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INDIRECT INTERACTIONS AMONG DENDROPHAGES: PORCUPINES PREDISPOSE PINYON PINES TO BARK BEETLE ATTACK

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Abstract

Discerning linkages among trophic levels and untangling indirect interactions is essential to understanding structuring of communities and ecosystems. Indeed, indirect interactions among disparate taxa are often essential to the functional role of these species. The goal of this research was to test the hypothesis that the relationship between 2 dendrophagous taxa, the North American porcupine (*Erethizon dorsatum*) and the pine engraver beetle (*Ips hoppingi*), is an asymmetric indirect interaction mediated by a common host. We proposed that the porcupine predisposes the papershell pinyon pine (*Pinus remota*) to colonization by pine engraver beetles. We examined porcupine tree selection, 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. Although attacks by beetles were evident on both damaged and undamaged trees, successful colonization was greater ($\chi^2 = 75.3$, df = 3, $P < 0.01$) on pines damaged by porcupines. Intensity of porcupine attack, indexed by number of feeding scars and area of bark removed, also was associated with subsequent colonization by beetles. 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 phloem with higher concentrations of fructose and glucose and lower percent composition of limonene, sabinene, and terpinolene than uncolonized trees. Our findings supported our hypothesis of an indirect interaction between these dendrophages. We rejected alternative explanations (e.g., that these dendrophages preferred similar trees or that beetles facilitated porcupine damage) for this relationship based on the biology of *Ips* and their selection of host trees. We propose that release of volatile terpenes as a result of porcupine feeding and reallocation of carbon resources as a response to stress explains the facilitation of beetle colonization in porcupine-damaged trees. Our findings parallel those observed in other systems involving indirect effects and fit within the framework of integrated theories explaining host plant-herbivore interactions.

Key Words: dendrophages*, Erethizon dorsatum*, indirect effects, *Ips hoppingi*, *Pinus remota*, plant-herbivore interactions

1. 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, which 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 (Christensen 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). Insects and vertebrates can interact to influence species composition, organic decomposition, and soil properties within an ecosystem (Sharpe et al., 1995; Elkinton et al., 1996). Several studies have shown that attack by one consumer can increase susceptibility to attack by others. Browsing by mammalian herbivores can lead to increased densities of leaf-eating (Martinsen et al., 1998) and galling insects

(Roininen et al., 1997; Olofsson and Strengbom ,2000). 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). Although the impact of herbivory on dendrophagic insects has received less attention, Conner and Rudolph (1995) suggested that pecking at resin wells by red-cockaded woodpeckers (*Picoides borealis*) may increase susceptibility of cavity trees to infestation by bark beetles (*Dendroctonus frontalis.*) Similarly, defoliation of jack pine (*Pinus banksiana*) by the jack pine budworm (*Choristoneura pinus pinus)* led to increased colonization by subcortical insects (Wallin and Raffa, 2001).

We examine a novel interaction involving 2 dendrophagic species and their tree hosts to advance our understanding of plant-herbivore interactions. Previous research effort in this area has focused on leaf-eaters and defoliation. The cost to defend, repair, and replace bark damaged by dendrophages likely differs from damage produced by defoliators, warranting examination of a model system involving indirect interactions among a host plant and 2 dendrophages. Our study animals, the porcupine (*Erethizon dorsatum*) and bark beetles (Coleoptera: Scolytidae), are taxonomically distinct dendrophagous taxa occurring sympatrically in many wooded ecosystems. Their phloem-feeding activities impact nutrient flow within the host tree, as opposed to nutrient production (by defoliators) or nutrient storage and acquisition (by root pathogens). Phloem feeding causes wounding or girdling, thereby altering translocation of carbohydrates and resulting in increased activity of bark beetles (Dunn and Lorio 1992).

Mechanisms of host attack exhibited by porcupines and bark beetles differ. The porcupine exploits a variety of habitat types (Roze and Ilse, 2003) and prefer to attack healthy, vigorous trees (Sharpe et al., 1995). A strict herbivore, it consumes deciduous leaves and herbaceous matter during spring and summer, but feeds primarily on inner bark and coniferous foliage during the winter and fall (Roze and Ilse, 2003). 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, emerge in spring and aggregation and development of multiple generations occurs through summer (Stark, 1982). Furthermore, they attack, feed, and oviposit in stressed or otherwise compromised conifers (Raffa et al., 1993) and exhibit greater host specificity at the species level (Wood, 1963; Cane et al., 1990). Events known or presumed to precipitate pine engraver and other bark beetle infestations include fire, severe drought, mechanical injury, lightning, and even cavity-nesting by the red-cockaded woodpecker (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 bark beetle attack by flushing out invaders. A secondary, or induced, response contains the infestation when the primary response is insufficient to repel attack (Berryman ,1972; Cates and Alexander, 1982; Raffa, 1991). Chemical and nutritional imbalances resulting from a variety of stressors diminish a host’s ability to mount a defensive response and increase the potential for pathogenic infection and increased susceptibility to bark beetle invasion (Hodges et al., 1979; Lorio 1993; Paine and Baker, 1993).

Porcupines and pine engravers feed upon the papershell pinyon pine (*Pinus remota*) in the pinyon-juniper woodlands of the Edwards Plateau region of Texas (Ilse, 2001; Ilse and Hellgren 2001). Close observation of vigorous, healthy pines in this region often indicated extensive porcupine feeding scars. However, examination of dead and dying trees indicated additional presence of pine engraver beetles (*I. hoppingi*). These observations led to development of our hypothesis that porcupine-feeding activity acts similar to other mechanical stressors (e.g., fire, lightning, cavity-building), predisposing these pinyon pines to subsequent colonization by bark beetles and producing an asymmetric, indirect interaction between these 2 dendrophages. We compared morphological and physiological characteristics, as well as colonization success of *I. hoppingi*, of trees that were (target) or were not (nontarget) attacked by porcupines. We predicted that if a facultative association occurred among these taxa, we would observe greater colonization of pine engraver beetles on those trees that had been previously damaged by porcupines. We also predicted that we would discern differences in morphology and physiology of target and nontarget trees attributed to taxon-specific host selection.

2. Study area and methods

2.1 Study area

Research was conducted on the 2577-ha Kickapoo Caverns State Park (KCSP**;** Fig.1**)** located about 35 km north of Brackettville, Texas. The site (formerly recognized as Kickapoo Caverns State Natural Area) straddles Kinney and Edwards counties in the southwestern region of the Edwards Plateau. Topography was 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 were present on the site.

Shallow clay soils of east- and north-facing slopes supported pinyon-juniper-oak plant communities. In addition to papershell pinyon pine, dominant tree species included Ashe juniper (*Juniperus ashei*), plateau live oak (*Quercus fusiformis*), Texas persimmon (*Diospyros texana*), and vasey oak (*Q. 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 curtipenula*) and hairy tridens (*Erioneuron pilosum*) in more open areas. Shallow soils of the south- and west-facing slopes were dominated by guajillo plant communities, with pinyon pines restricted to lower slopes. 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 include threeawn and annual dropseed (*Sporobolus* spp.).

2.2 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) or by immobilizing animals in trees or dens by use of an adjustable pole-mounted syringe. We immobilized porcupines with a mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, A.H. Robbins, Richmond, VA) at a rate of 7 mg/kg body weight (Hale et al., 1994). 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, Manomet, Illinois) secured by nylon mesh collars.

2.3 Selection of trees by porcupines

We used radiotelemetry to locate and obtain visual observations on all animals at least twice weekly during 1997–1999. Triangulation was used only when an animal left the study site and lack of appropriate authorization or hunting seasons precluded our safe and/or lawful access. We 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. We tallied all trees $\geq$ 1.5 m in height because porcupines were rarely observed using trees shorter than this threshold.

2.4 Morphology of target vs. nontarget trees

We randomly established 20, 500–m transects (Fig.1) 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, we tagged the nearest porcupine-damaged (target) tree and a neighboring undamaged (nontarget) tree for a maximum of 20 pairs of trees per transect. Most transects had fewer than 20 pairs of trees due to low availability of nontarget trees. Diameter at root collar (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.

Limb structure of each tree was characterized as vertical if lateral limbs generally extended upward and horizontal if lateral limbs extended outward. Total number of porcupine feeding scars was recorded and area of bark removed (cm^2) was estimated for each target tree. Activity of bark beetles at each tree was characterized as: no beetle activity (N); attack only (A), evident by the presence of resin tubules but no successful colonization; or colonization (C), evident by the presence of $\geq$ 1 dead stems or branches resulting from beetle engravings. Morphological and beetle activity data on all transects were collected during June-August in 1997 and 1998.

2.5 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 in August-September 1998. 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 (μmol/mL; 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 holes to alleviate evaporative loss of hydrocarbons. Vials were removed after 24 h and the resin they contained was processed for subsequent gas chromatograph analysis of 7 monoterpenes (α-pinene, camphene, sabinene, β-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).

2.6 Statistical analyses

Selection of tree species by porcupines was determined by comparing use with availability using compositional analysis (Aebischer et al. 1993) and individual porcupines as the experimental unit. Analyses were restricted to porcupines with >20 locations in trees (n = 19) and to 4 groups of tree species: oaks, junipers, pinyon pines, and other. Tree availability was based on plot sampling.

Morphological and physiological data for all trees were averaged across each transect (n = 20); hence, transects were the experimental units. To explore porcupine selection, average values for target and nontarget trees on each transect were compared using paired t-tests and significance was set at $P < 0.05$. The relationship between porcupine damage (target, nontarget) and beetle activity (none, attacked, colonized) on individual trees was examined with a χ^2 test of independence. In addition, morphological and physiological 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 and the activity-classification interaction. Resin chemistry data were entered as percent composition of 8 dominant monoterpenes and subjected to angular transformation before analysis. Correlation analyses were performed to determine if percent composition of individual monoterpenes was associated with area of exposed xylem resulting from porcupine herbivory. Alpha levels were Bonferroni-adjusted for correlation analyses of monoterpene concentrations to P = 0.0024.

3. Results

3.1 Selection of trees by porcupines

Thirty-seven porcupines (24F;13M) were equipped with radio collars and were tracked > 1 month during the 3-year study period, yielding 1,496 total locations. Visual observations comprised 1,401 of the locations. Eighty percent of those locations (n =

1,118) were in trees, 14% (n = 197) were on the ground, and only 6% (n = 86) were located in dens.

We 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. Trees were used nonrandomly ($\chi^2_3 = 35.6$, $P < 0.001$) by the 19 porcupines included in the analysis. Pinyon pines ranked highest in selection, and were preferred ($P < 0.05$) in all pairwise comparisons with other tree groups. Oaks ranked second, and were preferred ($P < 0.05$) relative to junipers and other trees.

3.2 Morphology of transect trees

Data were collected on 366 trees (183 pairs). Four morphological characteristics differed between target and nontarget trees (Table 2). Porcupines used trees that were greater in girth, taller, greater in crown diameter, and thicker-barked. *Post hoc* analyses of those 5 characteristics revealed that diameter at root collar was significantly correlated 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 (χ^2 = 35.2, df = 1, P < 0.0001). Similarly, beetle colonization was associated with horizontal limb structure (χ^2 = 13.6, df = 2, $P < 0.001$). Of beetle-colonized trees, 83% (83 of 100) had horizontal limb structure vs. 62.5% (15 of 24) attacked trees and 56.9% (33 of 58) of trees with no beetle activity.

Trees damaged by porcupines were more likely to be colonized by bark beetles, and undamaged trees were more likely to free from beetle attack (χ^2 = 75.3, df = 3, $P <$ 0.01, Fig. 2). However, tree characteristics varying by level of beetle activity were not entirely consistent with those associated with porcupine use of trees (Table 2). Larger trees were more likely to be fed upon by porcupines and colonized by beetles; however, resin flow did not vary across levels of beetle activity. 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 (Table 2) was greater ($P < 0.055$) on colonized, nontarget trees ($\bar{x} \pm$ SE = 3.1 ± 0.8 m^2/ha) than any other combination of beetle activity and tree class (pooled $\bar{x} \pm$ SE = 1.4 ± 0.3 m^2/ha, all cell $\bar{x}$ between 1.1 and 1.8 m^2/ha).

Number of porcupine scars was correlated positively with area of bark that had been removed ($r = 0.90$, $P < 0.0001$). Area of bark removed was less ($P < 0.001$) on trees that exhibited no beetle activity or attack only (pooled $\bar{x} \pm$ SE = 303 cm^2 ± 75) than on trees that had been colonized ($\bar{x}$ ± SE = 989 cm^2 ± 152).

3.3 Physiology of transect trees

Target trees had greater resin flow than nontarget trees (Table 2). Plant moisture stress did not differ between target and non-target trees (P > 0.05) and 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 µmol/mL ± 0.020; fructose: 0.417 µmol/mL ± 0.023). Trees that were colonized by beetles had higher levels of both these sugars (glucose: 0.451 µmol/mL ± 0.021, $P < 0.01$; fructose: 0.455 µmol/mL ± 0.022, $P < 0.03$) than trees that had no beetle activity or had been attacked only (glucose: 0.389 µmol/mL ± 0.019; fructose: 0.395 µmol/mL ± 0.022). An interaction in fructose concentration across levels of beetle activity and by tree classification approached significance ($P < 0.08$). Undamaged trees that were colonized by beetles tended to have higher levels of fructose (0.544 µmol/mL ± 0.04) than target trees (0.422 µmol/mL ± 0.03) and undamaged trees with no beetle activity or attack only (0.386 µmol/mL ± 0.02). Fructose concentrations also were higher in undamaged colonized trees than all target trees (0.422 µmol/mL ± 0.03).

The most abundant monoterpenes in target and nontarget trees (n = 120) were α-pinene, β-pinene, and limonene (Table 3). Alpha-pinene concentration was correlated negatively with sabinene ($r = -0.36$, $P < 0.0017$), β-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 ($r = 0.40$, $P < 0.0005$), β-pinene and myrcene ($r = 0.72$, $P < 0.0001$), β-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 ($r = 0.97$, $P < 0.0001$).

Of the terpenes we examined, only myrcene concentration differed between target and 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 porcupine damage 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% ± 1.9) than trees with other combinations of beetle activity and porcupine damage (pooled $\bar{x}$ = 0.4% ± 0.1).

4. Discussion

Our findings are compatible with our predictions that porcupine bark-feeding activity predisposes pinyon pines to subsequent bark beetle activity. Our results do not unequivocally define the mechanism that explains our observations. However, we propose and elaborate 2 non-exclusive and likely interacting mechanisms responsible for the facilitative association observed in our study. These mechanisms are, first, that porcupine damage is a stressor needed for successful colonization by bark beetles, and second, that porcupine damage causes release of volatile terpenes, which in turn cue pine engraver beetles to the status of potential colonization sites. In addition, we will reject alternative explanations regarding the direction of the indirect interaction.

The first mechanism, that porcupine damage represents an additional stressor requisite to infestation by these bark beetles, is supported by our result that trees damaged by porcupines were more likely to be colonized by bark beetles than undamaged trees. In addition, trees colonized by bark beetles had, on average, 3 times as much bark removed by porcupines as non-colonized trees. Association of beetles with trees in areas of higher pinyon pine basal area in this study further 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 among within-plant processes (growth-differentiation hypothesis; Lorio, 1986). Consistent with our results, Lombardero et al. (2000) found that resin flow induced by wounding in *Pinus taeda* was lowest in trees with smaller crowns and in areas of high basal density. Successful colonization by beetles was likely facilitated because of the diminished resistance by the host tree. We 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). 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.

Porcupines may select pinyon pines over more abundant species to optimize nutrient acquisition and thermoregulation. Coniferous species provide thermal advantages over deciduous species (Clarke and Brander , 1973) and frequently constitute the preferred feeding and resting trees of porcupines (Dodge, 1967; Griesemer, 1995; Speer and Dilworth, 1978). We observed that feeding by porcupines on oaks was restricted to leaves and acorns in the canopy, 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, oak leaves and acorns are higher in protein than pine bark and cambium (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.

Paired sampling on transects allowed us to eliminate site favorability as a cause for tree selection by porcupines. Significant correlations of height, crown diameter, bark thickness, and resin flow with diameter at root collar indicate that size is the dominant factor in intraspecific selection of trees. Similar findings of size-related selectivity by porcupines have been reported (Krefting et al., 1962; Tenneson and Oring, 1985; Sullivan et al., 1986). Trees colonized by beetles also were larger than nontarget trees. 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 optimization (Roze, 1989).

We reject alternative explanations regarding the direction of the indirect interaction. First, it is unlikely that beetles are predisposing subsequent feeding by porcupines because beetles are facultative colonizers, usually requiring stressed hosts (but see Santoro et al., 2001), whereas porcupines are not limited by host health. Facilitation of beetle attack by porcupine feeding exemplifies an asymmetrical process. Porcupines, because of their size, sharp incisors, and large claws, select large, healthy trees from which they can easily remove bark. *Ips*, however, is a facultative parasite that generally attacks stressed or injured hosts (Raffa et al., 1993; but see Santoro et al., 2001). Unlike the porcupine, which is not dependent on a single 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. Furthermore, successful brood production by all scolytid beetles requires recently dead tissue (Raffa et al., 1993). Hence, the engraving pattern typical in the course of colonization by *Ips* beetles results in death of the colonized host limb/whole tree, rendering it unavailable for use by porcupines.

We also reject the alternative explanation that the relationship we observed was a result of similar tree preferences by the 2 dendrophages in our study system. This explanation was similarly discussed and ultimately rejected for a budworm *(Choristoneura pinus pinus)*–bark beetle (*Ips grandicollis*)–woodborer (*Monochamus carolinensis*) system (Wallin and Raffa, 2001). Porcupines and beetles exhibited several differences in tree selection, especially physiologically. Our data indicate that biochemical variability may influence porcupine diet selection, but minimally. We found no correlation between feeding activity of porcupines and levels of limonene, in contrast to Snyder and Linhart (1997). Target and nontarget trees of porcupines differed for only 1 physiological measure, myrcene concentration. On the other hand, as discussed below, the biochemical composition of trees colonized by beetles differed from uncolonized trees for several terpenes and carbohydrates. Association of increased beetle colonization on trees with higher levels of glucose and fructose was not surprising given nutritional requirements of the pine engraver (Haack and Slansky, 1987).

We propose that the second mechanism to explain the directional nature of the association between beetle colonization and porcupine feeding activity is that damage by porcupines causes release of volatile terpenes, thereby cueing pine engraver beetles to presence of toxic substances and availability of potential pheromone precursors. Such a mechanism parallels that observed for defoliator-conifer-bark beetle models of host-herbivore interactions (Wallin and Raffa, 1999; Erbilgin et al., 2003). In those systems, variation in monoterpene content and composition of the induced defenses of a host tree led to variation in the relative aggregation or inhibition of bark beetles (*Ips pini*; Erbilgin et al., 2003). Defoliation intensity, which is analogous to amount of bark removed in our study, directly altered monoterpene composition and was inversely related to monoterpene concentration over long time frames ($\geq$ 12 months; Wallin and Raffa, 1999, 2001).

Beetles, in contrast to the porcupine, appeared to select trees based on monoterpene characteristics of resin. High levels of limonene are toxic to many bark beetles (Harborne, 1993) and explain increased beetle activity on trees in our study area exhibiting low proportions of this monoterpene. Loreto et al. (2000) reported increased emissions of limonene and α-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. Similar responses to herbivore-induced volatile plant terpenes and other plant chemicals have been reported for parasitic wasps (Turlings et al., 1990) and anthocorid predators (Drukker et al., 2000).

Chemical reactions between host monoterpenes and pheromone production are complex and have not been identified completely for *I. hoppingi*. However, myrcene and α-pinene serve as pheromone precursors in other species of pine engraver beetles (Hughes, 1974; Renwick et al., 1976; Hughes and Renwick, 1977; Byers et al., 1979). 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 attributed this lack of specificity to recent phylogenetic divergence of these beetles. Based on the close phylogenetic relationship among these species of *Ips*, we speculate that myrcene and α-pinene may be suitable pheromone precursors for *I. hoppingi*.

The overwhelming dominance of monoterpene composition by α-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). We postulate that *I. hoppingi* is either an α-pinene obligate species or harbors *Bacillus cereus* and is therefore able to biosynthesize this monoterpene, as in *Ips paraconfusus* (Brand et al. 1975). Beetles attacked or colonized trees with lower levels of sabinene and terpinolene, which were terpenes that were correlated negatively with concentrations of α-pinene.

We acknowledge that a stronger test of our hypothesis would have included experimental manipulation of trees or demonstrating the temporal sequence of dendrophagy. Alternatively, long-term temporal observation across a quantified range of bark removal by porcupines (*sensu* Wallin and Raffa, 2001) also would also strengthen our inference. However, we were constrained by the limited number of pinyon pines of comparable size and possessing physiological characteristics preferred by porcupines that were also free of porcupine and/or beetle damage (Ilse, 2001). Conservation concerns on the study area also precluded the ability to artificially inflict damage requisite to experimental manipulation. Therefore, we were unable to adequately test our hypothesis with an experimental manipulation at our study site. However, our detailed observational data supports the hypothesis and rejects alternative explanations.

The novel aspect of our work is the focus on the indirect effects of a vertebrate dendrophage on a insect dendrophage with the same host plant, as opposed to the large body of work exploring effects of insect defoliators on host plant suitability to other insect herbivores. However, the proposed mechanisms for the association between porcupines and bark beetles fit within the framework of integrated theories explaining host plant-herbivore interactions. First, the porcupine feeding process can be generalized to a mechanical stress to the host tree, rendering it susceptible to invertebrate infestation. The outcome of the invertebrate attack likely depends on the interaction among seasonal timing of initial damage by porcupines, attack magnitude by beetles, and the induced-defense response of the stressed host (Raffa and Berryman, 1983), which is a trade-off best explained by the growth-differentiation model of plant resistance (Lorio, 1986; Herms and Mattson, 1992). Second, the putative mechanism linking the 2 dendrophages involves release of chemical cues (e.g., monoterpenes) from the host tree that are triggered by the mechanical damage. The specific composition and concentration of these cues can either trigger beetle aggregation or inhibit beetle attraction (Erbilgin et al., 2003). We suggest that the differential nature of the induced response by host plants to varying types of wounding (e.g., defoliation, root pathogenic infection, bark removal) be examined.

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Table 1. Availability and use of dominant tree species by porcupines on Kickapoo Caverns State Park, southwestern Texas, USA, 1996-1999.

	Availability[a] (*n* =965)		Use (*n* = 1092)	
Tree species	*n*	%	*n*	%
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

[a] Based on 300, 0.04 ha fixed-radius plots.

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

	Porcupines					Beetles[a]						
	Target		Nontarget			None		Attacked		Colonized		
Characteristic	$\bar{x}$	SE	$\bar{x}$	SE	P [b]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	P [c]
DRC (cm)[d]	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^2/ha)[e]	3.1	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

[a] Means for each characteristic with the same letter are not different at $\alpha = 0.05$ level of significance.

[b] Main effect of porcupine damage (present or absent).

[c] Main effect of level of beetle activity.

[d] Diameter at root collar.

[e] See text for discussion of interactive effects.

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

	Porcupines			Beetles [a]			
Monoterpene %	Target	Nontarget	P [b]	None	Attacked	Colonized	P [c]
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 [d]	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

[a] Means for each monoterpene with the same letter are not different at $\alpha = 0.05$ level of significance.

[b] Main effect of porcupine damage (present or absent).

[c] Main effect of level of beetle activity.

[d] See text for discussion of interactive effects.

Figure Captions

Fig. 1. Location of study site, Kickapoo Caverns State Park, in southwestern Texas, USA with solid bars delineating vegetation transects.

Fig. 2. Association of bark beetle activity on target (porcupine-damaged) and nontarget (non-damaged) pinyon pines on Kickapoo Caverns State , in southwestern Texas, USA. N = no beetle activity; A = beetle attack only, C = beetle colonization.

Figure 1

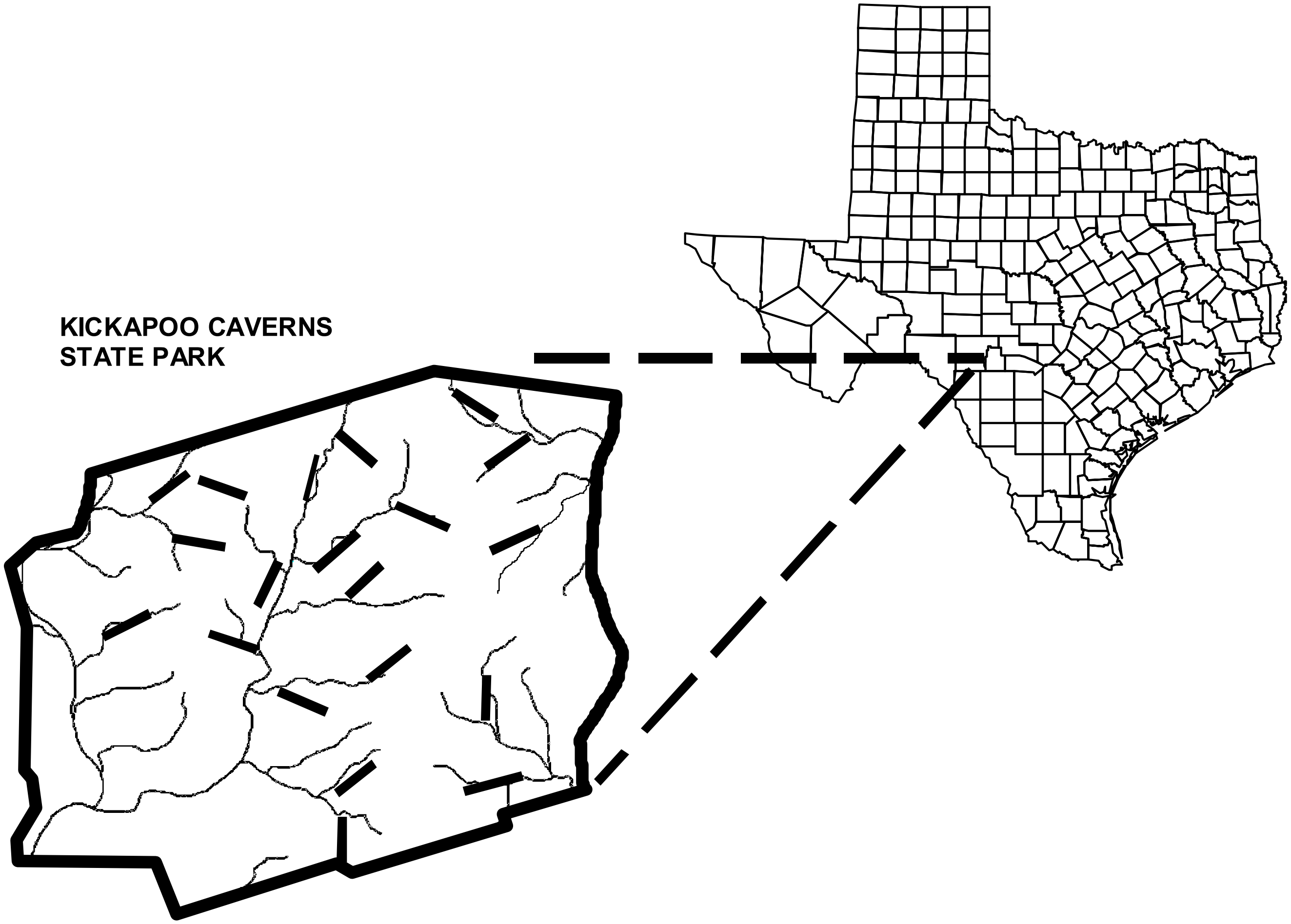
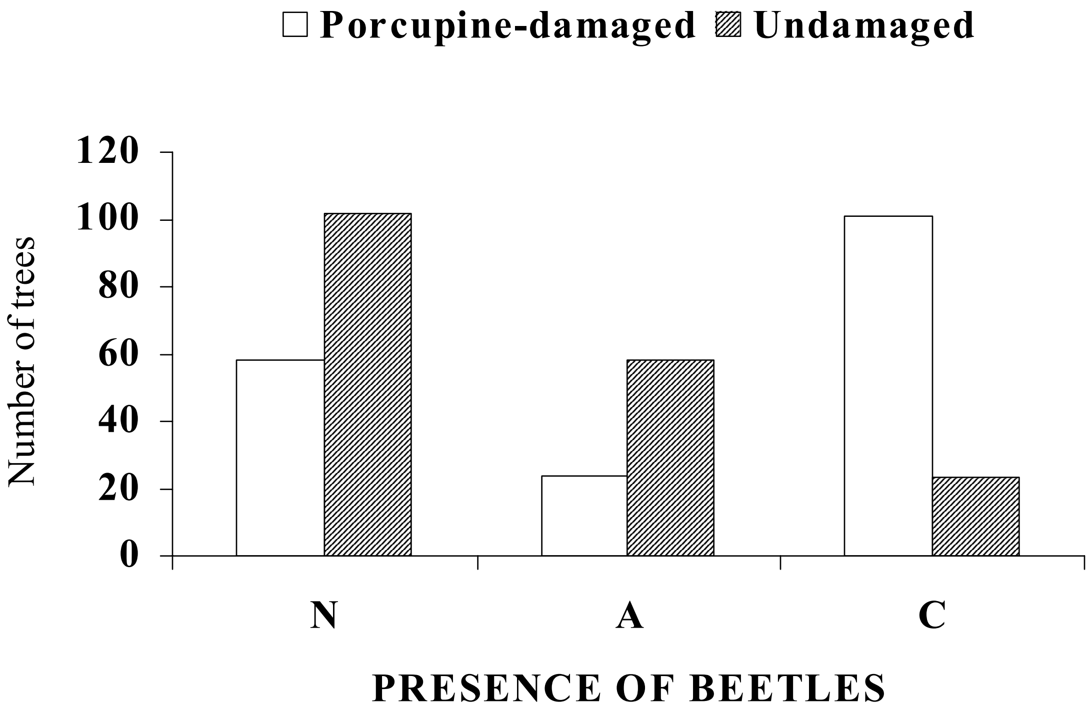


Figure 2


☐ Porcupine-damaged ▨ Undamaged
Number of trees
120
100
80
60
40
20
0
N
A
C
PRESENCE OF BEETLES