonene and  $\alpha$ -pinene in artificially wounded needles of the Mediterranean pine (*Pinus pinea*). Hence, bark removal by the porcupine and resultant vaporization of limonene may alert the beetle to levels of this hydrocarbon

I found no direct relationship among myrcene,  $\alpha$ -pinene, and bark beetles; however, the relationship between bark beetles and monoterpenes is complex. These 2 terpenes serve as pheromone precursors in other species of pine engraver beetles (Hughes 1974, Renwick et al. 1976a, Hughes and Renwick 1977, Byers et al. 1979). Ipsdienol, ipsenol, and *cis*-verbenol have been identified in the aggregation pheromones of *I. paraconfusus* (D. L. Wood 1982, Borden 1984) and can be biosynthesized from myrcene vapors (Hughes 1974, Hughes and Renwick 1977, Byers et al. 1979). Similarly,  $\alpha$ -pinene is a precursor to *cis*- and *trans*-verbenol (Renwick et al. 1976a, Hughes and Renwick

1977), and can be biosynthesized by these beetles. The process is enhanced by presence of the bacteria (*Bacillus cereus*) found in the gut of adult *I. paraconfusus* (Brand et al. 1975).

Cane et al. (1990) reported a lack of pheromone specificity occurring between *I. confusus* and *I. hoppingi*, which are closely related to *I. paraconfusus* but are host-specific to pinyon pines. They attribute this response to recent phylogenetic divergence of these beetles. Currently *I. confusus* is associated with *P. monophylla*, *P. edulis*, *P. quadrifolia*, and *P. californium* throughout the desert-southwestern United States. *I. hoppingi* is found east and south of the range of *I. confusus*. It commonly is associated with *P. cembroides* in Mexico and Texas, *P. discolor* in southern Arizona and New Mexico, and *P. remota* in Texas. Chemical reactions between host monoterpenes and pheromone production are complex and have not been identified completely for *I. hoppingi*. However, based on the close phylogenetic relationship among these species of *Ips*, I speculate that myrcene and  $\alpha$ -pinene may be suitable pheromone precursors for *I. hoppingi*.

Beetles attacked or colonized trees with lower levels of sabinene and terpinolene, which were terpenes that were correlated negatively with high levels of  $\alpha$ -pinene. The overwhelming dominance of monoterpene composition by  $\alpha$ -pinene in all groups of trees may have masked an association between beetle colonization and this terpene. Alpha-pinene, a major constituent of pines and other conifers, is particularly dominant in pinyon pines. Percent composition of this monoterpene ranges from about 10% in Ponderosa pine (Sturgeon 1979, Snyder 1992) to > 90% in populations of Mexican pinyon pine (*Pinus cembroides*) in the Big Bend region of Texas (Zavarin and Snajberek 1985). I

postulate that *I. hoppingi* is either an  $\alpha$ -pinene obligate species or harbors *B. cereus* and is therefore able to biosynthesize this monoterpene.

The role of camphene is less clear. Adult males and females of *D. brevicornis* and *D. frontalis* exposed to camphene vapors are able to oxidize the hydrocarbon into camphenol, but the role of this product in bark beetle pheromone production and subsequent colonization has not been determined (Renwick et al. 1976b).

I propose that feeding activity by porcupines “advertises” the presence of specific monoterpenes and represents an additional stressor requisite to infestation by these bark beetles. Association of beetles with trees of diminished crown density and in areas of high pinyon pine basal area in this study emphasizes the role of stress in insect outbreaks (Hodges and Lorio 1975, Mattson and Haack 1987, Paine and Baker 1993). Under these conditions, balance of nutrients necessary for growth and defense responses of the tree is compromised because of lower levels of photosynthates and increased competition for nutrients (Lorio 1986). Successful colonization by beetles is facilitated because of the diminished resistance by the host tree. I postulate that injury to trees by porcupines elicits a similar response, causing the tree to displace nutrients used for growth to the wound site for defense (Christiansen et al. 1987), leaving it more vulnerable to insect attack.

#### *Experimental manipulation*

Several factors may have contributed to the lack of observed response by trees and beetles to the experimental manipulation. Conservation concern for the rare papershell pinyon pine precluded a larger sample size for manipulation. Additionally, limited availability of trees with no prior porcupine or bark beetle damage resulted in use of trees that were not comparable in size or physiology to those used by porcupines. Higher levels

of limonene, a toxic monoterpene, and lower levels of fructose and glucose on experimental trees may explain the lack of prior- and post-manipulation attack by bark beetles.

The patchiness of bark removal and random selection of within-tree sampling sites may have hindered my ability to detect differences in measured variables. In contrast, Dunn and Lorio (1992) reported a decrease in downward translocation of carbohydrates after artificially girdling loblolly pines (*Pinus taeda*). Hodges and Pickard (1971) reported increases in simple hexose sugars following lightning damage. Similarly, Hodges and Lorio (1969) reported increases in sugars in drought-stressed conditions. Widespread damage imposed by lightning or bark girdling might have elicited a stronger response because these types of damage are of greater magnitude than the patchy bark removal evident in this particular system.

My experimental results may have been biased by examining only effects of artificially removed bark and excluding possible effects of porcupine salivary secretions. Qualitative and quantitative host responses may be dependent on the type of damage incurred. Natural herbivory often elicits stronger defense responses by the host than artificial wounding (Haukioja and Neuvonene 1985, Stout et al. 1994). Hartley and Lawton (1990) reported that addition of caterpillar (*Spidopterea littoralis*) saliva to artificially wounded birch (*Betula pendula*) resulted in increased levels of phenylalanine ammonia lyase (PAL) comparable to those elicited by natural herbivory. Turlings et al. (1990) reported differential release of terpenes between artificially damaged corn (*Zea mays*) seedlings and those treated with oral secretions of the herbivorous beet armyworm larvae (*Spodoptera exigua*). Regurgitant alone did not elicit as strong a response by

parasitic wasps (*Cotesia marginiventris*) to volatile terpenes. These studies indicate that physical damage and salivary secretions act synergistically.

Field studies are inherently limited by confounding effects of weather patterns and microsite differences. Although these factors can be controlled in laboratory settings, effects associated with natural field conditions are overlooked. Robust ecological studies should incorporate field and laboratory components. A stronger test of my hypothesis might have included introduction of beetles to damaged and undamaged trees and then a measurement of beetle response; however, I was limited in my ability to perform these manipulations because of the rarity of the papershell pinyon pine.

Lack of statistical significance also should be considered with caution. Statistical significance can not always be equated with biologic significance. Species with heightened chemoreception capabilities may be affected by minute changes in olfactory stimulants that are below limits of assay precision. Likewise, *I. hoppingi*, measuring < 5 mm in length, may be susceptible to statistically insignificant changes in resin flow. In these situations, it is prudent to examine apparent trends in biological and ecological responses and evaluate their importance in accordance with the individual species and its basic ecology and natural history.

#### *Ecological and Conservation Implications*

My findings are compatible with my predictions that porcupine bark-feeding activity predisposes pinyon pines to subsequent bark beetle activity; however, my data and results do not define unequivocally the mechanism that explains my observations. The most parsimonious explanation for the association between beetle colonization and porcupine feeding activity may be the increased vaporization of volatile terpenes cuing



pine engraver beetles to presence of toxic substances and availability of potential pheromone precursors. Additionally, disruption of carbon allocation by reallocation of photosynthates to terpenes and resins surrounding feeding scars, and therefore away from the remainder of the tree, puts the tree at increased vulnerability to beetle infestation.

The dominant mechanism facilitating beetle invasion in the absence of porcupines, or in areas of diminished porcupine activity, appears to be host stress, resulting in diminished availability or increased competition for nutrients. This mechanism is evident by increased colonization of trees in areas of diminished crown density or in areas of higher pinyon pine basal area. Lori (1986) suggested that nutrients are used for growth and cellular responses and resin formation. A balance must be attained by the tree for acquisition and use of these nutrients. Based on Lorio's (1986) observations and review, photosynthates are used for tree growth during spring. Resin duct formation increases later in the year during transformation between formation of early- and late-wood formation (Blanche et al. 1992). Because resin flow is often a primary defense against bark beetle attack, spring is a more favorable period for bark beetle attack. Christiansen et al. (1987) took the concept further, and suggested that energy expenditures required to synthesize terpenes after wounding depleted carbon stores for successful defense against beetles. Essentially, host vulnerability to attack is increased seasonally due to growth response and may be further exacerbated by injury or drought that strain carbon reserves.

Implications of this indirect ecological interaction to conservation of the pinyon pine are ambiguous. Predominance of multiple stems, characteristic of the papershell pinyon pine, is an effective means of diminishing vulnerability to porcupines and bark beetles because the tree can effectively lose one or more major main stems and remain

viable. Although sustained or increased herbivory might affect individual tree viability, directional selection over time resulting from feeding activity may lead to increased fitness of trees that are chemically and morphologically less attractive to these dendrophages. Sturgeon (1979) reported that ponderosa pines in areas historically associated with western pine beetle invasion exhibited higher proportions of limonene than trees in areas without a history of beetle invasion. Linhart et al. (1989) reported that Abert's squirrels (*Sciurus aberti*) and the porcupine can act as agents of natural selection by their feeding activities on ponderosa pine.

The paradigm that bark beetle invasion is catastrophic to wooded ecosystems may be invalid in a system incorporating the pine engraver *I. hoppingi*, which is often associated with endemic local outbreaks (Raffa et al. 1993). On the contrary, by thinning individual localized stands, this particular pine engraver may be creating more suitable growing conditions for pinyon pines that otherwise may compete for space and for nutrients as a result of crowded growing conditions.

Facilitation of beetle attack by porcupine feeding is not a symmetrical process. Porcupines, because of their size, sharp incisors, and large claws, are able to remove bark easily from healthy trees, and this is evident by their selection of larger healthy trees. *Ips*, however, is a facultative parasite that attacks only stressed or injured hosts (Raffa et al. 1993). Unlike the porcupine that is not dependent on the host tree for survival, the pine engraver spends much of its life cycle within the inner bark of the host, leaving only to disperse to a new host.

My research underscores the need to identify and examine interactive processes involved in structuring wooded systems, particularly those inhabited by rare species. *I.*

*hoppingi*, because of its recent taxonomic divergence (Cane et al 1990), has received limited attention. It is important that a better understanding of its association with host constituents and potential mediators, such as the porcupine, be developed. Bark beetles originated during the Permian Period at about the same time conifers were becoming conspicuous in the northern hemisphere (Bright and Stock 1982). The current viability of both is an example of coevolution. A better understanding of the roles of other taxa and subsequent indirect effects is vital to fully understand these processes and essential to development of effective management practices. Although, current conditions in the system investigated in this study do not warrant active management, the population of pinyon pines should be monitored for potential changes in viability and recruitment. This manuscript represents Welder Wildlife Contribution No. \_\_\_\_\_.

#### **ACKNOWLEDGMENTS**

I am indebted to D. Stuart and D. Klepper for invaluable logistical, technical, and field assistance. E. C. Hellgren, D. M. Leslie, Jr., R. Masters, and W. Ross provided valuable research suggestions. Tommy Reeder and the Mark Lacy family assisted in capturing and handling of porcupines. Bruce Kimball of the U.S. Department of Agriculture and Donna Chrz of the Department of Horticulture at Oklahoma State University were instrumental in GC-MS and HPLC analyses of terpenes and carbohydrates. Funding for this research was provided by the Rob and Bessie Welder Wildlife Foundation, Max McGraw Wildlife Foundation, Theodore Roosevelt Memorial Fund, Oklahoma Cooperative Fish and Wildlife Research Unit (Okla. State Univ., Okla. Dep. Wildl. Conserv., U.S.G.S. Biol. Resource Div., Wildl. Manage. Inst., cooperating)

Sigma Xi, Texas Parks and Wildlife Department and the American Society of Mammalogists.

#### LITERATURE CITED

Bailey, D. K., and F. G. Hawksworth. 1979. Pinyons of the Chihuahuan Desert region.

*Phytologia* **44**:129-133.

Barbosa, P., and M. R. Wagner. 1989. Phloem and wood-boring insects. Pages 225-243

*in* Introduction to forest and shade tree insects. Academic Press, New York.

Berryman, A. A. 1972. Resistance of conifers to invasion by bark beetles-fungus

associations. *Bioscience* **22**:598-602.

Betancourt, J. L. 1987. Paleoecology of the pinyon-juniper woodlands. Pages 129-139

*in* Proceedings of the pinyon-juniper conference, Reno, NV. U.S. Forest Service, USDA Gen. Tech. Rep. INT 215.

Blanche, C. A., J. D. Hodges, and T. E. Nebeker. 1985. Changes in bark beetle

susceptibility: indicators in a lightning-struck pine. *Canadian Journal of Forest Research* **15**:397-399

Blanche, C. A., P. L. Lori, Jr., R. A. Sommers, J.D. Hodges, and T. E. Nebeker. 1992

Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts, and resin flow. *Forest Ecology and Management* **49**:151-165.

Borden, J. H. 1984. Semiochemical-mediated aggregation and dispersal in the

Coleoptera. Pages 123-149 *in* T. Lewis, ed. *Insect communication*. Academic Press, New York.

- Brand, J. M., J. W. Bracke, A. J. Markowitz, D. L. Wood, and L. E. Browne. 1975. Production of verbenol pheromone by a bacterium isolated from bark beetles. *Nature* **254**:136-137.
- Bright, D. E., and M. W. Stock. 1982. Taxonomy and geographic variation. Pages 46-73 in J. B. Mitton and K. B. Sturgeon, editors. *Bark beetles in North American conifers: a system for the study of evolutionary biology*. University of Texas Press, Austin.
- Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management* **48**:1050-1053.
- Byers, J. A., D. L. Wood, L. E. Brown, R. H. Fish, B. Piatek, and L. B. Hendry. 1979. Relationship between a host plant compound, myrcene and pheromone production in the bark beetle *Ips paraconfusus*. *Journal of Insect Physiology* **25**:477-482.
- Cane, J. H., L. D. Merrill, and D. L. Wood. 1990a. Attraction of pinyon pine bark beetle, *Ips hoppingi* to conspecific and *I. confusus* pheromones (Coleoptera:Scolytidae). *Journal of Chemical Ecology* **16**:2791-2798.
- Cates, R. G., and H. Alexander. 1982. Host resistance and susceptibility. Pages 212-263 in J. B. Mitton and K. B. Sturgeon, eds. *Bark Beetles in North American conifers: a system for the study of evolutionary biology*. Univ. of Texas press, Austin.
- Christiansen, E., R. H. Warring, and A. A. Ferryman. 1987. Resistance of conifers to bark beetles attack: searching for general relationships. *Forest Ecology and Management* **22**:89-106.

- Christensen, K. M., and T. G. Whitham. 1993. Impact of insect herbivores on competition between birds and mammals for pinyon pine seeds. *Ecology* **74**:2270-2278.
- Clarke, S. H., and R. B. Brander. 1973. Radiometric determination of porcupine surface temperature. *Physiological Zoology* **46**:230-237.
- Cognac, D. C. 1996. Estimating diameter growth for pinyon and juniper trees in Arizona and New Mexico. USDA Forest Service, Research Note INT-RN-429. 6pp.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:81-116.
- CONNER, R. N., and D. C. Rudolph. 1995. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. *Wilson Bulletin* **107**:81-92.
- Coulson, R. N., and J. A. Wittwer. 1984. Phloem boring insects. Pages 511-551 *in* Forest entomology: ecology and management. John Wiley and Sons, New York.
- Davis, W. R., and D. J. Schmidly. 1994. Pages 206-208 *in* The mammals of Texas. Texas Parks and Wildlife Department, Austin.
- Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* **65**:1780-1786.
- Dodge, W. E. 1967. The biology and life history of the porcupine, (*Erethizon dorsatum*) in western Massachusetts. Ph.D. Thesis. University of Massachusetts, Amherst. 133pp.

- Dunn, J. P., and P. L. Lori, Jr. 1992. Effects of bark girdling on carbohydrate supply and resistance of loblolly pine to southern pine beetle (*Dendroctonus frontalis* Zimm.) attack. *Forest Ecology and Management* **50**:317-330.
- Elkinton, J. S., W. M. Healy, J. P. Buonccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith, and A. M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* **77**:2332-2342.
- Gerdol, R., P. Acumen, R. Marchesni, and L. Braggazza. 2000. Water-and nutrient-use efficiency of a deciduous species, *Vaccinium myrtillus*, and an evergreen species *V. vitis-idaea*, in a sub-alpine dwarf shrub in the southern Alps, Italy. *Oikos* **88**:19-32.
- Griesemer, S. J. 1995. Habitat selection by porcupines in central Massachusetts. M.S. Thesis University of Massachusetts, Amherst. 79pp.
- Haack, R. A., and F. Slansky, Jr. 1987. Nutritional ecology of wood-feeding coleoptera, lepidoptera, and hymenoptera. Pages 449-486 in F. Slansky, Jr. and J. G. Rodriguez, eds. *Nutritional ecology of insects, mites, spiders, and related invertebrates*. John Wiley & Sons, New York.
- Hale, M. B., S. J. Griesemer, and T. K. Fuller. 1994. Immobilization of porcupines with tiletamine hydrochloride and zolazepam hydrochloride (Telazol). *Journal of Wildlife Disease* **30**:429-431.
- Hale, M.B., and T. K. Fuller. 1996. Porcupine (*Erethizon dorsatum*) demography in central Massachusetts. *Canadian Journal of Zoology* **74**:480-484.
- Harborne, J. B. 1993. Hormonal interactions between plants and animals. Pages 104-127 in *Ecological biochemistry*. Academic Press, New York.

- Hartley, S. E., and J. H. Lawton. 1990. Biochemical aspects and significance of the rapidly induced accumulation of phenolics in birch foliage. Pages 105-132 in D. W. Tallamy and M. J. Raupp, editors. *Phytochemical induction by herbivores*. John Wiley & Sons, Inc, New York.
- Haukioja, E., and S. Neuvonen. 1985. Induced long-term resistance of birch foliage against defoliators: defensive or incidental? *Ecology* **66**:1303-1308.
- Hodges, J. D., W. W. Elam, W. F. Watson, and T. E. Nebeker. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera:Scolytidae) attacks. *Canadian Entomologist* **11**:889-896.
- Hodges, J.D., and P. L. Lori, Jr. 1969. Carbohydrate and nitrogen fractions of the inner bark of loblolly pines under moisture stress. *Canadian Journal of Botany* **47**:1651-1657.
- Hodges, J. D., and P. L. Lori, Jr. 1975. Moisture stress and composition of xylem oleoresin in loblolly pine. *Forest Science* **21**:283-290.
- Hodges, J. D., and L. S. Pickard. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Canadian Entomologist* **103**:41-51.
- Hughes, P. R. 1974. Myrcene: a precursor of pheromones in *Ips* beetles. *Journal of Insect Physiology* **20**:1271-1275.
- Hughes, P. R., and J. A. A. Renwick. 1977. Neural and hormonal control of pheromones in the bark beetle *Ips paraconfusus*. *Physiological Entomology* **2**:117-123.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* **22**:477-504.



- Johnston, C. A., and R. J. Naiman. 1990. Browse selection by beaver: effects on forest composition. *Canadian Journal of Forest Research* **20**:1036-1043.
- Krefting, L. W., J. H. Stoeckeler, B. J. Bradle, and W. D. Fitzwater. 1962. Porcupine-timber relationships in the Lake States. *Journal of Forestry* **60**:325-330.
- Lajtha, K., and F. J. Barnes. 1991. Carbon gain and water use in pinyon-pine-juniper woodlands of northern New Mexico: field versus phytotron chamber measurements. *Tree Physiology* **9**:59-67.
- Lanier, G. N. 1970. Biosystematics of North American *Ips* (Coleoptera:Scolytidae) Hoppings group IX. *Canadian Entomologist* **122**:1235-1238.
- Linhart, Y. B., M. A. Snyder, and S. A. Habeck. 1989. The influence of animals on genetic variability within ponderosa pine stands, illustrated by the effects of Abert's squirrel and porcupine. Pages 141-148 *in* A. Teele et al., editors. Multi-resource management of Ponderosa Pine Forests. USDA Forest Service. Gen. Tech rept. RM-185.
- Little, E. L. 1966. A new pinyon variety from Texas. *Wrightia* **3**:181-187.
- Loreto, F, P. Nascetti, A. Graverini, and M. Manozzi. 2000. Emission and content of monoterpenes in intact and wounded needles of the Mediterranean Pine *Pinus pinea*. *Functional Ecology* **14**:589-596.
- Lorio, P. L., Jr. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *Forest Ecology and Management* **14**:259-273.
- Lorio, P. L., Jr. 1993. Environmental stress and whole-tree physiology. Pages 88-101 *in* T. J. Schwatter and G. M. Filip, eds. Beetle-pathogen interactions in conifer forests. Academic Press, Ltd.

- Martin, T. E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evolutionary Ecology* **2**:37-50.
- Martinsen, G. D., E. M. Driebe, and T. G. Whitham. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology* **79**:192-200.
- Mattson, W. J., and R. A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* **37**:110-118.
- McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* **73**:2059-2075.
- McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* **191**:92-94.
- McReady, R. M., J. Guggolz, V. Silviera, and H. S. Owens. 1950. Determination of starch and amylase in vegetables. *Analytical Chemistry* **22**:1156-1158.
- National Oceanographic and Atmospheric Administration. 1999. Texas Climatological. National Climatic Data Center, Asheville, North Carolina, USA.
- Nebeker, T. E., and J. D. Hodges. 1985. Thinning and harvesting practices to minimize stand disturbance and susceptibility to bark beetle and disease attacks. Pages 263-271 *in* Branham, S. J., and R. C. Thatcher, editors. Proceedings of the Integrated Pest management Research Symposium. USDA, Forest Service, Gen. Tech. Rept. Rep. SOH-56.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization - availability data. *Journal of Wildlife Management* **38**:541-545.

- Paine, T. D., and F. A. Baker. 1993. Abiotic and biotic predisposition. Pages 61-79 in T. D. Schwatter and G. M. Filips, editors. Beetle-pathogen interactions in conifer forests. Academic Press, Ltd.
- Paine, T. D., F. M. Stephen, and R. G. Cates. 1988. Moisture stress, tree suitability, and southern pine beetle population dynamics. Pages 85-97 in T. D. Paine and H. Saakermäa editors. Integrated control of Scolytid bark beetles. Proceedings of IUFRO Working Party and XVII International Congress of Entomology Symposium, Vancouver, B.C.
- Raffa, K. F., T. W. Phillips, and S. M. Salom. 1993. Strategies and mechanisms of host colonization by bark beetles. Pages 103-128 in D. Schwatter and G. M. Filips, editors. Beetle-pathogen interactions in conifer forests. Academic Press, Ltd.
- Raffa, K. F. 1991. Induced reactions in conifer-bark beetle systems. Pages 245-276 in Tallamy, D. W., and M. J. Raup, editors. Phytochemical induction by herbivores. John Wiley & Sons, Inc., New York.
- Redman, A. M. and J. M. Scriber. 2000. Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids. *Oecologia* **125**:218-228.
- Reichman, O. J., and C. S. Smith. 1985. Impact of pocket gopher burrows on underling vegetation. *Journal of Mammalogy* **66**:720-725.
- Renwick, J. A. A., P. R. Hughes, and I. S. Krull. 1976a. Selective production of *cis*- and *trans*-verbenol from (-)- and (+)- $\alpha$ -pinene by a bark beetle. *Science* **191**:199-201.

- Renwick, J. A. A., P. R. Hughes, G. B. Pitman, and J. P. Vite'. 1976b. Oxidation products of terpenes identified from *Dendroctonus* and *Ips* bark beetles. *Journal of Insect Physiology* **22**:725-727.
- Ritchie, G. A., and T. M. Hinckley. 1975. The pressure chamber as an instrument for ecological research. *Advancements in Ecological Research* **9**:165-254.
- Roze, U. 1984. Winter foraging by individual porcupines. *Canadian Journal of Zoology* **62**:2425-2428.
- Roze, U. 1989. *The North American porcupine*. Smithsonian Institution Press, Washington, D. C.
- Russo, V. M., J. Williamson, K. Roberts, J. R. Wright, and N. Maness. 1998. <sup>13</sup>C-nmr spectroscopy to monitor sugars in pith of internodes of a *sh2* corn at developmental stages. *HortScience* **33**:980-983.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240-285.
- Sharpe, G. W., C. W. Hendee, W. F. Sharpe, and J. C. Hendee. 1995. Insects and mammals. Pages 140-161 *in* Introduction to forests and renewable resources. McGraw Hill Inc. New York.
- Smith, R. H. 1977. Monoterpenes of ponderosa pine xylem resin in western United States. Unites States Department of Agriculture Forest Service General Technical Report PSW-1.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* **16**:269-311.

- Snyder, M. A. 1992. Selective herbivore by Abert's squirrel mediated by chemical variability in ponderosa pine. *Ecology* **73**:1730-1741.
- Snyder, M. A., and Y. B. Linhart. 1997. Porcupine feeding patterns: selectivity by a generalist herbivore? *Canadian Journal of Zoology* **75**:2107-2111
- Speer, R.J., and T. G. Dilworth. 1978. Porcupine winter foods and habitat utilization in central New Brunswick. *Canadian Field Naturalist* **92**:271-274.
- Spencer, D. A. 1964. Porcupine fluctuations in past centuries revealed by dendrochronology. *Journal of Applied Ecology* **1**:127-149.
- Stahle, D. W., and M. K. Cleaveland. 1988. Texas drought history reconstructed and analyzed from 1698 to 1980. *Journal of Climate* **1**:59-74.
- Stark, R. W. 1982. Generalized ecology and life cycle of bark beetles. Pages 21-45 in J. B. Mitton and K. B. Sturgeon, editors. *Bark beetles in North American conifers: a system for the study of evolutionary biology*. University of Texas Press, Austin.
- Stout, M. J., J. Workman, and S. S. Duffy. 1994. Differential induction of tomato foliar proteins by arthropod herbivores. *Journal of Chemical Ecology* **20**:2575-2594.
- Stricklan, D. J., J. T. Flinders, and R. G. Cates. 1995. Factors affecting selection of winter food and roosting resources by porcupines in Utah. *Great Basin Naturalist* **55**:29-36.
- Sturgeon, K. B. 1979. Monoterpene variation in Ponderosa pine xylem resin related to western pine beetle predation. *Evolution* **33**:803-814.
- Sullivan, T. P., W. T. Jackson, J. Pojar, and A. Banner. 1986. Impact of feeding damage by the porcupine on western hemlock-Sitka spruce forests of north-coastal British Columbia. *Canadian Journal of Forest Research* **16**:642-647.

- Tallamy, D. W., and M. J. Raup. 1991. Phytochemical induction by herbivores. John Wiley & Sons, Inc. New York. 431 pp.
- Tenneson, C., and W. Oring. 1985. Winter food preferences of porcupines. *Journal of Wildlife Management* **49**:28-33.
- Tomlin, E. S., E. Antonejevic, R. I. Alfaro, and J. H. Borden. 2000. Changes in volatile terpene and diterpene resin acid composition of resistant and susceptible white spruce leaders exposed to simulated white pine weevil damage. *Tree Physiology* **20**:1087-1095.
- Turlings, C. J., J. H. Tumlinson, and W. J. Lewis. 1990. Exploitation of herbivore induced plant odors by host-seeking parasitic wasps. *Science* **250**:1251-1253.
- Warring, R. H., and B. D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. *Science* **155**:1248-1254.
- Wells, P. V. 1987. Systematics and distribution of pinyons in the late Quarternary. Pages 104-108 *in* Proceedings of the pinyon-juniper conference, Reno, NV. U.S. For. Serv. Gen. Tech. Rep. INT 215.
- Wood, B. W., and J. L. McMeans. 1981. Carbohydrate changes in various organs of bearing and non-bearing pecan trees. *Journal of American Society of Horticultural Science* **106**:758-761.
- Wood, D. L. 1963. Studies on host selection by *Ips confusus* (Le Conte) (Coleoptera:Scolytidae). California University Publication in Entomology **27**:241-282.

- Wood, D. L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review of Entomology* **27**:411-446.
- Woods, C. A. 1973. *Erethizon dorsatum*. *Mammalian Species* 29:1-6.
- Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. *Ecology* **73**:981-991.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**:413-466.
- Zavarin, E., and K. Snajberk. 1985. Monoterpenoid and morphological differentiation within *Pinus cembroides*. *Biochemical Systematics and Ecology* **13**:89-104.

Table II.1 Availability and use of dominant tree species by porcupines on the Kickapoo Caverns StatePark, Kinney and Edwards counties, Texas, 1996-1999.

| Tree species           | Availability <sup>a</sup> ( <i>n</i> = 965) |    | Use ( <i>n</i> = 1092) |     |
|------------------------|---|----|------------------------|-----|
|                        | <i>n</i>                                    | %  | <i>n</i>               | %   |
| Ashe juniper           | 350   | 36 | 155                    | 14  |
| Oak species            | 253   | 26 | 393                    | 35  |
| Texas persimmon        | 216   | 22 | 2                      | 0.2 |
| Papershell pinyon pine | 146   | 15 | 542                    | 50  |

<sup>a</sup> Based on 300, 0.04 ha fixed-radius plots.



Table II.2. Morphological characteristics of pinyon pines differing with regard to porcupine and bark beetle activity on the Kickapoo Caverns State Park, Kinney and Edwards counties, Texas, 1996-1999. Values represent average of 20 transect means.

| Characteristic                               | Porcupines |      |           |      |                       | Beetles <sup>a</sup> |      |           |     |           |     |                       |
|--|------------|------|-----------|------|-----------------------|----------------------|------|-----------|-----|-----------|-----|-----------------------|
|  | Target     |      | Nontarget |      | <i>P</i> <sup>b</sup> | None                 |      | Attacked  |     | Colonized |     | <i>P</i> <sup>c</sup> |
|  | $\bar{x}$  | SE   | $\bar{x}$ | SE   |                       | $\bar{x}$            | SE   | $\bar{x}$ | SE  | $\bar{x}$ | SE  |                       |
| DRC (cm)                                     | 22.3       | 1.1  | 12.4      | 0.5  | < 0.001               | 14.8 A               | 0.6  | 15.2 A    | 0.9 | 23.6 B    | 0.9 | < 0.001               |
| Height (m)                                   | 4.6        | 0.2  | 3.2       | 0.1  | < 0.001               | 4.4 A                | 0.2  | 4.6 A     | 0.3 | 7.1 B     | 0.3 | < 0.001               |
| Crown diameter (m)                           | 4.1        | 0.2  | 2.3       | 0.1  | < 0.001               | 2.7 A                | 0.2  | 2.7 A     | 0.2 | 4.1 B     | 0.2 | < 0.001               |
| Crown density (%)                            | 88.7       | 1.7  | 88.2      | 1.7  | 0.755                 | 88.1AB               | 0.2  | 91.8A     | 0.2 | 84.3B     | 0.2 | 0.147                 |
| Bark thickness (cm)                          | 0.8        | 0.03 | 0.4       | 0.02 | < 0.001               | 0.4 A                | 0.03 | 0.4 A     | 0.0 | 0.8 B     | 0.0 | < 0.001               |
| Basal area (m <sup>2</sup> /ha) <sup>d</sup> | 1.3        | 0.2  | 1.5       | 0.2  | 0.424                 | 1.5 A                | 0.3  | 1.3 A     | 0.3 | 2.0 B     | 0.4 | < 0.04                |
| 24-hr Resin flow (mL)                        | 2.6        | 0.3  | 1.4       | 0.2  | < 0.001               | 1.9                  | 0.2  | 2.0       | 0.3 | 2.6       | 0.3 | 0.09                  |

<sup>a</sup> Means for each characteristic with the same letter are not different at  $\alpha = 0.05$  level of significance.

<sup>b</sup> Main effect of porcupine damage (present or absent).

<sup>c</sup> Main effect of level of beetle activity.

<sup>d</sup> See text for discussion of interactive effects.

Table II.3. Percent composition of seven monoterpenes occurring in papershell pinyon pines used by porcupines and pine engraver beetles on the Kickapoo Caverns State Park, Kinney and Edwards counties, Texas, 1999. Values represent average of 20 transects (3 pairs of trees/transect).

| Monoterpene %         | Porcupines   |              |                       | Beetles <sup>a</sup> |              |              |                       |
|-----------------------|--------------|--------------|-----------------------|----------------------|--------------|--------------|-----------------------|
|                       | Target       | Nontarget    | <i>P</i> <sup>b</sup> | None                 | Attacked     | Colonized    | <i>P</i> <sup>c</sup> |
| α-pinene              | 86.15 ± 1.83 | 82.63 ± 2.16 | 0.1187                | 80.14 ± 2.28         | 86.30 ± 3.03 | 88.9 ± 1.96  | 0.1201                |
| Camphene <sup>d</sup> | 0.39 ± 0.06  | 0.56 ± 0.10  | 0.3864                | 0.37 ± 0.07A         | 0.38 ± 0.10A | 0.67 ± 0.28B | 0.0223                |
| Sabinene              | 0.60 ± 0.21  | 0.79 ± 0.25  | 0.4483                | 0.62 ± 0.17A         | 1.65 ± 0.60B | 0.15 ± 0.08A | 0.0218                |
| β-pinene              | 5.04 ± 0.91  | 6.65 ± 0.97  | 0.1298                | 7.64 ± 1.06          | 4.8 ± 1.27   | 4.11 ± 1.09  | 0.2111                |
| Myrcene               | 0.63 ± 0.11  | 1.08 ± 0.14  | 0.0084                | 1.03 ± 0.15          | 0.86 ± 0.19  | 0.61 ± 0.14  | 0.4413                |
| Limonene              | 6.79 ± 0.98  | 7.89 ± 1.11  | 0.2957                | 9.82 ± 1.25B         | 5.26 ± 1.40A | 5.38 ± 0.93A | 0.0247                |
| Terpinolene           | 0.37 ± 0.11  | 0.44 ± 0.11  | 0.6043                | 0.34 ± 0.09A         | 0.91 ± 0.28B | 0.17 ± 0.05A | 0.0138                |

<sup>a</sup> Means for each monoterpene with the same letter are not different at α = 0.05 level of significance.

<sup>b</sup> Main effect of porcupine damage (present or absent).

<sup>c</sup> Main effect of level of beetle activity.

<sup>d</sup> See text for discussion of interactive effects.

Fig. II.1. Study site, Kickapoo Caverns State Natural Area in Kinney and Edwards counties, Texas.

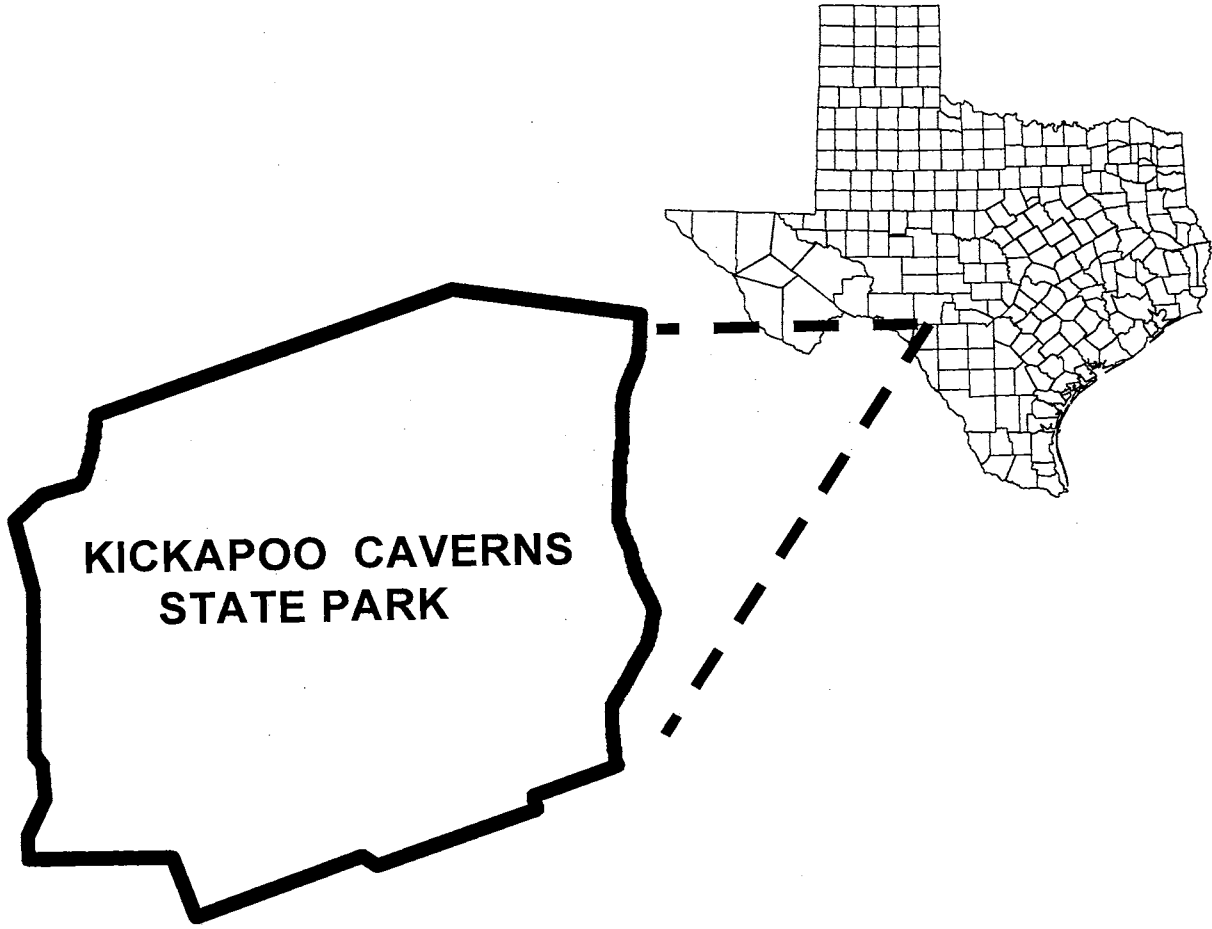


Fig. II.2. Transects established for sampling of porcupine- and bark beetle-damaged trees on Kickapoo Caverns State Natural Area in Kinney and Edwards counties, Texas.

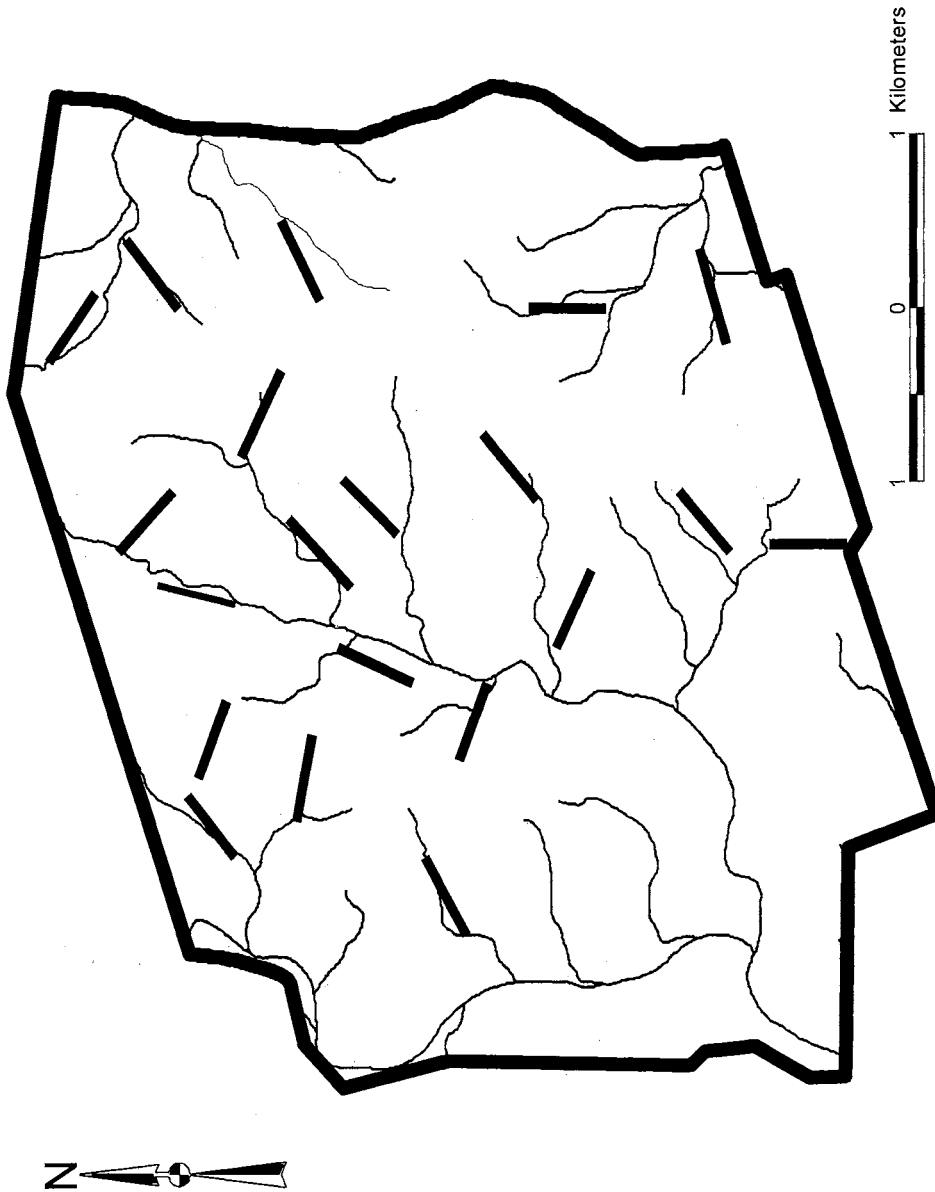


Fig. II.3. Association of bark beetle activity on porcupine-damaged and non-damaged pinyon pines on Kickapoo Caverns State Natural Area, Kinney and Edwards counties, Texas.

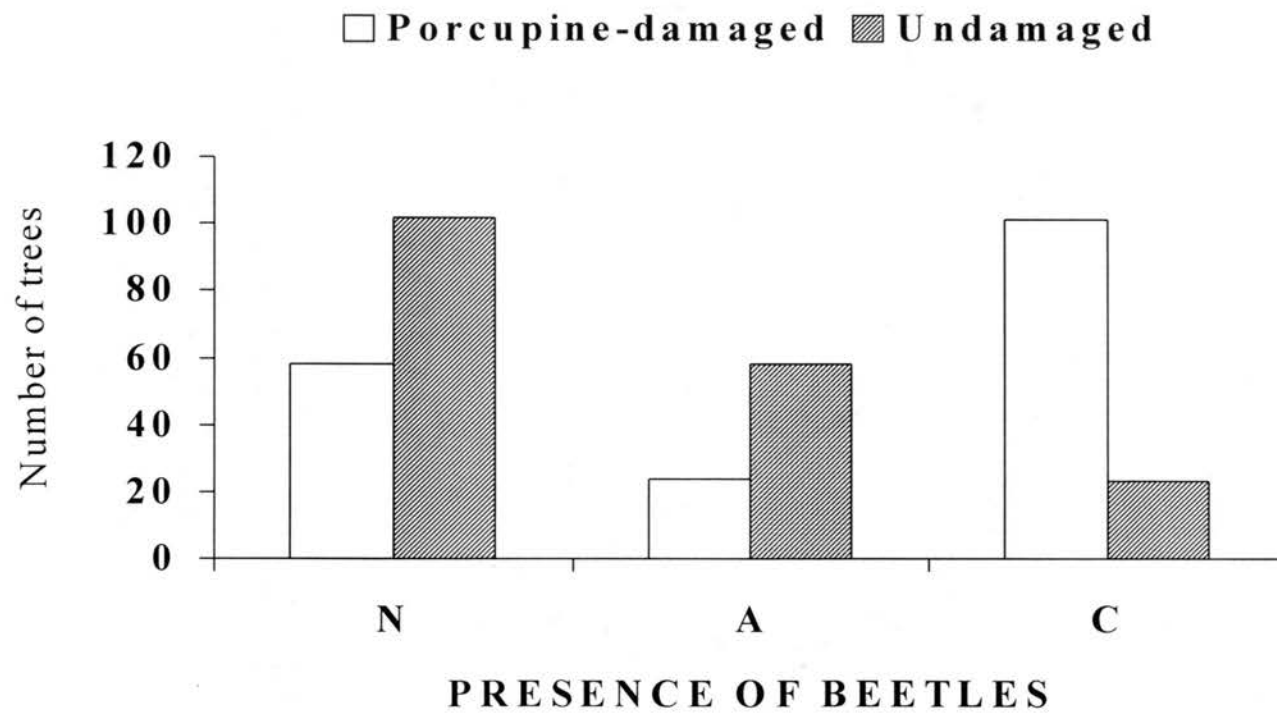




Fig. II.4. Comparison of resin flow on control and manipulated (bark removed) pinyon pines on Kickapoo Caverns State Natural Area in Kinney and Edwards counties, Texas.

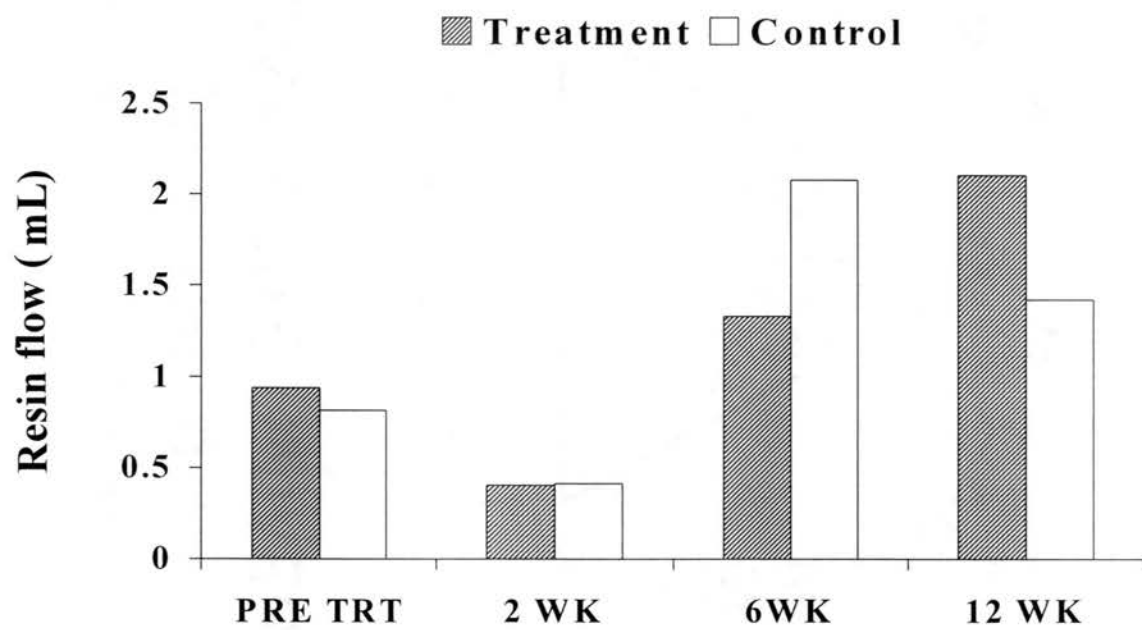


Fig. II.5. Comparison of glucose (a) and fructose (b) concentrations on control and manipulated (bark removed) pinyon pines on Kickapoo Caverns State Natural Area in Kinney and Edwards counties, Texas.

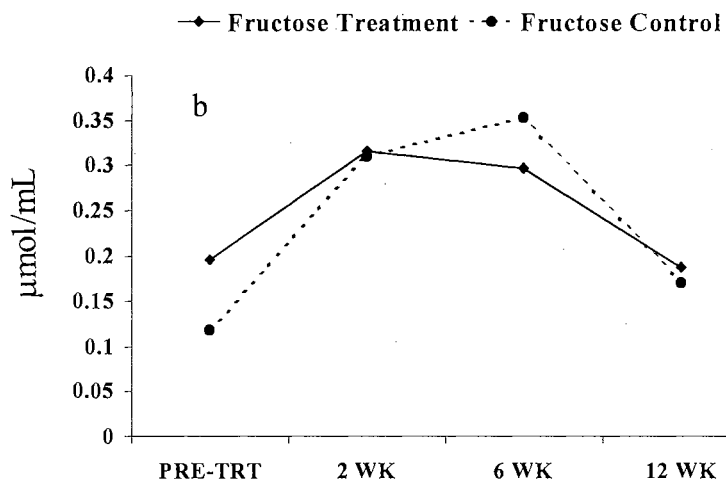
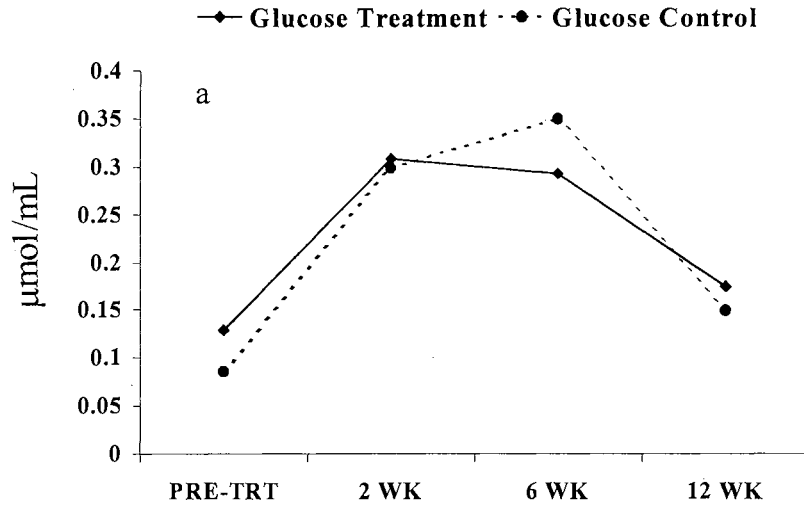


Fig. II.6. Comparison of percent composition of seven major monoterpenes on control and manipulated (bark removed) pinyon pines on Kickapoo Caverns State Natural Area, Kinney and Edwards counties, Texas.

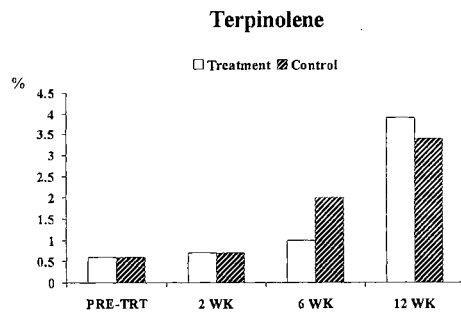
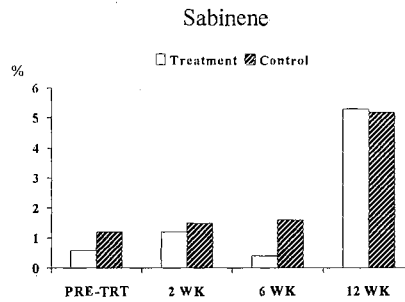
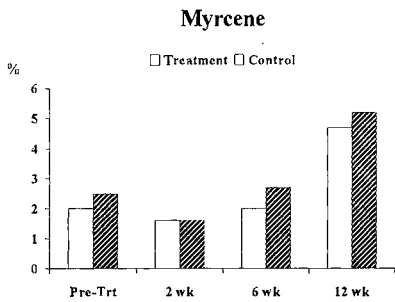
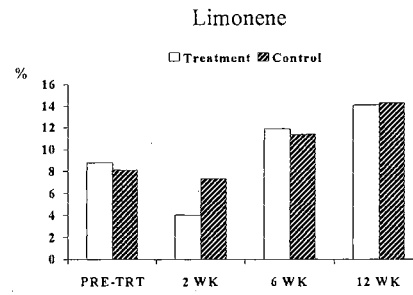
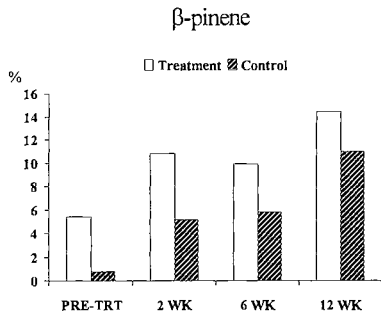
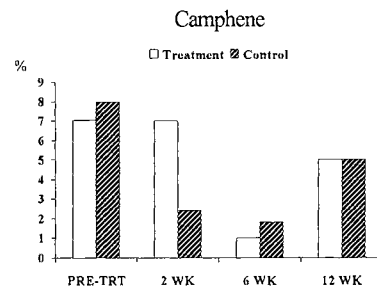
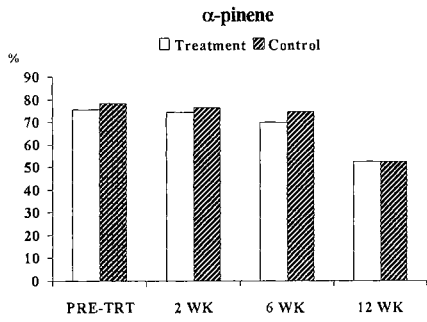
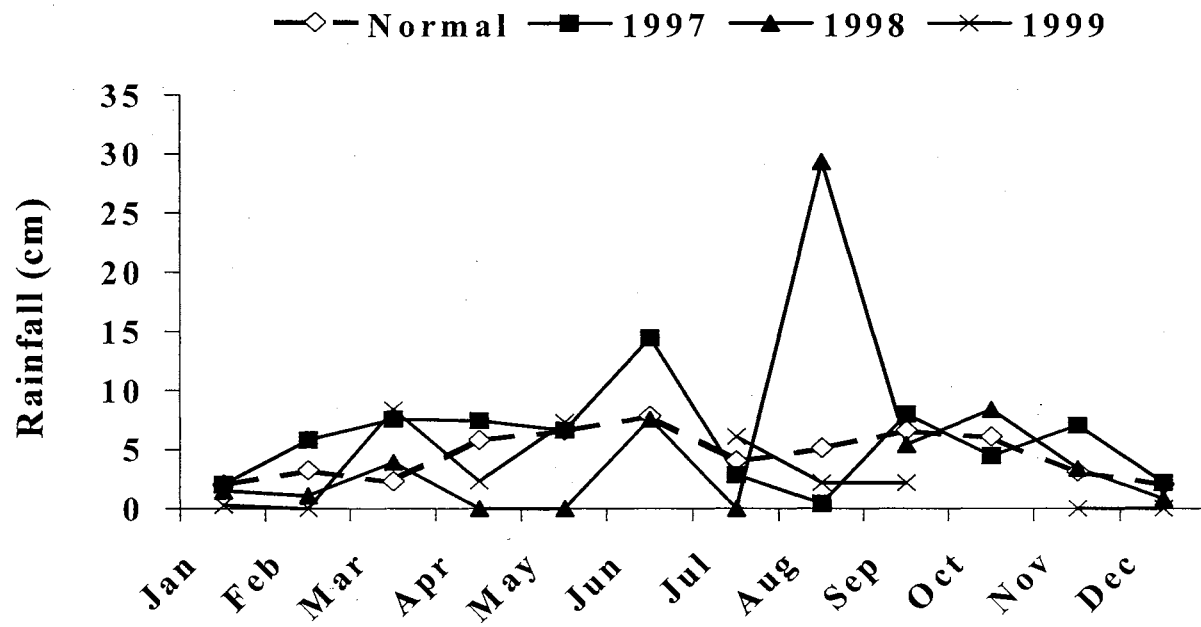


Fig. II.7 Monthly precipitation patterns in Kinney and Edwards counties, Texas 1997-1999.

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## CHAPTER III

### PORCUPINE EXPANSION AND ESTABLISHMENT IN THE EDWARDS PLATEAU OF TEXAS: A DENDROECOLOGICAL EXPLORATION

**ABSTRACT**— Ecological patterns can often be detected by analysis of annual growth rings of trees. I used a dendroecological approach to authenticate North American porcupine (Erethizon dorsatum) expansion into the Edwards Plateau of Texas. My study area, Kickapoo Caverns State Park, was the site of grazing and brush control management for over 50 years. These practices were discontinued in 1986 when the site was purchased by the Texas Parks and Wildlife Department. Tree-ring analysis of 430 cores and cross sections extracted from feeding scars on papershell pinyon pines (Pinus remota) on the site revealed that porcupines began expanding into this area about 30 years ago. Rare until the middle to late 1980s, porcupines recently have increased in numbers in the Edwards Plateau. I propose that a combination of climatic and land-use changes, accompanied by predator control, facilitated establishment of porcupines in this region.

### INTRODUCTION

The North American porcupine (Erethizon dorsatum) is distributed throughout Canada, most of the United States and parts of northern Mexico (Moody and Doniger, 1956; Dodge, 1982; Woods, 1973; Roze, 1989). Ecological study of this species has been conducted primarily in Canada (Harder, 1979; Payette 1986), the northern United States (Roze, 1989; Hale and Fuller, 1996; Griesemer et al., 1998), and the western United States (Tenneson and Oring, 1985; Sweitzer, 1990; Stricklan et al., 1995). Despite its occurrence and expanding range into southwestern states, little attention has addressed

porcupine activity in this region (Taylor, 1935; Reynolds, 1957; Davis and Schmidly, 1994).

Expansion of porcupines into the Edwards Plateau region of Texas (Davis and Schmidly, 1994) is of particular significance because the area harbors a disjunct relict population of the papershell pinyon pine (*Pinus remota*; Wells, 1987). Formerly prolific throughout the Chihuahuan Desert region, this pine is now restricted to scattered populations in northeastern Mexico and the Big Bend and Edwards Plateau regions of Texas (Wells, 1987), and porcupines feed preferentially on this species (Ilse 2001; see Chapter II). Warmer, drier conditions, typical of post-Pleistocene climate change, resulted in development of these refugial populations (Wells, 1966; Van Devender and Spaulding, 1979; Betancourt, 1987; Wells, 1987). However, the diminished range of this conifer may increase the possibility of its extirpation.

Strict herbivores, porcupines feed on a variety of vegetation, concentrating on herbaceous species in spring and summer. However, they are noteworthy for their bark-feeding activity, particularly in autumn and winter. During these seasons they become more arboreal, feeding primarily on phloem and cambium of coniferous trees (Spencer, 1964; Dodge, 1967; Roze, 1984). The porcupine, with its widespread geographic distribution, exploits a variety of habitat types (Woods, 1973) and can attack healthy vigorous trees (Sharpe et al., 1995). Although trees may be girdled in the process, damage frequently is limited to rectangular or ovate patches positioned above convenient resting branches (Spencer, 1964).

Removal of bark by porcupines leaves a distinctive scar at the feeding site on the tree. Radial growth is suspended on the face of the exposed xylem, but continues on

undamaged surfaces (Fig. III.1). Therefore, counting rings from the current year to the site of the lesion allows dating of wound inception. Dendrochronology has been used successfully to document patterns of distribution of porcupines (Spencer, 1964; Payette, 1986), caribou (Rangifer tarandus; Morneau and Payette, 2000), and spruce bud worms (Choristoneura occidentalis; Swetnam and Lynch, 1989).

My objective was to use dendrochronology to describe and reconstruct the recent expansion of porcupines into the ecologically sensitive Edwards Plateau region (Diamond et al. 1997). Age distributions of feeding scars were examined to detect changes in distribution and relative abundance of porcupines. I complemented these data with a review of land-use history in the area to explain my findings.

**METHODS AND MATERIALS**---Research was conducted on the 2577-ha Kickapoo Caverns State Park (KCSP, formerly Kickapoo Caverns State Natural Area) located approximately 35 km north of Brackettville, Texas. The site straddles Kinney and Edwards counties in the southwestern region of the Edwards Plateau. Topography is predominantly steep limestone hills and deep canyons with elevations ranging from 482 to 610 m. Average annual rainfall is approximately 45 cm (National Oceanic and Atmospheric Administration, 1999) and is bimodal, peaking in spring and fall (Fuhlendorf and Smeims, 1997; Bryan et al. 1999). No standing water or active springs are present on the site.

Shallow clay soils of east and north facing slopes supported pinyon-juniper-oak plant communities. In addition to the relict papershell pinyon pines, dominant tree species included Ashe juniper (*Juniperus ashei*), plateau live oak (*Quercus fusiformis*), Texas persimmon (*Diospyros texana*), and vasey oak (*Quercus pungens* var. *vaseyana*). Woody

shrubs included evergreen sumac (*Rhus virens*), guajillo (*Acacia berlandieri*) prickly pear (*Opuntia* spp.), and Roemer acacia (*Acacia roemeriana*). Ground cover was represented by cedar panicgrass (*Dichanthelium pedicellatum*) and cedar sedge (*Carex planostachys*) in shaded areas, and sideoats grama (*Bouteloua curtipendula*) and hairy tridens (*Erioneuron pilosum*) in more open areas.

Shallow soils of the south and west facing slopes were dominated by guajillo plant communities and pinyon pines were restricted to lower slope regions. Shrub species included guajillo, coyotillo (*Karwinskia humboldtiana*) and leatherstem (*Jatropha dioica*). Grasses included threeawn (*Aristida* spp.) and red grama (*Bouteloua trifida*).

Mottes of plateau live oak mixed with vasey oak and Ashe juniper were common in canyons and drainages where moisture was more abundant and soil was deeper. Pinyon pines and netleaf hackberry (*Celtis reticulata*) also occurred in these areas, but were less common. Dominant grasses included threeawn and annual dropseed (*Sporobolus* spp.).

A master chronology was prepared by extracting complete cores from the outer bark to the center of 10 randomly selected pinyon pines widely dispersed across the study area. Cores collected for dating porcupine range expansion and population fluctuations activity were extracted from feeding scars on trees along 20, 500-m transects previously established within wooded areas of known porcupine activity (Fig. III.2). Two cores or cross sections were extracted from a minimum of 10 trees located on or near each transect. One sample from each tree, selected by appearance, represented the oldest porcupine feeding scar. These samples were collected to determine the approximate date of initial porcupine expansion into KCSP. Subsequent samples on each tree were randomly selected to detect establishment and population fluctuations of porcupines within the area.

No more than 1 scar of the same age, based on appearance, was collected from the same tree. Cores were extracted using a 45.7-cm increment borer (Forestry Suppliers, Jackson, MS) with the bit started at the perimeter of the scar and directed to intercept the scar surface just inside the callous tissue, or intersection of new wood with the scar face (Spencer, 1964). Cross sections of branches were collected using a bow saw (Forestry Suppliers, Jackson, MS).

Core samples were initially placed in a plastic core holder (Forestry Suppliers, Jackson, MS) and allowed to dry before being placed in grooved wooden blocks for sanding. Surfaces of cores and cross sections were prepared by repeated sanding with progressively finer grades of sandpaper (60-600 grit). Date of scar inception was determined using a binocular dissecting microscope and counting rings back from the year of collection to the ring bearing the scar .

Cross-dating and identification of marker rings was accomplished using the list-method described by Yamaguchi (1991). Narrow annual growth rings were recorded for each specimen. Cores were then compared for shared narrow rings for cross-dating purposes. Separate frequency distributions were constructed for the oldest porcupine feeding scars and for randomly selected scars. Scar distributions also were compared with local rainfall data.

**RESULTS**---Dates from 10 trees collected for the master chronology ranged from 34 years (1965) to 120 years (1879). Narrow growth rings during the last 50 years were identified for 1952-1956, 1977, 1988, 1991, 1998, and 1999. These signature years coincided with periods of low rainfall and aided in cross-dating all samples. Among the 488 feeding scar samples, 88% ( $n = 430$ ) could be reliably dated to  $\pm 2$  years of scar

formation. One hundred seventy-eight samples represented the oldest scars and 252 samples represented random scars.

The oldest feeding scars were dated to the early 1970s (Fig. III.3), but were limited and intermittent until a decade later. Distribution of random scars (Fig. III.4) indicated that porcupine activity increased in the next 2 decades with peaks in 1987-88, 1991, 1994, and 1998. Porcupine activity tracked rainfall patterns with an approximate 1-year time lag (Fig. III.5).

**DISCUSSION**--My data indicate that porcupines occurred within the study area a minimum of 30 years ago. I conservatively estimated reliability of my sample dates because it was not always possible to discern if feeding occurred in the growing season or during the dormant season. Similarly, cores and cross sections were collected during the growing season and it was not always possible to detect onset of new growth. Older scars likely existed but were not evident in my sample. I was unable to extract cores from the oldest scars on all trees because stem and branch configuration prevented positioning of the increment borer. Trees bearing older scars may have died as a result of porcupine activity or other natural causes. However, persistence of trees older than the earliest dated feeding scar, evident in the master chronology trees, indicate that age of stands was not a factor affecting detection of older scars. Additionally, I observed numerous vigorous trees bearing extensive feeding scars. Girdling, and subsequent mortality of trees, as a result of feeding by porcupines is most common where branches are arranged symmetrically around the main stem, allowing the porcupine to conveniently grasp and remove bark from the same relative position around the entire tree (Spencer, 1964). Asymmetrical branching characteristic of the papershell pinyon pine generally precludes

this type of bark removal. Hence, it is improbable that porcupine-induced mortality was responsible for the observed lack of older feeding scars.

Age distribution of random scars was similar to distribution of oldest scars and validated the lack of earlier porcupine feeding scars. It is doubtful that scars were obliterated by callous tissue, or formation of new wood surrounding the wound. Spencer (1964) reported that the growth response of P. edulis, another pinyon pine of the subsection Cembroides (Price et al., 1998), was well-suited to preservation of dendrochronological records because the callous tissue is insufficient to obscure external evidence of the wound.

Porcupines frequently remain in or near the same feeding tree for 1-4 days (Spencer, 1964; Roze, 1989, personal obs.). In some regions, winter home ranges are diminished because the animals use feed-trees near den sites (Smith, 1979; Craig and Keller, 1986). I ameliorated biases associated with these behavioral characteristics by randomly sampling trees dispersed throughout the study site and by limiting collection of cores from an individual tree. Therefore, I believe that my data accurately reflect porcupine feeding activity and serve as an indirect index not only to occurrence but population size.

Although evidence of porcupines within the study region dates to 1970, my data indicate that it is unlikely that the population became well established before the 1980s. These dates correspond to anecdotal sightings by local residents who report that porcupines have been observed in the area only during the last 15-20 years. Likewise, Davis and Schmidly (1994) reported a westward and southward expansion of porcupines in Texas.

These data also correspond with those of T. P. Harlan (Laboratory of Tree Ring Research, University of AZ, Tucson, unpublished data) who collected core data in 1974 on another site in Edwards county. Tree ages in that sample ( $n = 20$ ) ranged from 45 years to 307 years. Porcupine damage was noted on only 1 tree, but broken limbs from a severe ice storm that winter were reported for 6 trees. My limited sample was collected for ring-growth comparison only; therefore, it is likely that older trees were overlooked. Damage from the ice storm in 1974 also may have eliminated older, more vulnerable trees.

Distribution of random feeding scars indicates that porcupines may have experienced several population fluctuations occurring at 3-4 year intervals. Alternatively, these fluctuations may simply reflect a decrease in use of pinyon pines during these periods. Porcupines consume a variety of food resources focusing on inner bark during winter (Dodge, 1967; Roze, 1989). In addition to winter use of pinyon pines, I observed females using pines extensively in spring and summer immediately following parturition (Ilse and Hellgren, In Press). During arid conditions, porcupines also were observed frequently feeding on fruits of prickly pear. These observations, combined with the association of decreased feeding scars during periods of limited rainfall, validate my contention that the animals may be switching to alternative food resources during drought conditions.

The dendrochronological data adequately described movement and establishment of porcupines into the region; however, examination of related ecological factors is requisite to explaining why this range expansion has occurred. Historical land-use practices conceivably influenced expansion of porcupines into the Edwards Plateau. There is no reported evidence of porcupines in this region before settlement, indicating the



possibility that open prairie and savannah communities were inadequate to support this dendrophagic mammal. European settlement of the region resulted in increased stocking of domestic herbivores and a concomitant decrease in fuel load and fire intensity (Fuhlendorf et al., 1996). Overgrazing, fire suppression, and climatic change affected long-term vegetation dynamics (Fuhlendorf and Smeims, 1997) and facilitated invasion and establishment of pinyon-juniper woodlands across the Southwest (Blackburn and Tuellar, 1970). These woodlands constitute more suitable habitat for the porcupine and likely enhanced its successful expansion into this region.

Management of Kickapoo Caverns State Park supported goat, sheep, and cattle ranching for 63 years before acquisition by the Texas Parks and Wildlife Department (TPWD) in 1986 (Bryan et al., 1999). Mechanical treatments such as cabling, chaining, and hydroaxing were used to promote grazing suitability. Stocking rates of sheep and goats ranged from 3,500 animals in 1937 to 2,000 animals in 1986 and during periods of sufficient precipitation, up to 200 cattle also were stocked on the property (Bryan et al., 1999). During the 1950s through 1970s, cabling and chaining was continued with some rotational grazing and reseeding of non-native grasses including King ranch bluestem (*Bothriochloa ischaemum* var. *songarica*), buffleggrass (*Cenchrus ciliaris*) and blue panicgrass (*Panicum antidotale*). Manipulation of vegetation was discontinued following acquisition by TPWD and preservation of the papershell pinyon pine was a primary conservation goal (Bryan et al. 1999). Earlier perturbations and vegetative changes may have prevented the porcupine from establishing a viable population. Although the porcupine has never been the subject of grazing studies, I believe the population eruption following discontinuation of these activities may be more than coincidental.

Lack of predation pressure may have contributed to the recent porcupine proliferation in this region. Organized predator control has been used in the Edwards Plateau since the early 1900's to benefit goat and sheep ranching operations (Nunley, 1996). Coyotes (Canis latrans) were extirpated from the region for many years as a result of combined efforts by the Texas Animal Damage Control Agency and private ranchers. These carnivores began returning to the Edwards Plateau in the 1950-1970 period and renewed efforts at control were initiated. (Nunley, 1996). In Kinney and Edwards counties, control efforts targeting coyotes, bobcats (Lynx rufus), and feral hogs (Sus scrofa) have been ongoing for > 20 years. Properties adjacent to Kickapoo Caverns State Natural Area have been sites of much of this effort (M. Mapston, Texas Animal Damage Control, pers. comm.) Occasional sightings of mountain lions (Felis concolor) have been reported; however, alternative prey, including opossum (Didelphus virginianus), desert cottontail (Sylvilagus auduboni), black-tailed jackrabbit (Lepus californicus), squirrels (Spermophilus spp.), and a variety of mice and rats (Muridae) abound in the area and constitute more easily available prey than the quill-defended porcupine.

I propose that a combination of land-use practices, changing climate, and predator control contributed to successful establishment and expansion of the porcupine in the Edwards Plateau region. Although porcupines occurred on the property before purchase by TPWD, the population, as reflected by feeding scars, was limited until the 1980s. The population, despite possible fluctuation, continued to grow in the late 1990s ( $\lambda = 1.03$ ; Ilse and Hellgren, In Press).

**ACKNOWLEDGMENTS**—I am indebted to Dave Stuart and Daniel Klepper for invaluable logistic and technological support for this research. I also am grateful to Dr.

Steve Schwartz for allowing me to use his lab and dissecting microscope for tree ring analysis. Funding for the study was provided by Rob and Bessie Welder Wildlife Foundation, Max McGraw Wildlife Foundation, Texas Parks and Wildlife Department, Oklahoma Cooperative Fish and Wildlife Research Unit (Okla. State Univ. Oklahoma Dep. of Wildlife Conserv., U.S.G.S. Biol. Resour. Div., Wildl. Manage. Inst. Cooperating), Sigma Xi, Theodore Roosevelt Memorial Fund, and The American Society of Mammalogists. This manuscript represents Welder Wildlife Contribution Number \_\_\_\_\_.

#### LITERATURE CITED

- BETANCOURT, J. L. 1987. Paleoecology of the pinyon-juniper woodlands. Pages 129-139 in Proceedings of the pinyon-juniper conference. Reno NV. USDA Forest Service Gen. Tech. Rept. INT 215.
- BLACKBURN, W.H., AND P. T. TUELLER. Pinyon and juniper invasion in back sagebrush communities in east-central Nevada. Ecology 51:841-848.
- BRYAN, K., L. HEDGES, AND T. ROBERTS. 1999. Resource management plan for Kickapoo Caverns State Park. Draft Report for Texas Parks and Wildlife Department
- CRAIG, E. H., AND B. L. KELLER. 1986. Movements and home range of porcupines (*Erethizon dorsatum*) in Idaho shrub desert. Canadian Field Naturalist 100:167-173.

- DAVIS, W. R., AND D. J. SCHMIDLY. 1994. Porcupine. Pages 206-208 in The mammals of Texas. Texas Parks and Wildlife Department, Austin.
- DIAMOND, D. D., C. D. TRUE, AND K. HE. 1997. Regional priorities for conservation of rare species in Texas. *Southwestern Naturalist* 42:400-408.
- DODGE, W. E. 1967. The biology and life history of the porcupine (*Erethizon dorsum*) in western Massachusetts. Ph.D. dissertation. University of Massachusetts, Amherst. 133pp
- DODGE, W. E. 1982. Porcupine. In: Chapman, J. A., and G. A. Feldhamer, editors. Wild mammals of North America: biology, management, and economics. Johns Hopkins University Press, Baltimore. pp 355-366.
- FUHLENDORF, S. D., F. E. SMEIMS, AND W. E. GRANT. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards plateau of Texas, USA. *Ecological Modelling* 90:245-255.
- FUHLENDORF, S. D., AND F. E. SMEIMS. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetative Science* 8:819-828.
- GRIESEMER, S. J., T. K. FULLER, AND R. M. DEGRAAF. 1998. Habitat use by porcupines (*Erethizon dorsatum*) in central Massachusetts: effects of topography and forest composition. *American Midland Naturalist* 140:271-279.
- HALE, M. B., AND T. K. FULLER. 1996. Porcupine (*Erethizon dorsatum*) demography in central Massachusetts. *Canadian Journal of Zoology* 74:480-484.
- HARDER, L. D. 1979. Winter feeding by porcupines in montane forests of southwestern Alberta. *Canadian Field Naturalist* 93:405-410.

- ILSE, L. M., AND E. C. HELLGREN. **In Press.** Demographic and behavioral characteristics of North American porcupines (*Erethizon dorsatum*) in pinyon-juniper woodlands of Texas. *American Midland Naturalist*.
- MOODY, P. A., AND D. E. DONIGER. 1956. Serological light on porcupine relations. *Evolution* 10:47-55.
- MORNEAU, C., AND S. PAYETTE. 2000. Long-term fluctuations of a caribou population revealed by tree-ring data. *Canadian Journal of Zoology* 78:1784-1790.
- NATIONAL OCEANOGRAPHIC AND ATMOSPHERIC ADMINISTRATION. 1999. Texas Climatology. National Weather Data Center, Asheville, NC, USA.
- NUNLEY, G. L. 1996. The re-establishment of the coyote in the Edwards Plateau in Texas. In: Rollins, D, C. Richardson, T. Blankenship, K. Canon, and S. Henke, editors. *Coyotes in the southwest: a compendium of our knowledge*. Symposium Proceedings. Pp55-64.
- PAYETTE, S. 1986. Recent porcupine expansion at tree line: a dendroecological analysis. *Canadian Journal of Zoology* 65:551-557.
- PRICE, R. A., A. LISTON, AND S. H. STRAUSS. 1998. Phylogeny and systematics of *Pinus*. In: Richardson, D. M., editor. *Ecology and biogeography of Pinus*. Cambridge University Press, Cambridge, UK. Pages 49-68.
- REYNOLDS, H. G. 1957. Porcupine behavior in the desert-shrub type of Arizona. *Journal of Mammalogy* 33:418-419.
- ROZE, U. 1984. Winter foraging by individual porcupines. *Canadian Journal of Zoology* 62:2425-2428.

- ROZE, U. 1989. The North American Porcupine. Smithsonian Press, Washington, D. C. 261pp.
- SHARPE, G. W., C. W. HENDEE, W. F. SHARPE, AND J. C. HENDEE. 1995. Insects and mammals. Pages 140-161 in Introduction to forests and renewable resources. McGraw Hill Inc., New York.
- SMITH, G. W. 1979. Movements and home range of the porcupine in Northeastern Oregon. Northwest Science 53:277-282.
- SPENCER, D. A. 1964. Porcupine fluctuations in past centuries revealed by dendrochronology. Journal of Applied Ecology 1:127-149.
- STRICKLAN, D., J. T. FLINDERS, AND R. G. CATES. 1995. Factors affecting selection of winter food and roosting resources by porcupines in Utah. Great Basin Naturalist 55:29-36.
- SWEITZER, R. A. 1990. Winter ecology and predator avoidance in porcupines in Great Basin porcupines (*Erethizon dorsatum*). M.S. Thesis. University of Nevada, Reno. 64pp.
- SWETNAM, T. W., AND A. M. LYNCH. 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. Forest Science 35:962-986.
- TAYLOR, W. P. 1935. Ecology and life history of the porcupine (*Erethizon dorsatum epixanthum*) as related to the forests of Arizona and the southwestern United States. University of Arizona Bulletin 6:1-177.
- VAN DEVENDER, T. R., AND W. G. SPAULDING. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701-710.

- WELLS, P. V. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. *Science* 153:970-975.
- WELLS, P. V. 1987. Systematics and distribution of pinyons in the late quaternary. Proceedings of the pinyon-juniper conference. Reno, NV. U.S. Forest Service, USDA, Gen. Tech Rep. INT 215:104-108.
- WOODS, C. A. 1973. *Erethizon dorsatum*. *Mammalian Species* 29:1-6.
- YAMAGUCHI, D. K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21:414-416.

Fig III.1. Cross-section of porcupine feeding scar on papershell pinyon pine branch.



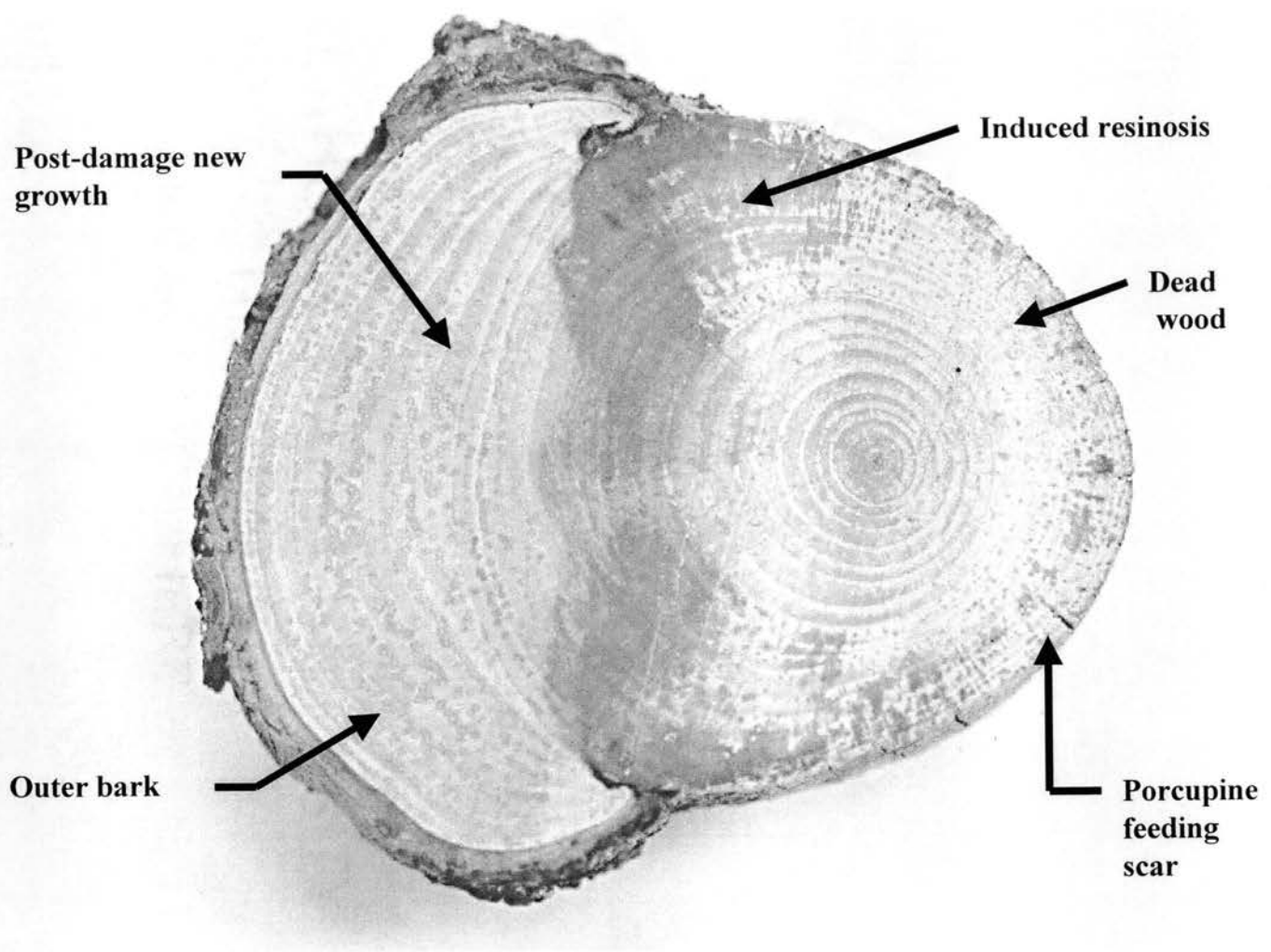


Fig. III.2. Transects established on Kickapoo Caverns State park, Kinney and Edwards counties, Texas, Texas.

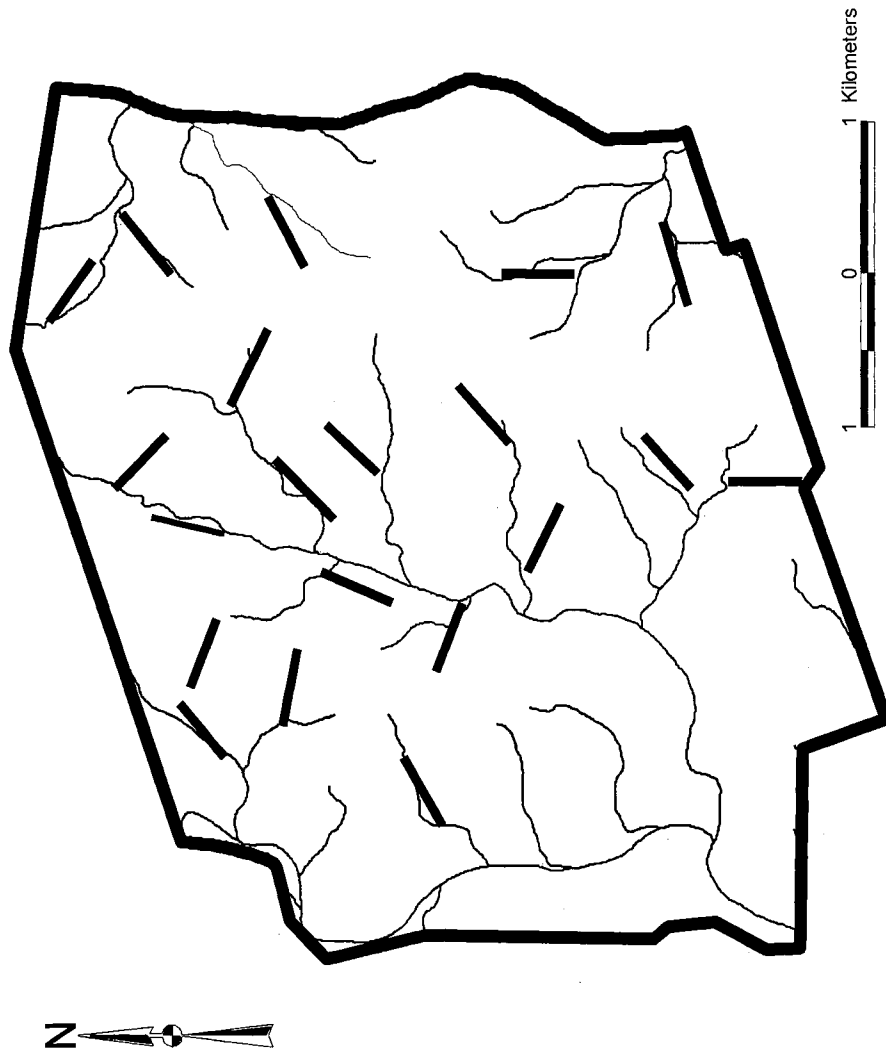


Fig. III.3. Histogram of oldest porcupine feeding scars collected from papershell pinyon pines ( $n = 178$ ) by year of scarring on Kickapoo Caverns State Park, Kinney and Edwards counties, Texas.

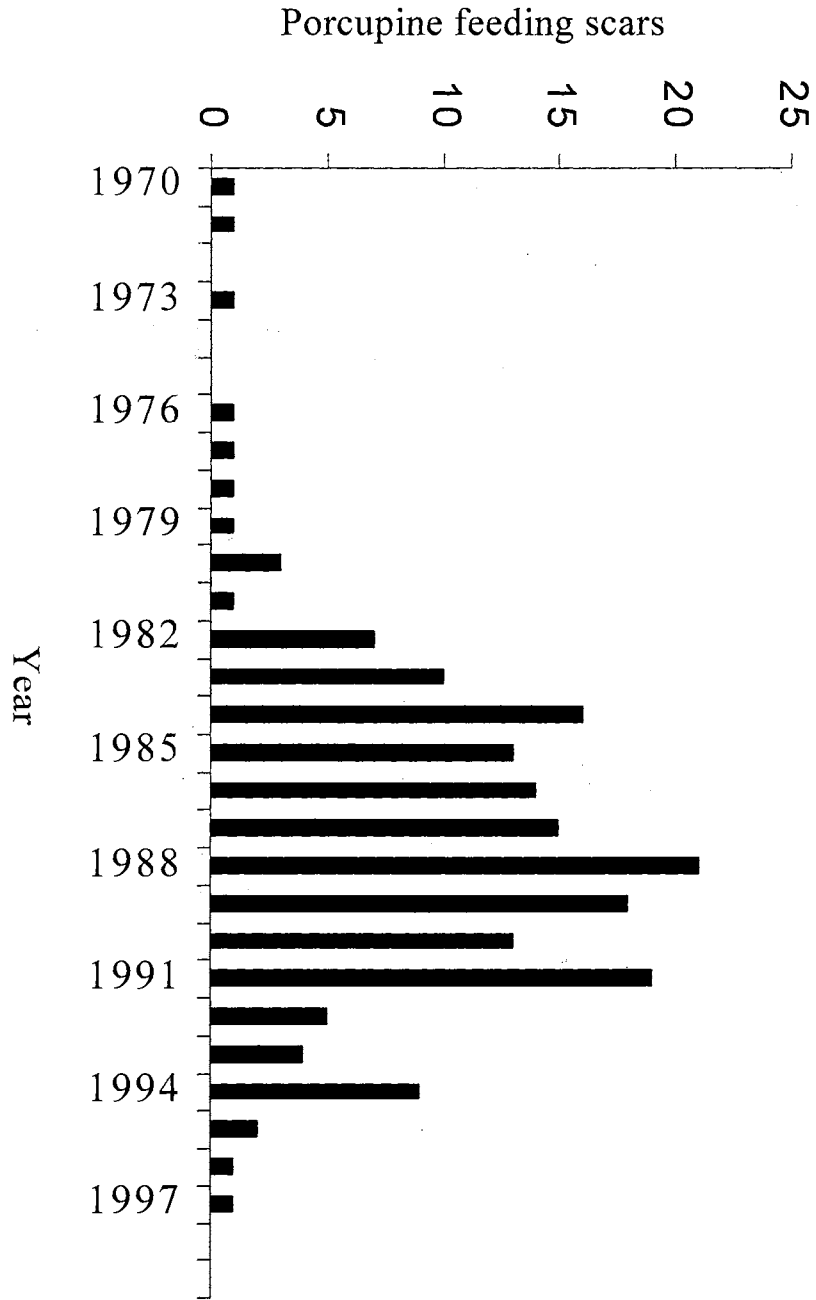


Fig. III. 4. Histogram of random porcupine feeding scars collected from papershell pinyon pines ( $n = 252$ ) by year of scarring on Kickapoo Caverns State park, Kinney and Edwards counties, Texas.

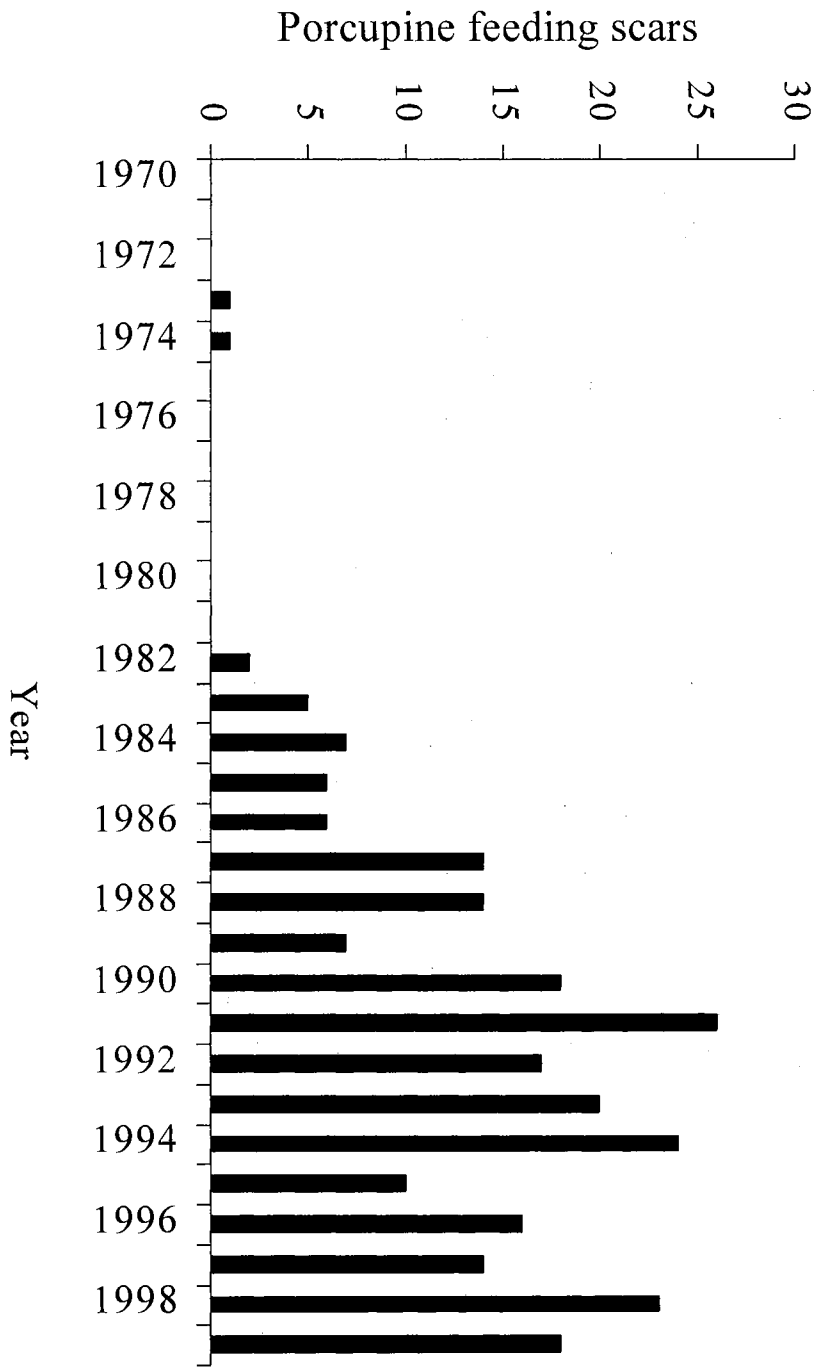
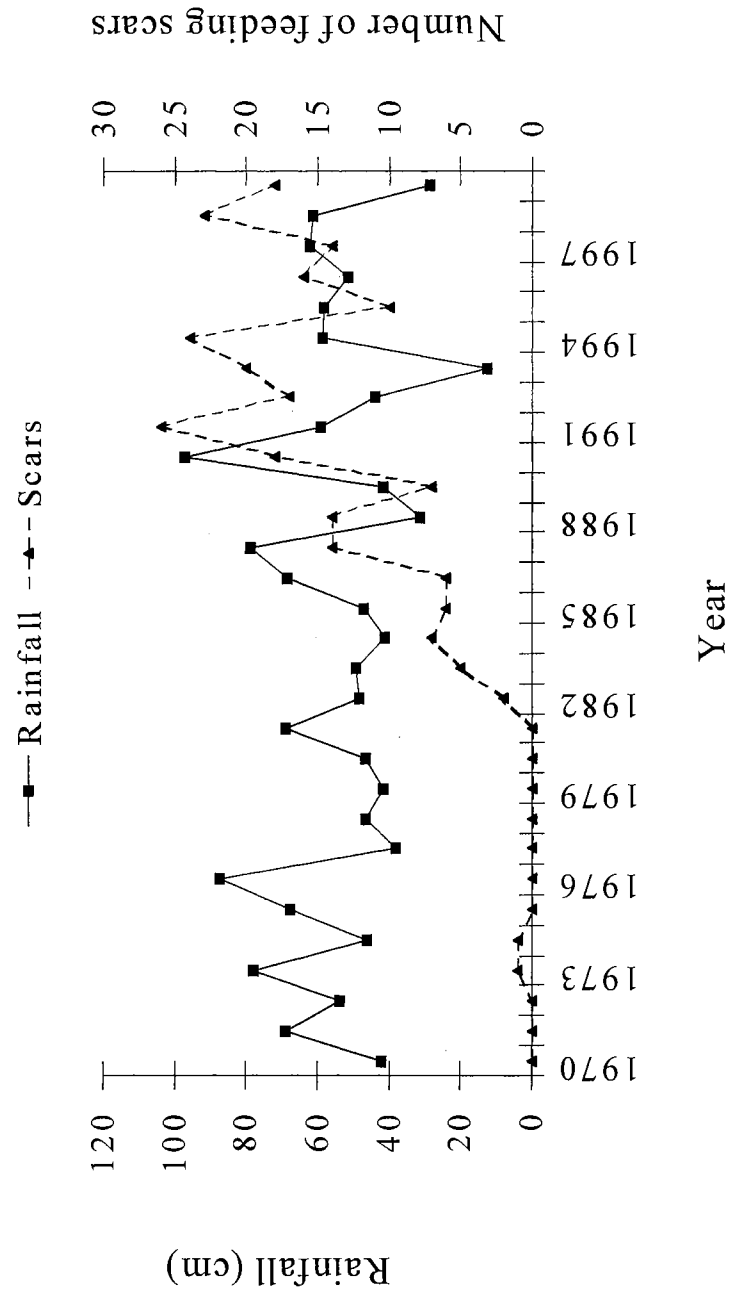


Fig. III.5. Relationship among porcupine feeding scars, rainfall, and year on Kickapoo Caverns State Park, Kinney and Edwards counties, Texas.





APPENDIX  
MORPHOMETRIC DATA OF CAPTURED PORCUPINES

APPENDIX. Morphometric data for porcupines captured at Kickapoo Caverns State Natural Area, Kinney and Edwards counties Texas, 1997-1999.

| SEX | AGE | MASS<br>(kg) | TOTAL <sup>a</sup><br>LENGTH(mm) | TAIL <sup>b</sup><br>LENGTH(mm) | NECK <sup>c</sup><br>(mm) | HIND FOOT <sup>d</sup><br>LENGTH(mm) | UPPER INCISOR<br>LENGTH (mm) | LOWER INCISOR<br>LENGTH (mm) |
|-----|-----|--------------|----------------------------------|---------------------------------|---------------------------|--------------------------------------|------------------------------|------------------------------|
| F   | A   | 6.0          | 520.0                            | 230.0                           | 27.5                      | 70.0                                 | 14.8                         | 28.0                         |
| F   | A   | 6.8          | 530.0                            | 205.0                           | 26.0                      | 75.0                                 | 19.0                         | 23.5                         |
| F   | A   | 4.5          | 500.0                            | 190.0                           | 26.5                      | 85.0                                 | na                           | na                           |
| F   | A   | 4.5          | 500.0                            | 190.0                           | 26.5                      | 85.0                                 | na                           | na                           |
| F   | A   | 8.1          | 535.0                            | 220.0                           | 30.0                      | 80.0                                 | 16.0                         | 16.0                         |
| F   | A   | 7.3          | 570.0                            | 230.0                           | 31.0                      | 84.0                                 | 17.0                         | 17.0                         |
| F   | A   | 8.1          | 570.0                            | 200.0                           | 31.0                      | 85.0                                 | 16.3                         | 17.9                         |
| F   | A   | 6.7          | 545.0                            | 220.0                           | 29.0                      | 75.0                                 | 13.3                         | 19.6                         |
| F   | A   | 7.2          | 535.0                            | 185.0                           | 29.0                      | 85.0                                 | na                           | na                           |
| F   | A   | 7.7          | 555.0                            | 185.0                           | 25.0                      | 84.0                                 | 18.0                         | 20.0                         |
| F   | A   | 8.5          | 550.0                            | 170.0                           | 28.0                      | 88.0                                 | 20.1                         | 18.1                         |
| F   | A   | 5.8          | 640.0                            | 190.0                           | 23.4                      | 84.0                                 | 18.9                         | 24.5                         |
| F   | A   | 3.5          | 520.0                            | 230.0                           | 22.0                      | 75.0                                 | 19.4                         | 21.4                         |
| F   | A   | 5.9          | 510.0                            | 230.0                           | 24.0                      | 65.0                                 | 15.9                         | 19.4                         |
| F   | A   | 6.7          | 565.0                            | 200.0                           | 26.0                      | 75.0                                 | 14.4                         | 20.7                         |

APPENDIX Cont. Morphometric data for porcupines captured at Kickapoo Caverns State Natural Area, Kinney and Edwards counties, Texas, 1997-1999.

| SEX | AGE | MASS<br>(kg) | TOTAL <sup>a</sup><br>LENGTH(mm) | TAIL <sup>b</sup><br>LENGTH(mm) | NECK <sup>c</sup><br>(mm) | HIND FOOT <sup>d</sup><br>LENGTH(mm) | UPPER INCISOR<br>LENGTH (mm) | LOWER INCISOR<br>LENGTH (mm) |
|-----|-----|--------------|----------------------------------|---------------------------------|---------------------------|--------------------------------------|------------------------------|------------------------------|
| F   | A   | 5.0          | 520.0                            | 215.0                           | 23.5                      | 90.0                                 | 11.3                         | 16.3                         |
| F   | A   | 8.0          | 560.0                            | 210.0                           | 30.0                      | 80.0                                 | 14.5                         | 19.6                         |
| F   | A   | 6.7          | 530.0                            | 210.0                           | 23.5                      | 75.0                                 | 15.1                         | 22.9                         |
| M   | A   | 12.7         | 730.0                            | 230.0                           | 38.0                      | 105.0                                | na                           | na                           |
| M   | A   | 9.1          | 610.0                            | 260.0                           | 33.0                      | 120.0                                | 26.0                         | 31.0                         |
| M   | A   | 9.1          | 655.0                            | 265.0                           | 28.0                      | 95.0                                 | 20.9                         | 24.4                         |
| M   | A   | 11.6         | 710.0                            | 245.0                           | 30.0                      | 111.0                                | 20.7                         | 31.5                         |
| M   | A   | 6.6          | 550.0                            | 250.0                           | 20.0                      | 82.0                                 | 20.0                         | 23.0                         |
| M   | A   | 8.0          | 610.0                            | 270.0                           | 27.0                      | 105.0                                | 25.2                         | 35.6                         |
| F   | Y   | 4.7          | 515.0                            | 240.0                           | 28.0                      | 80.0                                 | 13.0                         | 15.0                         |
| F   | Y   | 4.1          | 490.0                            | 155.0                           | 24.5                      | 75.0                                 | 9.0                          | 11.0                         |
| F   | Y   | 5.5          | 560.0                            | 195.0                           | 21.5                      | 85.0                                 | 10.9                         | 16.1                         |
| F   | Y   | 4.3          | 495.0                            | 215.0                           | 23.5                      | 90.0                                 | 13.2                         | 16.4                         |
| M   | Y   | 4.2          | 450.0                            | 160.0                           | 22.0                      | 80.0                                 | 15.0                         | 18.0                         |
| M   | Y   | 4.7          | 525.0                            | 230.0                           | 23.0                      | 92.0                                 | 16.4                         | 20.9                         |

APPENDIX Cont. Morphometric data for porcupines captured at Kickapoo Caverns State Natural Area, Kinney and Edwards counties Texas, 1997-1999.

| SEX | AGE | MASS<br>(kg) | TOTAL <sup>a</sup><br>LENGTH(mm) | TAIL <sup>b</sup><br>LENGTH(mm) | NECK <sup>c</sup><br>(mm) | HIND FOOT <sup>d</sup><br>LENGTH(mm) | UPPER INCISOR<br>LENGTH (mm) | LOWER INCISOR<br>LENGTH (mm) |
|-----|-----|--------------|----------------------------------|---------------------------------|---------------------------|--------------------------------------|------------------------------|------------------------------|
| M   | Y   | 6.2          | 555.0                            | 285.0                           | 24.0                      | 95.0                                 | 12.8                         | 16.1                         |
| M   | Y   | 4.8          | 520.0                            | 187.0                           | 21.0                      | 87.0                                 | 10.0                         | 13.1                         |
| M   | Y   | 4.5          | 505.0                            | 195.0                           | 22.7                      | 78.0                                 | 15.1                         | 16.2                         |
| F   | J   | 3.5          | 300.0                            | 150.0                           | 27.0                      | 46.5                                 | 10.5                         | 12.5                         |
| F   | J   | 3.0          | 390.0                            | 170.0                           | 23.0                      | 67.0                                 | na                           | na                           |
| F   | J   | 3.6          | 400.0                            | 165.0                           | 20.0                      | 75.0                                 | 6.5                          | 10.1                         |
| M   | J   | 2.0          | 375.0                            | 147.0                           | 15.0                      | 72.0                                 | 10.0                         | 11.8                         |
| M   | J   | 3.1          | 440.0                            | 180.0                           | 21.5                      | 70.0                                 | 10.5                         | 15.9                         |
| M   | J   | 2.6          | 400.0                            | 165.0                           | 17.0                      | 70.0                                 | 13.0                         | 14.0                         |

<sup>a</sup> Measured along vertebral column from distal tip of tail to tip of snout

<sup>b</sup> Measured from distal tip of tail to caudal vertebra

<sup>c</sup> Circumference

<sup>d</sup> Includes claw

7  
VITA

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