ORIGINAL ARTICLE

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Relationships among Key deer, insect herbivores, and plant quality

Abstract Deer can have severe effects on plant communities, which in turn can affect insect communities. We studied the effects of Key deer herbivory on the incidence of insect herbivores that occur within deer habitats in the lower Florida Keys, within the National Key Deer Refuge (NKDR). We analyzed plant chemistry (tannins, nitrogen) and surveyed for the occurrence of insects (above the browse tier) among plant species that were either deer-preferred or less-preferred. Results indicated higher levels of foliar tannins on islands with fewer Key deer and larger amounts of foliar nitrogen on islands with a high density of Key deer. Consequently, leaf miners were significantly more abundant on islands with high deer density, irrespective of deer-preference of plant species. On islands with a high deer density, incidence of leaves damaged by chewing insects was lower on preferred plant species but greater on less-preferred species than on islands with fewer deer. No apparent patterns were evident in the distribution of leaf gallers among plant species or islands with different deer density. Our results imply that plant nutrition levels—either preexisting or indirectly affected by deer deposition—are more important than plant defenses in determining the distribution of insect herbivores in the NKDR. Although high densities of the endangered Key deer have negative effects on some plant species in the NKDR, it seems Key deer might have an indirect positive influence on insect incidence primarily above the browse tier. Further research is warranted to enable fuller understanding of the interactions between Key deer and the insect community.

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Introduction

Ungulates can have a wide variety of effects on natural areas and can affect individual organisms, populations, communities, and ecosystems (Jones et al. 1993; Hobbs 1996; Waller and Alverson 1997; Rooney 2001; Russell et al. 2001; Rooney and Waller 2003). Ungulate populations, especially white-tailed deer (*Odocoileus virginianus*), have dramatically increased in North America, because of changes in land use and management practices (Leopold et al. 1947; McShea et al. 1997; Cote et al. 2004). These high densities of deer can have serious consequences for local natural communities where browsing pressure is strong (Jones et al. 1993; Russell et al. 2001).

Herbivory by white-tailed deer usually affects plant populations, which in turn can indirectly affect other organisms within the community. For example, deer herbivory may change plant biomass, plant species composition, plant quality, microhabitat, and ultimately forest structure, which can affect the abundance and diversity of invertebrates associated with deer habitat (Stewart 2001). Depending on the nature of effect of ungulates, insect response can be positive, negative, or neutral (Strauss 1991; Roininen et al. 1997; Rambo and Faeth 1999; Feber et al. 2001; Stewart 2001; Herder et al. 2004). Herbivores can induce a response from host plants that may or may not defend the plant from subsequent herbivory (Karban and Myers 1989). For example, browsing of plants by deer might induce defenses, for example an increase in leaf toughness, that deters insect herbivores (Shimazaki and Miyashita 2002). Another possible interaction is prior insect herbivory reducing the likelihood of deer browsing on the shared host plant (Strauss 1991). Effects of mammals that induce defenses that change plant chemistry can

also positively affect insects that sequester the chemical for their own defenses (Martinsen et al. 1998).

In this study we examined the effects of the federally endangered Key deer (*Odocoileus virginianus clavium*), a diminutive subspecies of white-tailed deer, on insect distribution in the lower Florida Keys within the National Key Deer Refuge (NKDR). The population size of Key deer has increased substantially over the last 50 years (Lopez 2001), with 75% of the population residing on two islands in the NKDR and lower deer densities on the other islands (Lopez et al. 2004a). High densities of Key deer on these two islands caused heavy browsing pressures that affected plant species composition and forest regeneration (Barrett and Stiling 2006). This browsing on plant species could also cause phytochemical responses (e.g. induced defenses) and, in turn, affect the distribution of insect herbivores associated with deer habitat among the islands. Although deer are usually selective browsers, and associated insect communities can be less dense on deer-preferred species and more dense on avoided species, the constant regeneration of browsed plants can result in increased densities of insects on preferred plants (Stewart 2001). We therefore also examined plant species that were preferred and less-preferred by Key deer for insect occurrence. We analyzed plant chemistry and surveyed insects on these plant species in Key deer habitats to determine whether the incidence of insect herbivores is lower on islands with high deer density than on islands with a lower deer density, because of induced defense among plant species. Specifically, we expected plant species preferred by deer to have a greater foliar tannin content on islands with high densities of Key deer, and thus lower incidence of insect herbivores. Less-preferred plant species on islands with different deer densities should, conversely, have a similar tannin content and a similar incidence of insect herbivores.

Materials and methods

Study area

The study was conducted in the lower Florida Keys within the NKDR boundaries (24°36′N–81°18′W to 81°34′W). The climate is subtropical with evident wet (May–October) and dry (November–April) seasons. The mean annual temperature is ∼25.2°C and mean annual rainfall is ∼100 cm. Soils vary from blue-gray marl to black peaty muck and are underlain by oolitic limestone (exposed in many areas), which is continuous with Miami oolite of the Florida mainland (Dickson III 1955). Vegetation in the lower Keys is primarily of West Indian origin (Stern and Brizicky 1957).

The NKDR archipelago contains lowland, upland, saline, and freshwater environments. Two types of vegetative cover—hardwood hammock and mangrove wetlands—were used in this study with habitat descriptions based on Folk (1991). Hardwood hammock is a climax successional community formed by tropical hardwood plant species that occur in uplands. Common woody tree and shrub species include: Jamaica dogwood (*Piscidia piscipula*), gumbo-limbo (*Bursera simaruba*), pigeon plum (*Coccoloba diversifolia*), blackbead (*Pithecellobium keyense*), willow bustic (*Bumelia salicifolia*), white stopper (*Eugenia axillaris*), Spanish stopper (*Eugenia foetida*), and maiden bush (*Savia bahamensis*). Extended periods of saltwater inundation and poor nutrient exchange in mangrove wetlands produces mostly stunted woody plant species including: black mangrove (*Avicennia germinans*), red mangrove (*Rhizophora mangle*), white mangrove (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*).

Experimental design

Key deer use both hammock and mangrove habitats to different extents (Lopez 2001; Lopez et al. 2004b) and can have sever effects on some plant species within each habitat (Barrett and Stiling 2006). These two deer habitats are present in the NKDR on islands with a natural gradient of Key deer density from high (> 17 deer km^{-2}) to medium (3–10 deer km^{-2}) and low (< 1 deer km^{-2}) (Lopez 2001; Lopez et al. 2004a). Whole islands or large subdivided islands were used as independent samples, with four sites for insect surveys per deer-density category: *high* deer density—Big Pine (North, Central, South) and No Name; *intermediate* deer density—Big Torch (North, South), Middle Torch, and Little Torch; and *low* deer density—Ramrod, Summerland, Cudjoe, and Sugarloaf. Sites for insect surveys were separated by $> 1,500$ m among and within islands.

Five plant species were sampled from each island: *R. mangle* and *A. germinans* in mangrove wetlands and *Pithecellobium keyense*, *Coccoloba diversifolia*, and *E. foetida* in hardwood hammocks. Both *R. mangle* and *Pithecellobium keyense* are regarded as deer-preferred plant species whereas *Coccoloba diversifolia*, *A. germinans*, and *E. foetida* are less-preferred species (Klimstra and Dooley 1990; Barrett and Stiling 2006). For each of these plant species the density (within species) of individuals > 1.2 m tall was similar among the islands, although the relative density of less-preferred plant species was 20% higher on islands with high Key deer density than on islands with fewer deer (Barrett and Stiling 2006). Densities of preferred plant species within the browse tier (< 1.2 m tall) were, moreover, significantly lower on islands with many deer than on islands with fewer deer (Barrett and Stiling 2006). Resource availability for insect herbivores was, therefore, not uniformly distributed among islands over the Key deer density gradient.

Insect surveys

Insect surveys were conducted seven times from January to December in 2003. For each plant species, five indi-

vidual plants were selected haphazardly during each survey period. On the five plants per species, insects were surveyed haphazardly on 200 leaves (or leaflets) per individual plant. The surveyed plants selected were taller than the browse tier (> 1.2 m tall) yet still had foliage present within the browse tier (< 1.2 m tall); thus direct effects of deer herbivory were avoided by surveying plant foliage above the browse tier, although Key deer browsing could potentially persist on foliage within the browse tier and indirectly affect plant chemistry. Insects were categorized by feeding guild: leaf miners, leaf chewers, and leaf gallers. Leaf miner abundance was quantified by counting the number of mines (i.e. individual trails) per leaf. For leaf chewers, a leaf was either recorded as damaged (i.e. notches, holes) or undamaged. Key deer usually eat whole leaves (leaving the petiole intact), so insect damage was easily distinguished from deer damage. Galls were categorized as < 5 or > 5 per leaf. For all deer-density treatments, however, a ratio of nearly 3:1 for abundance of the two categories of gall was observed for all plant species except for *Pithecellobium keyense*, for which the ratio was almost 1:1. Because of lack of variation among the islands, categories of gall abundance were therefore pooled for analysis. Means from insect surveys were for 7,000 leaves per plant species on each island (summarized over seven surveys in 2003 from the five individual plants per species on each island).

Foliar chemical analysis

For chemical analyses of plant foliage, five to ten leaves per plant species (from five individuals per site) were collected from each study island in 2003. Leaves were collected twice in the dry season (January and March) and twice in the wet season (June and August). Leaves were oven-dried at 50°C for approximately 48 h. The dried leaves were then milled to a fine powder. Foliar tannin content was analyzed using a tannic acid standard following the procedure of Hagerman (1987); foliar tannin content was therefore expressed as mL mg^{-1} tannic acid equivalent (TAE). Leaves were also analyzed for amount of nitrogen by using a CE Instruments NC2100 CN Analyzer (CE Elantech, Lakewood, NJ, USA). Tannin and nitrogen data were each summarized for each plant species per study island.

Data analysis

Differences between numbers of miners, chewers, and galls among islands were each analyzed with split-plot ANOVA with deer density (low, medium, high) and plant species as fixed factors and island (random factor) nested within deer density. Because deer browsing differentially affects plant species, plant species were analyzed in separate groups as either preferred or less-preferred. Insect data from less-preferred plant species

were either square root or log-transformed before analysis to improve the normality or homogeneity of variance.

Different amounts of foliar nitrogen and tannins for plant species (dichotomized by deer-preference) among islands were each tested with split-plot ANOVA with deer density and plant species as factors and island nested within deer density. Nitrogen and tannin data were square root-transformed before analysis to meet parametric assumptions. All statistical analyses were tested for significance at the $P = 0.05$ level.

Results

For foliar TAE of preferred species, there was a significant effect of deer density ($F_{2,9} = 5.43$, $P = 0.028$), and plant species ($F_{1,9} = 18.24$, $P < 0.001$), but not their interaction ($F_{2,9} = 0.30$, $P = 0.746$). Similarly, for less-preferred plant species, foliar TAE varied significantly among deer density ($F_{2,9} = 5.26$, $P = 0.031$) and plant species ($F_{2,18} = 72.41$, $P < 0.001$), but not their interaction ($F_{2,18} = 0.85$, $P = 0.510$). Islands with low deer density had the highest TAE concentrations, irrespective of deer–plant preference (Fig. 1). For preferred plant species, foliar nitrogen did not vary with deer density ($F_{2,9} = 1.52$, $P = 0.270$), but varied among plant species ($F_{1,9} = 100.1$, $P < 0.001$), although their interaction was not significant ($F_{2,9} = 0.09$, $P = 0.915$).
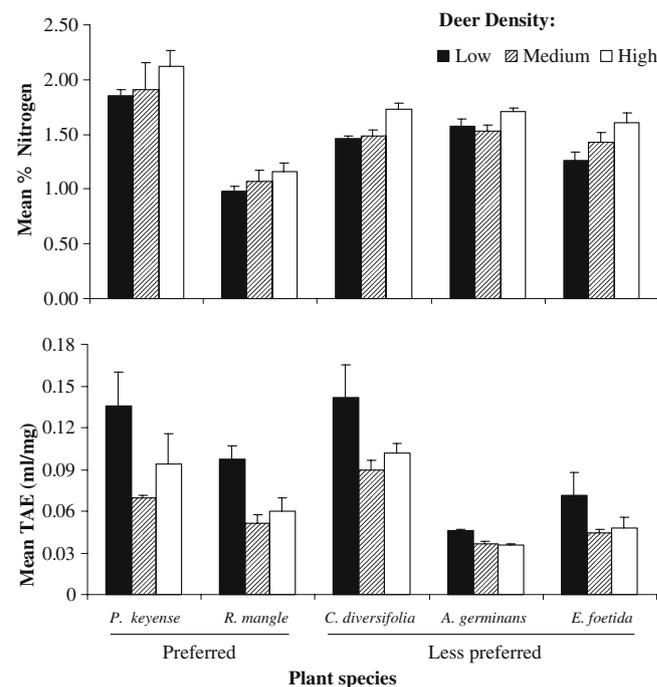
Fig. 1 Mean (+SE) foliar nitrogen (%) and tannic acid equivalent (*TAE*) (mL mg^{-1}) of plant species from islands with low, medium, and high deer density. *Pithecellobium keyense* and *R. mangle* are deer-preferred plant species. The other species are less-preferred

Foliar nitrogen of less-preferred species varied significantly among deer density ($F_{2,9}=15.18$, $P=0.001$), and among plant species ($F_{2,18}=6.70$, $P=0.007$), but their interaction was not significant ($F_{4,18}=1.04$, $P=0.415$). For all plant species, a pattern of higher foliar nitrogen was evident on islands with high deer density (Fig. 1).

Because *R. mangle* lacked leaf miners, only *Pithecellobium keyense* was analyzed as a deer-preferred plant species using one-way ANOVA. There was a marginal difference ($F_{2,9}=3.57$, $P=0.072$) in miner abundance for *Pithecellobium keyense* among deer treatments—it was slightly higher for islands with high deer density. For less-preferred species, effect of deer-density ($F_{2,9}=7.83$, $P=0.011$) and effect of plant species ($F_{2,18}=88.48$, $P<0.001$) were significant, although the interaction was not ($F_{4,18}=2.22$, $P<0.107$). Islands with high deer density had the highest leaf miner abundance for all plant species (Fig. 2).

For leaf chewer damage on preferred plant species there was a marginally significant effect of deer density ($F_{2,9}=4.05$, $P=0.056$) and a significant plant species effect ($F_{1,9}=12.84$, $P=0.006$), although the interaction was not significant ($F_{2,9}=0.13$, $P=0.880$). Leaf chewer damage was higher for both preferred species on islands with low deer density. For less-preferred species there was a significant effect of deer density ($F_{2,9}=5.58$, $P=0.026$) and plant species ($F_{2,18}=8.32$, $P=0.003$), but not a significant interaction ($F_{4,18}=0.48$, $P=0.747$). Leaf chewer damage was greater on islands with high deer density for all less-preferred species (Fig. 2). For all plant species, damage per leaf from chewers was usually $<50\%$.

Because *R. mangle* lacked leaf galls, only *Pithecellobium keyense* was analyzed as a deer-preferred plant species using one-way ANOVA, and no effect of deer density on leaf gall occurrence was evident ($F_{2,9}=0.14$, $P=0.870$). For less-preferred plant species there was no evident deer-density effect ($F_{2,9}=2.15$, $P=0.173$), but the species effect was significant ($F_{2,18}=22.72$, $P<0.001$), as was the interaction ($F_{4,18}=4.20$, $P=0.014$). Overall, no clear pattern was evident for incidence of leaf gallers among deer-density treatments or plant species (Fig. 2).

Discussion

We found little evidence of induced defense affecting patterns of insect distribution among plant species in the NKDR. Overall, on islands with high density of deer, plant tannins were lower whereas nitrogen and insect incidence were higher than on islands with fewer deer. Plant chemistry had no observable effect on leaf galler abundance in this study, possibly because leaf gallers may not be greatly affected by plant chemistry or nutrition (Hartley and Lawton 1992). Our study nevertheless indicates that higher levels of nutrients (e.g. nitrogen) increase insect occurrence in both mangrove (especially on *A. germinans*) and hammock habitats on islands with many deer.

Because deer browsing may not always affect subsequent herbivory by insects (Strauss 1991), perhaps the most parsimonious explanation of our results is bottom-up effects of plant nutrition on herbivore abundance for both Key deer and insects. Mammalian and insect herbivores have been shown to respond positively to bottom-up factors that cause an increase in their abundance and/or occurrence in nutrient-enriched areas (Mattson 1980; Hunter and Price 1992; Ball et al. 2000). Because herbivore fitness usually depends on nitrogen concentration in plants (Polis and Strong 1996), preexisting relatively high nutrient levels on Big Pine and No Name keys may be affecting both Key deer and insect herbivore populations independently. It seems, moreover, that plant chemistry (tannin levels) might limit Key deer distribution among islands, because deer numbers were lower on islands with high foliar tannin content.

Circumstantial evidence suggests, however, that Key deer distribution and population levels could be determined by other factors. For example, Key deer are
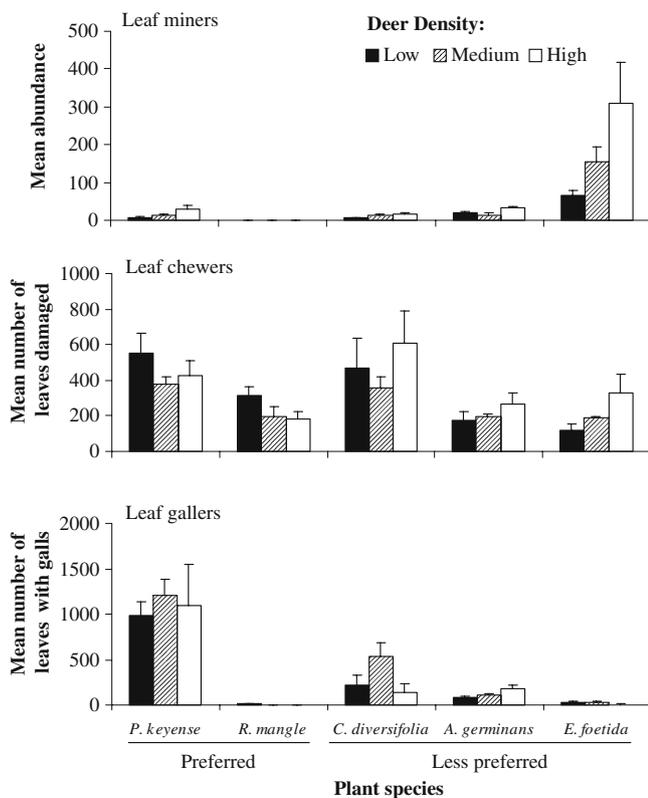
Fig. 2 Mean ($+$SE) abundance of leaf miners, number of chewed leaves, and number of leaves with galls, per plant species, on islands with low, medium, and high deer density. Means are for 7,000 leaves per plant species (summarized from randomly sampling 200 leaves on five individuals per plant species each month on each island over 7 months in 2003). *Pithecellobium keyense* and *R. mangle* are deer-preferred plant species. The other species are less-preferred

mainly found on Big Pine and No Name keys because these two islands:

1 contain one-third of the upland area in the NKDR, which deer utilize heavily for bedding, fawning, and forage (Silvy 1975; Lopez et al. 2004b);
2 contain substantial pineland communities that historically have been actively managed, e.g. prescribed fire (Dickson III 1955; Folk 1991), and are thus heavily utilized by Key deer because of a high diversity of forage species, for example shrubs and herbaceous cover (Folk 1991; Carlson et al. 1993; Barrett 2004);
3 have year-round freshwater sources (unlike other keys in the NKDR), a primary factor of Key deer distribution among islands (Folk 1991; US Fish and Wildlife Service 1999);
4 contain regions of anthropogenic influence (handouts of food and water) that result in larger group sizes and local site fidelity of Key deer (Lopez et al. 2004b; Peterson et al. 2005).

Key deer eat a wide range of plant species to meet dietary requirements (Klimstra and Dooley 1990), and Big Pine, being the largest island with the most plant community types and highest plant diversity in the NKDR (Dickson III 1955; Folk 1991; Barrett and Stiling 2006), provides diverse forage and habitats to meet deer needs. Key deer regularly consume *R. mangle*, a principal food plant (Klimstra and Dooley 1990; Barrett and Stiling 2006), yet it has low nitrogen content compared with other plant species (Fig. 1); accordingly, nitrogen may not be an exclusive factor affecting Key deer population dynamics; it has, for example, been suggested that phosphorus limitation affects Key deer reproduction (Folk and Klimstra 1991). Finally, we speculate that tannins do not affect deer feeding behavior or distribution because during feeding trials Key deer did not discriminate when consuming the same plant species collected from different islands (e.g. Big Pine, Middle Torch, Sugarloaf, etc.) (Barrett and Stiling 2006) even though foliar tannin content varies among the islands (Fig. 1). Also, neither tannins nor nitrogen notably affect Key deer choice among plant species (M.A. Barrett, unpublished data).

Consequently, an alternative explanation to bottom-up effects affecting both Key deer and insects is that high deposition rates from Key deer results in increased nitrogen levels in plants and this subsequently affects insect populations on islands with many deer. Ungulates can alter nutrient cycles and increase soil nitrogen by deposition of feces and urine (Hobbs 1996; McNaughton et al. 1997; Knapp et al. 1999); this, in turn, can affect nutrient enrichment of plant species. This indirect consequence of nutrient deposition by ungulates could positively affect insect herbivore populations by increasing plant quality (e.g. Olofsson and Strengbom 2000). Although tidal flushing could affect nutrient exchange in mangrove wetlands, animal deposition can still affect plant quality. For example, Onuff et al. (1977) found higher insect numbers and insect damage to mangrove species on islands in Florida where bird rookeries were present, because of increased nutrient deposition from guano. Because nitrogen concentrations were higher for all surveyed plant species in hammock and mangrove communities on islands with a high density of Key deer, we infer that nutrient enrichment from Key deer deposition (though not directly tested) affected insect distribution more than plant defense.

Plant quality aside, less leaf chewer damage on deer-preferred species on islands with high deer density could be because of reduced patch size (resource availability), because these plant species were less abundant because of heavy browsing. Reduced availability of resources because of browsing pressure can concomitantly cause lower invertebrate abundance (Rambo and Faeth 1999). Different responses of miner and chewer populations on deer-preferred species among islands with few and many deer could also be explained by different responses of specialist (e.g. miners) and generalist (e.g. chewers) herbivores to patch size dynamics (Bach 1988). With regard to plant quality, increased plant damage by chewers on islands with low deer density could be a result of herbivores feeding more, not less, on plants low in nitrogen to meet nutritional requirements (Slansky Jr and Feeny 1977). Although the reason for the lower tannin content of plants on high deer-density islands is unclear, it is probably a consequence of carbon/nutrient balance (Bryant et al. 1983) and a plant strategy for escaping herbivory by establishing a cost–benefit trade-off of plant defense (tannins) for rapid regrowth (nitrogen) (van der Meijden et al. 1988).

It seems that plant quality potentially affected by Key deer deposition on islands with high deer density positively affects the incidence of phytophagous insects above the browse tier. Deer can nonetheless have severe negative effects on invertebrates within the browse tier (Allombert et al. 2005). Although insects were not surveyed within the browse tier in this study, the absence or very low densities of preferred plant species <1.2 m tall caused by heavy Key deer browsing probably has severe detrimental consequences for the associated insect community. The net effect of Key deer on insect herbivores, therefore, could be negative on islands with many deer.

Although effects of the endangered Key deer on plant communities are evident, further research is warranted to enable understanding of the complex interactions of herbivore populations in the NKDR. Specifically, future work should consider effects of deer deposition on plant quality, browsing effects on insects within the browse tier, and deer effects on insect diversity and other trophic levels (e.g. insect predators/parasitoids).

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