An Analysis of Key Deer Herbivory on Forest Communities

in the Lower Florida Keys

by

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ABSTRACT

The Key deer (*Odocoileus virginianus clavium*) population has increased from less than 80 individuals in the 1950s to approximately 700 by 2000. Over two-thirds of the Key deer population resides on two islands out of a potential 26 islands within their range. The skewed distribution resulted in high deer densities on Big Pine, No Name, and Big Munson keys. The objective of the study was to evaluate the effects of Key deer herbivory in mangrove, buttonwood, hammock and pineland habitats between islands with low, medium, and high densities of deer. Host-plant choice trials were conducted to determine Key deer selection among plant species. Subsequent analyses on vegetation were then compared by deer preference categories: preferred and nonpreferred plant species. Vegetation quadrats, deer exclosures, nursery plant species, and baseline vegetation data were used to examine the effects of Key deer browsing on plant communities. For most analyses, browsing impacts were not evident for the entire plant assemblage (e.g. all plant species combined, diversity, species richness etc.), but were noticeable when plant species were dichotomized by deer preference. The strongest negative impacts of browsing were seen for highly preferred woody plant species, such as *Bursera simaruba, Erithalis fruticosa, Bumelia celastrina, Rhizophora mangle, Jacquinia keyensis,* and *Guapira discolor,* which all had very low densities on high deer density islands. Some nonpreferred species exhibited a positive relationship with high deer densities, such as *Eugenia spp., Piscidia piscipula,* and *Coccoloba diversifolia* among others. Urbanization also influenced Key deer herbivory in that Key deer tend to aggregate in urban environments, which increased browsing pressure in adjacent hammock habitats. Fire played an important role by increasing the percent cover of preferred herbaceous species in pinelands especially in deer exclosure plots. Fire and Key deer browsing also interacted by decreasing hardwood species invasion into pineland habitat. Key deer

have a strong influence on plant community structure on islands with large deer herds. Management efforts, such as contraception, public education on the ramifications of feeding wildlife, and sustainable/suspended development of lands in the National Key Deer Refuge is warranted to benefit Key deer and to deter increased browsing pressure.

CHAPTER 1

INTRODUCTION

Background

White-tailed deer (*Odocoileus virginanus*) have been studied extensively in North America, mainly for game species management. Current management practices, including predator control and habitat protection have increased deer populations above historical levels. White-tailed deer at such high levels [or deer irruptions (Leopold 1947)] can have major impacts on plant communities in the areas they inhabit (Hough 1965; Anderson and Loucks 1979; Alverson et al. 1988; Anderson 1994; Johnson et al. 1994; McClaren 1996; Ward et al. 2000; Cornett et al. 2000; Castleberry et al. 2000; Wright et al. 2000). Therefore, there is much impetus to maintain deer populations at non-destructive densities.

Ungulates can produce both direct and indirect effects on forest composition and structure (Rooney and Waller 2003) and have various consequences at different spatial scales (McLaren 1996). For example, herbivore effects can be seen at the plant level through direct mortality or overcompensation (Paige 1992; Seagle 2003; but see Belsky 1986), at the community level by changing species composition or by accelerating or retarding succession (Connel and Slayter 1977; Ball et al. 2000; Coomes et al. 2003), and at the ecosystem level by altering nutrient cycles (McNaughton 1976; Seagle et al. 1992; Hobbs 1996; Frank and Groffman 1998). Herbivore density can determine the magnitude of these effects on local vegetation, especially direct plant damage. Heavy levels of deer herbivory on young browse-sensitive woody plant species can cause regeneration failure and eventually lead to their local extinction (Alverson et al. 1988). This, in turn, may allow less palatable or less frequently browsed plant species to become dominant (Dyksterhuis 1949; Mcshea et al. 1997). Furthermore, this change in forest community structure could lead to loss or change in composition of other native biota, including insects (in Miller et al. 1992; Rambo and Faeth 1999), small mammals (Ostfeld et al. 1996; Flowerdew and Ellwood 2001) and birds

(Casey and Hein 1983; DeCalesta 1994; Mcshea and Rappole 2000). Due to the various consequences (and magnitudes thereof) of deer browsing mentioned above, some might consider deer to be keystone species (Waller and Alverson 1997). Although browsing effects have been studied in white-tailed deer populations (Russell et al. 2001), few quantitative studies exist for Florida Key deer (*Odocoileus virginianus clavium*) herbivory and subsequent effects on forest regeneration.

Key Deer

The diminutive Key deer, a subspecies of the white-tailed deer, is a member of the Cervidae family, in the order Artiodactyla, and class Mammalia. Key deer were first recognized as a subspecies when described by Barbour and Allen (1922). Its body is stockier, legs shorter, and skull shorter and relatively wider than other deer (USFWS 1999). Adults measure around 63 to 76 cm at the shoulder and have an average weight of 25 to 35 kg for males and 20 to 30 kg for females (USFWS 1999).

Key deer were probably isolated from the mainland population around 4000-6000 years ago due to rising sea levels during the melting of the Wisconsin Glacier (Hoffmeister 1974). In the late 16th century, Key deer were noted by early explorers and reported to range from Key Vaca to Key West (De Pourtales 1877; Dickson 1955). As human encroachment increased, the Key deer range declined to an area between West Summerland Key and Sugarloaf Key (Klimstra et al. 1974; Lopez 2001), a substantial decrease in range (approximately 60 km). Key deer population estimates were not officially documented earlier than the 1950s (Dickson 1955); but since then, land managers and researchers have increased efforts to estimate Key deer population size and resources (e.g. habitat evaluation).

The current population of Key deer is estimated to be 579-678 individuals (Lopez 2001) and has a potential distribution on approximately 26 islands (Folk 1992). Key deer movement between islands is not inconsequential; their movement is especially influenced by the availability of drinking water (USFWS 1999). Key deer consistently use islands with permanent freshwater sources, such as Big Pine and No Name keys. Although other islands have freshwater lenses, freshwater is neither abundant nor available year round (Dickson 1955; Hanson 1980; Klimstra 1990; Folk 1992; Ross et al 1992; Ross and O'Brien 1994).

Big Pine Key and No Name Key support more than two-thirds of the population of Key deer because they have permanent drinking holes and substantial pineland habitat (Folk 1992). Habitat selection by Key deer varies with season, time of day, and the sex and the age of the individual, though uplands (e.g. pineland, hardwood hammock, urban areas) are usually preferred over lowlands (buttonwood transition, mangrove) (Lopez 2001). However, Key deer can aggregate in urban areas (mainly on Big Pine and No Name) where group sizes have increased dramatically (Folk and Klimstra 1991). Though urban deer may remain in the residential areas for a substantial amount of time, "wild" deer may roam greater distances. On Big Pine and No Name keys, mean ($\pm$ SE) annual home range size of Key deer females was 42 $\pm$ 4 ha with mean ($\pm$ SE) daily movements of 302 $\pm$ 13 m (Lopez 2001). Key deer have conspicuous patterns of activity and habitat use, and established trails from years of daily use can be readily seen in many of the deer's movement corridors (USFWS 1999). Some of these paths lead directly to *Rhizophora mangle* stands where significant browsing was evident (personal observation).

Within the home range of Key deer, a diversity of food plants may be found. Klimstra and Dooley (1990) found a total of 164 food plant species of which 28 plant species accounted for approximately 75% of the volume in rumen samples of Key deer. Although Key deer have a wide selection of food plants, they "prefer" certain plants over others. Key deer have a high saltwater tolerance (Folk 1992), such that *R. mangle* and *Avicennia germinans* can constitute 24% of the volume of their diet (Klimstra and Dooley 1990). Plant foods found in high percentage of rumen samples may either be "preferred" or are just more available (principal foods) (Dickson 1955; Klimstra and Dooley 1990; Folk 1992). The percentage of forage types in the deer diet indicate that leaves and newly grown stems of woody plants are most important, followed by fruits from woody plants, fruits and flowers of palms, forbs, and miscellaneous items, such as graminids, mushrooms, and pine needles (Dooley 1975).

Due to substantial increases in Key deer herds on certain islands, intense browsing by Key deer could affect rare tropical forests (e.g. pine rockland, hardwood hammock) and other endemic species in the lower Keys. It is usually not the day-to-day consumption of plants by herbivores that alters a plant community, but a dramatic increase or irruption of herbivores that can cause considerable changes (McShea

et al 1997). All deer food plants can be negatively impacted, yet highly preferred plant species can suffer particularly high losses (Anderson and Loucks 1979;Anderson 1994; Cornett et al 2000; Ward et al 2000).

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Study Area

The study was conducted in the lower Florida Keys within the boundaries (24° 36´ N – 81° 18´ W to 81° 34´ W) of the National Key Deer Refuge (NKDR). The climate is subtropical with evident wet (~May-October) and dry (~November-April) seasons. In the lower Keys, the mean annual temperature is ~ 25.2 °C and mean annual rainfall is ~ 100cm. Soils vary from blue-grey marl to black peaty muck and are underlain by oolitic limestone exposed in many areas (Dickson 1955). The surface of the Lower Keys is of Miami (oolite) limestone that can be traced to their Late Pleistocene development (Folk 1992). The vegetation has its origin in the south (Caribbean) and is mainly derived from Cuba (USFWS 1999).

The NKDR is a 352 km arc of low-lying islands that are approximately 5.4 m or less above sea level (Folk 1992). The Keys are bounded by Florida Bay and the Gulf of Mexico, and the Straights of Florida on the Atlantic Ocean (Folk 1992). The islands are separated by narrow northwest by southeast channels making them a unique study area. Each island can be considered an experimental unit with a different deer density and forest community structure.

Only 12 islands frequently used by Key deer were sampled in this study (see Figure 2.1). Many of the small outer islands are used only transiently by Key deer (Dickson 1955). Moreover, the small size of most of these islands makes it difficult to compare them to the larger islands. Nevertheless, a select few of the smaller outer islands (e.g. Howe, Big Munson) will be sampled because Key deer have been observed frequently on them (Dickson 1955; Folk 1992). The 12 islands are roughly arranged from a high to low density of Key deer from No Name to Sugarloaf (see Table 2.1).

Four habitat types (Figure 1.1) differing in percent coverage per island (Table 1.1) were sampled on each island: hardwood hammock, pine rockland, buttonwood transition, and mangrove wetland. Although the habitat types may be divided into smaller subcategories, a more general and comprehensive approach will be used in order to facilitate comparison between the islands. The following habitat descriptions are provided by Folk (1992):

Hardwood hammock

Hammocks are a climax successional community formed by tropical hardwood plant species that occur in uplands. The majority of the plant community is of West Indian origin. Much litter, produced by the hardwoods, accumulates organic matter that may develop into substantial soil. This acclimatizes the flora to mesic conditions. The closed canopy reduces the loss of soil moisture and moderates thermal extremes. Plant species tend to "clump" which makes rare species occur in a few places rather than being uniformly or randomly distributed. Therefore, every individual species may not always be sampled on each island. The most common plant species include: *Piscidia piscipula*, *Busera simaruba*, *Coccoloba diversifolia*, *Bumelia salicifolia*, *Eugenia axillaries*, *Eugenia foetida*, *Capparis flexuosa*, *Savia bahamensis* and *Chiococca alba* (herbaceous).

Pine rockland

The plant community with the highest elevation is pineland, which occurs 2m or more above sea level. This is considered a fire-climax system and may ultimately succeed into hammock in the absence of fire. The canopy is dominated by *Pinus elliottii* var. *densa*, while the mid-story contains *Coccothrinax argentata*, *Pithocellobium guadalupense* and *Thrinax morrisii*. The understory cannot be easily characterized since it depends on presence or absence of fire and the successional stage of the pineland. If fires are frequent then there may be a diverse range of herbaceous species. In the absence of fire, many hardwood species will occupy the understory leading to successional change. The soil is very shallow or in some cases completely absent. The pocketed limestone provides fresh drinking water after rain or in basins that connect with freshwater lenses. Pinelands are only found on Big Pine, Little Pine, No Name, Cudjoe, and Sugarloaf with relic stands on Howe and Knockemdown.

Buttonwood transition

Buttonwood transition is composed of salt tolerant species that inhabit areas that are adjacent to upland habitats. The main species found in this habitat are *Conocarpus erectus*, *Jacquinia keyensis*,

Maninkara bahamensis, *Bumelia celastrina*, *Maytenus phyllanthoides*, *Erithalis fruticosa*, and halophytic herbs. The openness of the habitat allows much sunlight to penetrate and reach the ground. As a result, many herbaceous species may occur where there is sufficient soil.

Mangrove wetland

The mangroves are mostly stunted due to extended periods of saltwater inundation and poor nutrient exchange. The habitat includes the three mangrove species: *Avicennia germinans*, *Rhizophora mangle*, and *Laguncularia racemosa* but is usually dominated by *A. germinans*. The herbaceous layer consists of *Batis maritime*, *Salicornia* spp., *Monanthacloe littoralis,* and *Borrichia frutescens*.

Each habitat is used to some extent by Key deer (feeding, bedding, fawning, etc.) and use varies by season (Silvy 1975; Folk 1992; Lopez 2001). Nonetheless, all of the habitats can be influenced by intense deer browsing on islands with high Key deer densities, such as Big Pine, No Name, and Big Munson keys. Therefore, it is necessary to study and quantify all of the plant species in each habitat to observe any effects of the increased Key deer population on local vegetation.

Objectives

The study aims to quantify the impacts of Key deer browsing on plant communities in the lower Florida Keys. To determine plant food preference by Key deer, cafeteria feeding trials were conducted. Deer preferences for plant species aided in determining browsing impacts among plant species in natural habitats. It is thought that islands of high-density deer will show a decrease in plant species density, especially seedlings and saplings (< 1.2m tall, in reach of Key deer) of preferred plant species. Deer herbivory rates (tested with nursery plants) were expected to be higher on islands with high deer densities. Also, preferred woody plant species densities and herbaceous cover and richness should be higher in fenced deer exclosures on No Name Key (a high deer density island). Many studies that involve deer exclosures show a striking difference in vegetation abundance, richness, and height class distribution within and outside exclosures (Alverson et al 1988; Anderson 1994; Anderson and Loucks 1979; Castleberry et al 2000; Cornett et al 2000; Ward et al 2000).

Temporal effects on plant communities caused by the increase in Key deer density were examined by comparing the present study to baseline vegetation data from Folk (1992). The deer densities ranged from approximately 50 animals in the 1950s to 200-300 animals in 1990s to 600-700 at present (Lopez 2001). The increased intensity of deer browsing should be reflected in the understory vegetation and perhaps midstory / canopy data between the present study and the previous study.

Hardwood hammock habitats adjacent to and distant from urban areas were sampled to compare Key deer impacts on vegetation. Key deer are prone to aggregate near urban development (Figure 1.2) due to presence of ornamentals, human handouts, and mowed land providing deer with favored herbaceous foods (Folk and Klimstra 1991; Lopez 2003). A higher density of Key deer can lead to intense browsing in areas near urban development. A strong deer effect should be noticeable between hammock stands adjacent to and distant from urban environments.

Woody and herbaceous vegetation was also compared in pineland habitat of burned and unburned areas on Big Pine and Sugarloaf keys. Fire history of the lower Keys was used to compare pinelands burned 10 years ago, 14 years ago, and unburned areas (not burned > 50 years) on islands with high and low Key deer densities. Furthermore, two exclosures in pineland on No Name were burned along with adjacent control plots. Vegetation data were compared from the time the plots were burned up to 1 year post-burn. Interacting and/or additive effects of fire-deer dynamics were expected to affect pineland plant communities.

Several hypotheses were examined. Hypotheses 1-4 refer to hammock, buttonwood, and mangrove habitats; hypothesis 5 refers to urban-hammock interface; and hypotheses 6-7 refer to pineland habitat.

1. Densities of seedlings and saplings (<1.2m tall) of preferred woody plant species should be greater on islands of low-density deer than on islands of high-density deer.
2. Plant richness and abundance will be greater inside of fenced deer exclosures than outside of the exclosures in adjacent control plots in hammock habitat.
3. Key deer herbivory rates will be higher on islands with high deer densities.

4. Plant composition should have changed on the plots between Folk's study (1992) and this study because of increased herbivory. Specifically, on islands with high deer densities, preferred plant species should decrease and nonpreferred species increase.
5. Richness and abundance of vegetation should be greater in hammock stands away from urban areas versus stands near urban areas on Big Pine.
6. Richness and abundance of vegetation should be lower in burned areas versus unburned areas on Big Pine due to high levels of herbivory because Key deer are known to forage recently burned areas.
7. Exclosures that were burned should have a higher richness and cover of herbaceous species and higher densities of preferred woody species than open (control) plots.

The Florida Keys is a fragile ecosystem. An increased population of a large herbivore such as the Key deer could greatly affect this delicate system. The outcome of this study may help in Key deer and habitat management. The project will provide land managers valuable information as to the effects of herbivores on recruitment of trees in hammock, pineland, buttonwood transition, and mangrove habitats. Although vegetation of mature trees may be out of reach to Key deer, seedlings and saplings are readily eaten. Thus, the whole age-structure of many tree species may be skewed towards mature individuals. When these senesce, there will be few saplings to replace them, and could result in local extinctions. Subsequent changes to plant composition could be detrimental to plant communities and wildlife that utilize the habitats, including Key deer.

Table 1.1. Percent habitat coverage for 12 islands frequently used by Key deer in the National Key Deer Refuge. Data is (partially) from Lopez (2001).

	% Habitat [1]					
Island	BW	MG	HM	FM	PL	DV
Big Pine	11	24	9	9	23	24
No Name	15	33	34	1	10	7
Big Munson	4	72	21	0	0	3
Big Torch	23	50	17	7	0	3
Middle Torch	27	39	27	5	0	2
Little Torch	21	33	16	1	0	29
Howe	17	72	11	0	0	0
Little Pine	19	52	15	1	13	0
Cudjoe	19	50	8	0	7	16
Sugarloaf	22	48	19	2	2	7
Summerland	22	40	10	0	0	28
Ramrod	15	31	26	5	0	23

[1] BW = Buttonwood, MG = mangrove, HM = hammock, FM = freshwater marsh, PL = pineland, DV = developed

Figure 1.1. Four major habitat types utilized by Key deer in the lower Florida Keys. Habitats are pine rockland (top left), hardwood hammock (top right), buttonwood transition (bottom left), and mangrove wetland (bottom right).

Figure 1.2. Urban (residential) area on Big Pine with a large Key deer herd.

CHAPTER 2

EFFECTS OF KEY DEER HERBIVORY ON FOREST STRUCTURE

Synopsis

Although most conservation studies investigate the effects of some factor (e.g. environmental or anthropogenic) on endangered species, this study was unusual by examining the effects of an endangered species on its environment. The endangered Key deer (*Odocoileus virginianus clavium*) have increased from approximately 50 animals in the 1950s to over 700 by 2000. Over two-thirds of the population resides on only a few islands in the lower Florida Keys. Therefore, impacts of Key deer herbivory on native plant species may be substantial on islands with high deer densities, such as Big Pine, No Name, and Big Munson. Using woody plant species in cafeteria feeding trials provided a relative preference index for Key deer plant selection. The index aided in determining browsing effects on highly preferred plant species and any indirect effects on nonpreferred species on islands with many deer. Vegetation quadrats were used to estimate deer herbivory effects on plant densities in hardwood hammock, buttonwood transition, and mangrove habitats throughout 12 islands categorized into treatments of high, intermediate, and low deer densities. Densities of highly preferred woody plant species < 1.2m tall (within Key deer reach) were significantly lower on high deer treatment islands, though the same species >1.2m tall did not differ in density among islands. Effects of deer treatment were not evident for most moderately preferred plant species, while significantly higher densities of some nonpreferred species on high deer treatment islands indicated possible competitive release. In addition, three fenced deer exclosures were established in hardwood hammock on No Name Key, a high-density deer island. After two and a half years, there was a mean increase in abundance and height of preferred woody species inside exclosures, while nonpreferred species increased significantly more in open plots, indicating a shift in plant species composition. Finally, in a field experiment, numerous nursery plants of eight native woody species were set in hammock and

mangrove habitats on six Keys (two from each deer treatment) over a 21 day period. Very high herbivory rates were observed on preferred plant species (predominately on high deer treatment islands) while the non-preferred species remained unbrowsed. Overall, data suggest that on high deer treatment islands, highly preferred (browse-intolerant) plant species might eventually fail to regenerate as young plants are over-browsed by Key deer, while unpalatable plant species become dominant. A balance must be found between maintaining sufficient numbers of Key deer and local food plant species.

Introduction

One is impressed with the amount of time Key deer spend feeding.

- Hardin et al. (1969)

Cervid studies are extensive given that many are game species, their populations can irrupt under certain conditions (Leopold 1943; McCullough 1997), and plant damage to crops and forest species can be wide-ranging and costly (Conover et al. 1995; Mcshea et al. 1997). Over-browsing by white-tailed deer (*Odocoileus virginianus*) is well documented in the northern United States (e.g. Leopold et al. 1947; Alverson et al. 1988; Hobbs 1996; Mcshea et al. 1997; Castleberry et al. 2000; Cornett et al. 2000; Webster and Parker 2000) but studies are generally lacking in the southeastern United States (Russell et al. 2001).

This project investigated the effects of Florida Key deer (*Odocoileus virginianus clavium*) herbivory on local plant species following an increase in the population over a 30-year period (Silvy 1975; Lopez 2001). Key deer, a subspecies of the white-tailed deer, are endemic to the lower Florida Keys. Historically, habitat loss and over-hunting lowered Key deer numbers resulting in federal listing as an endangered species and establishment of the National Key Deer Refuge (NKDR) in 1957 (USFWS 1999). Consequently, the Key deer population increased from approximately 50 animals in the 1950s to over 700 animals in 2000 (Lopez 2001). Key deer have a potential range of 26 islands (Folk 1992), but over two-thirds of the population reside on only two islands, Big Pine Key and No Name Key (Lopez 2001) resulting in a skewed distribution and relatively high Key deer densities on these islands. This provided for a distinctive study that considers the effects of an endangered species on unique plant communities, such as

hardwood hammock, a rare habitat considered imperiled in the state of Florida (Florida Natural Areas Inventory 1990).

High relative densities of white-tailed deer and subsequent increased browsing pressure can be detrimental to preferred plant species (Strole and Anderson 1992). Indeed, visible browse lines, around 1.2m high, which is approximately the Key deer's reach, are very noticeable in plant communities on Big Pine and No Name keys and on Big Munson (personal observation), part of an island complex off southern Big Pine. Evidence of browsing is usually detected on select plant species, however, even though Key deer may forage on over 160 plant species to meet dietary requirements (Klimstra and Dooley 1990).

To understand plant-deer density interactions, a critical assessment was required concerning the effects of Key deer on local vegetation. Because Key deer mainly browse on low growing plants within their reach (USFWS 1999; personal observation), it was hypothesized that seedling/sapling (<1.2 m tall) densities of woody preferred plant species should be lower on islands with many Key deer than on other islands with fewer deer. Also, preferred plant species abundance and height should increase in exclosures and decrease in control plots. Higher densities of nonpreferred plant species should be evident on high deer density islands and in open (no exclosure) plots. Finally, on islands with many deer, preferred plant species should be browsed at a higher rate and magnitude over a given time period (tested with potted plants), whereas nonpreferred plant species should be avoided.

Study Area

The study was conducted in the lower Florida Keys within the boundaries (24° 36´ N – 81° 18´ W to 81° 34´ W) of the National Key Deer Refuge (NKDR). The climate is subtropical with evident wet (~May-October) and dry (~November-April) seasons. In the lower Keys, the mean annual temperature is ~ 25.2°C and mean annual rainfall is ~ 100cm. Soils vary from blue-grey 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 1955).

Although the Key deer's range includes about 26 islands, most of them are used transiently - mainly during the wet season (Folk 1992; Lopez 2001). Around 12 islands of in the NKDR archipelago are

frequently used by Key deer and exhibit a deer density gradient: low (Sugarloaf, Cudjoe, Summerland, Ramrod), medium (Little Torch, Middle Torch, Big Torch, Howe, Little Pine), and high (Big Pine, No Name, Big Munson) (Table 2.1; Figure 2.1). Roel Lopez (Texas A & M University) provided Key deer densities (see Chapter 3). Each of the 12 islands contains hammock, buttonwood, and mangrove habitats. Pineland is also on 6 of the islands and is a highly utilized deer habitat, but fire history must be taken into account so herbivory in this habitat will not be discussed here (see Chapter 5 for pineland). Beach dune hammock, cactus hammock and buttonwood prairie were also not included because they are only found on certain islands. Vegetation in the lower Keys is primarily of West Indian origin (Stern and Brizicky 1957) and subsequent plant nomenclature follows Scurlock (1987) (Appendix 1). [Refer to Chapter 1 for more detailed descriptions of the islands, habitats, Key deer characteristics, etc.]

Methods

Cafeteria feeding trials

Because Key deer are selective browsers (Klimstra and Dooley 1990), cafeteria-feeding trials were conducted to understand the relative preference by Key deer for certain plant species. Subsequently, feeding trial results can aid in predicting the effects of herbivory on natural vegetation (Diaz 2000). To determine the relative preference of plant species by Key deer, cafeteria-feeding trials were conducted on Big Pine Key at four urban sites. Preliminary trials (5 per site) were conducted in March 2002 to allow Key deer to acclimate to the experiment, but the data were not used in analyses. After the acclimation period, seven trials were carried out per site for a total of 28 trials in 2002 from April 2 to May 5. Trials included male, female, adult and juvenile/yearling Key deer with a mean of five deer feeding per trial and 2-3 feeding at a time. Because trials were not conducted on individual deer, relative plant species preference can only be assessed at the population level. Key deer were apprehensive of the feeding station on days with excessive wind, so trials were not conducted on those days.

Seventeen woody plant species (Table 2.3) were selected for having a high frequency of occurrence throughout the 12 study islands (Dickson 1955; Folk 1992; personal observation) and by their incidence in Key deer rumen samples from a previous study (Dooley 1975). Stems of the 17 plant species

were clipped from branches >1.2m from the ground when possible, but stem lengths varied to obtain similar weights of consumable matter. Stems were collected from Big Pine, Middle Torch, and Sugarloaf keys and used in preliminary trials to acclimate Key deer to the feeding station (Figure 3) and to test deer selection for plant species from different islands. There were no differences in selection due to island source, so data were pooled for the trials. The stems were weighed to the nearest gram immediately before and after each trial and the leaves were counted; however, leaf number and leaf weight were highly correlated (Spearman's $r_s = 0.982$, $P < 0.01$) so only weight was analyzed. The clipped ends of the stems were secured on the feeding station in slots, 60cm from the ground, so deer could "pull" off the leaves, simulating natural herbivory. To control for species associations, stems of each species were randomly placed in the slots numbered 1-17 for each trial. The number "1" slot always faced north and the feeding station was set in the same location (per site) each trial. Cut stems of similar weights for each species were set-aside as controls to account for any weight loss due to evaporation; however, during the mean period of 1.5 hours between clipping stems and trial termination, weight loss per species was negligible.

Because Key deer are crepuscular, trials commenced at 6pm once per day. Deer were allowed 7 minutes (determined from acclimation trials) to feed before a trial was terminated. Leaves remaining on a stem after the trial were clipped and counted and the bare stem was weighed. The following equation determined wet consumable matter consumed (i.e. percent leaf weight):

$$\frac{\text{Pretrial stem (g) - post trial stem (g)}}{\text{Pretrial stem (g) - stem weight (g)}} \times 100 = \text{Percent leaf weight consumed}$$

For a simple example, suppose a cut stem weighed 50g. During the trial, the deer consumed many leaves and the post trial stem plus remaining leaves weighed 15g. After the remaining leaves were clipped, the stem alone weighed 10g. Therefore:

$$\frac{50\text{g} - 15\text{g}}{50\text{g} - 10\text{g}} \times 100 = 87.5\% \text{ leaf weight consumed}$$

Table 2.1. Attributes of 12 islands of frequent Key deer use in the NKDR.

Island Name	Key size km2	Key deer km-2	Deer category
Big Munson Key	0.48	31.25	High
No Name Key	4.91	21.59	High
Big Pine Key	25.03	17.74	High
Big Torch Key	6.32	7.91	Medium
Middle Torch Key	3.44	7.27	Medium
Little Pine Key	3.17	4.73	Medium
Little Torch Key	3.35	4.48	Medium
Howe Key	3.92	3.83	Medium
Sugarloaf Key	8.06	0.62	Low
Ramrod Key	4.33	0.46	Low
Summerland Key	4.75	0.42	Low
Cudjoe Key	14.35	0.35	Low

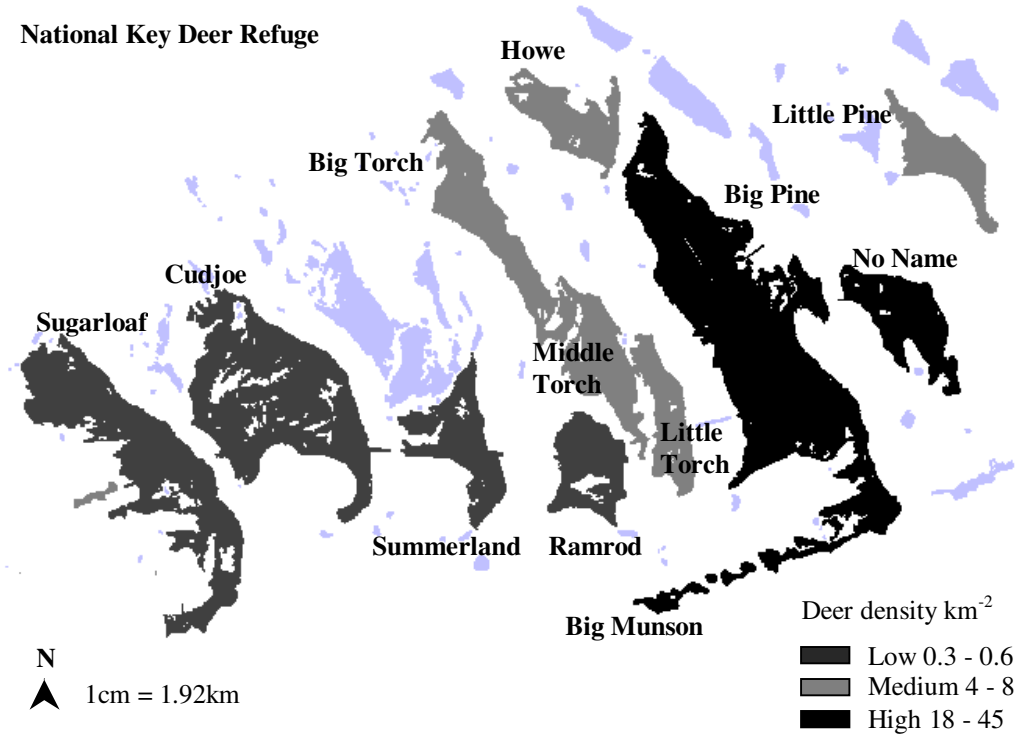

Figure 2.1. Twelve study islands of frequent Key deer use in the National Key Deer Refuge. Islands of different colors depict deer density treatments of low, medium and high.

Although a similar weight of consumable matter for each species during each trial is ideal for preference trials (Johnson 1980), the methodology only allowed a crude estimate for leaf weights consumed (i.e. stems were not eaten). The average bulk leaf weight was ~ 42g (+/- 7g) species $^{-1}$ trial $^{-1}$. The small differences in leaf weights were probably inconsequential and because relative proportions per species were used, test results should not be influenced. Nevertheless, a Rank Preference Index (RPI) was calculated (Johnson 1980) using Krebs/WIN software version 0.9 (Krebs 1989) to account for variable resource levels. *Resource levels* were mean leaf weights (g) that were held variable and *use* was the mean amount of leaf weight consumed (g) per species per site. The resource and use data were first assigned ranks, and the difference in ranks between use and resource was calculated by the equation (Johnson 1980):

$$t_i = r_i - s_i$$

where r_i = Rank of usage of resource i
s_i = Rank of availability of resource i
t_i = Rank difference (measure of relative preference)

For the feeding trials, RPI equaled the t_i value of each plant species averaged over sites. The plant species with the lowest RPI value was considered the most relatively preferred. For example, if species A had a RPI of -5.1 and species B had a RPI of 1.2 then species A is relatively preferred over species B. Furthermore, to calibrate plant preference, RPI was qualitatively compared to a Relative Preference Value (RPV) which was ranked by summing the mean percentage of leaf content consumed per plant species and the percent frequency of the plant species eaten (at least one bite) throughout the 28 trials.

Vegetation sampling

To examine the effects of Key deer herbivory on plant densities among islands, deer density treatments for the 12 study islands were: low density (<1 deer/km^2), medium density (1-10 deer/km^2), and high density (>10 deer/km^2) (Table 2.1). Vegetation was sampled in plant communities on each island and compared between the deer density treatments.

Vegetation sampling was conducted during the dry season from January to May of 2001 and 2002. To estimate the density (ha^{-1}) of plant species, a total of 200 nested quadrats were examined throughout the

12 islands in three habitat types: hammock (n = 5-10), buttonwood (n = 4), and mangrove (n = 6). A 1 x 50m quadrat was used to sample woody plant species with a diameter at breast height (dbh) < 12.7cm. Woody plant species were assigned to two height classes: <1.2m (within Key deer reach) and >1.2m. A 10 x 50m quadrat, bisected by the 1 x 50m quadrat, was used to estimate basal areas of large tree species with a dbh >12.7cm. Plant species that exhibited root suckering were recorded as individuals if they branched underground and the protruding stems were separated.

Basal areas ($m^2 ha^{-1}$) were compared to estimate stages of forest succession or stand age, which could cause differences in understory or sub-canopy structure and composition. For example, a higher basal area of a species should indicate higher seedling input for that species (Frelich and Lorimer 1985). Total basal areas (all species combined) were standardized by dividing by the number of plant species (>12.7cm dbh) sampled per habitat per island.

The density of each plant species < 1.2m high was compared between deer treatments to examine any direct effects of Key deer browsing (i.e. islands with many deer should have lower plant densities). Plant species densities >1.2m were compared to determine any initial differences in density of adult trees and shrubs that may affect the density of the < 1.2m class (i.e. via recruitment). Specifically, plant species that have a high density of adults may correspondingly have a relatively high number of seedlings and saplings (Alexander 1967).

To examine any differences in intrinsic habitat variables that might affect understory plant densities or composition, canopy cover was measured with a concave densiometer on a tripod (45cm high) placed every 10m along the 1m x 50m quadrat. The subsequent method for recording densiometer readings was according to Lemmon (1957). Four readings were taken by pivoting in four cardinal directions from a central point. On the concave lens there are 24 cells in a grid that are divided by ocular estimation into four quarters (points), thus totaling 96 points in the grid. The amount of sky was estimated by counting points representing non-occupied areas. Points counted were multiplied by 1.04 and subtracted from 100 to obtain percent canopy cover, which was averaged for the quadrat, then again for the habitat per island.

Vertical vegetation density was measured to determine any impacts of deer browsing on vertical structure of the understory plant community. A vegetation profile board was used to measure vertical

vegetation density following a method described by MacArthur and MacArthur (1961). The profile board (0.45m x 1.2m) had a black and white checkerboard pattern and two vertical ranges of 0-0.6m and 0.6-1.2m above the ground. The following protocol was followed for both vertical ranges in two opposite directions (180°) every 10m along the 1 x 50m vegetation quadrats for a total of 10 readings per range per quadrat. The profile board was faced in one direction and the researcher backed away while facing the board. When vegetative cover for a given vertical range obstructed 50% of the profile board, the researcher stopped and recorded the distance (maximum distance was 15m). A Vertical Obstruction Index (VOI) was calculated for each vertical range using the following formula (Hays et al 1981):

$$VOI = (\text{Log}_e 2) / \text{Distance in meters}$$

VOI measurements were summarized for each vertical range (0-0.6m and 0.6-1.2m) per quadrat. Quadrat data for each range were averaged for each habitat per island.

Deer exclosures

In August 2001, three square $37m^2$ deer exclosures were constructed on No Name Key in hardwood hammock with corresponding control plots. Although plots were randomly located, they were selected near roads (between 15m - 50m) to facilitate construction and decrease cost. Galvanized chain-linked fencing 1.8m high was erected to exclude Key deer, but was raised 15cm above the ground to allow access by other potential herbivores such as the lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), raccoon (*Procyon lotor*) and the Florida box turtle (*Terrapene carolina bauri*), a seed disperser (Liu et al. 2003).

Data were collected every 6 months from August 2001 to January 2004. Woody shrubs were quantified over the entire plot in the following height classes: < 5cm, 5cm – 0.6m, 0.6m – 1.2m, 1.2m – 1.8m, and > 1.8m. To limit edge effects, data were not recorded in a buffer zone (0.3m W x 2.1m H) within the plot perimeters. Percent cover of herbaceous species was quantified in nine circular plots ($1m^2$). However, herbaceous cover was too low and sporadic in both open and exclosure plots for any adequate comparisons, so it will not be discussed further.

Abundance data were summarized for each replicate plot per treatment (open/exclosure) by combining all height classes per species for each plot from the first (August 2001) and last (January 2004) sample date. The difference in plant abundance per species between the two times (abundance of last sample – abundance of first sample) was then calculated for each replicate plot. Positive values would indicate increases of plant species abundance and negative values a decrease of plant species abundance between the first and last sample date.

Every 6 months percent canopy cover was measured with a concave densiometer (see protocol above) including one sample in the center of the plot and samples taken in four cardinal directions 1.8m from the center. The data were averaged for each plot and time period.

Consumption rates of field-placed plants

In April 2002, potted plants were used in a field experiment to examine consumption rates of Key deer herbivory. Two islands from each deer density category were selected for the experiment: Big Pine Key and No Name Key (high), Big Torch Key and Little Torch Key (medium), and Cudjoe Key and Sugarloaf Key (low). Eight commercially available native plant species were purchased from a local nursery (Florida Keys Native Nursery, Plantation Key, FL) for the field experiment. First, the potted plants were numbered and the leaves were counted. Because deer tend to select larger plants over smaller plants (Anderson 1994; Augustine and Frelich 1998), the nursery plants were arranged so each island received similar sized plants with an overall similar number of leaves per species to decrease any initial variance and eliminate bias in plant size or available browse between treatments.

Sites that were at least 25m apart were randomly located in hammock and mangrove habitats and the potted plants were placed in groups (one of each species according to habitat) at the sites and randomly arranged approximately 5m apart at the following abundances per island: ten of both *R. mangle* and *A. germinans* individuals in mangrove habitat; and ten of each *B. simaruba*, *P. keyense*, *R. aculeata*, *C. diversifolia*, *E. foetida*, and *E. axillaries* individuals in hammock habitat. The nursery plants were set on the ground surface due to the extensive rocky substrate, and the pots were covered with loose rocks and organic debris. Initially, the height of each potted plant was measured from the pot-soil surface to the tip of

the leading shoot. Then, every simple leaf for most species and every leaflet of compound leaves for *B. simaruba* and *P. keyense* were counted. Plants were observed for browse and the leaves counted every 4hrs for the first 12 hrs, then every 24 hrs up to 550hrs (21 days). The plants were watered twice throughout the experiment.

Data Analysis

For feeding trials, differences in the proportion of leaf weight consumed were compared for plant species and site. For plant species, data were summarized across sites and the difference in the proportion of leaf weight consumed between plant species was tested for significance using a χ^2 procedure that tests if multiple proportions (k) are the statistically similar, following the formula (Zar 1999):

$$\chi^2 = \sum_{i=1}^{k} \frac{(\chi_i - n_i p)^2}{n_i pq}$$

where $p = \sum_{i=1}^{k} \chi_i \div \sum_{i=1}^{k} n_i$

$q = 1 - p$

χ_i = ith sample

n_i = ith sample size

The calculated χ^2 was compared to a critical $\chi^2_{0.05,\,v}$ where v = k –1 degrees of freedom. Statistical analyses only included plant species consumed with a frequency > 0 across sites. Background vegetation and adjacent habitats differed between feeding trial sites, which could elicit differential feeding behavior by deer; therefore, differences in proportion of leaf weight consumed per site was tested. Leaf weight consumed was summarized across plant species within sites and the same formula used above tested for differences among multiple proportions. A Tukey-type post hoc test with angular transformation was used to determine comparison-wise differences in proportions among the sites (Zar 1999). Potentially different groups of deer were present for each trial regardless of site causing intra-site replication per species to be suspect and precluded testing site x species interaction terms, though qualitative comparisons were made.

For vegetation quadrats, mean percent canopy cover, mean total basal areas (all species combined), and mean VOI (0-0.6m and 0.6-1.2m heights) were each tested using a two-way ANOVA with deer treatment (low, medium, high) and habitat type (mangrove, buttonwood, hammock) as fixed factors.

Some plant species were not present on certain islands currently or historically (Dickson 1955; Folk 1992; personal observation) which is likely an island effect not associated with deer browsing effects. These plant species were excluded from some analyses to eliminate bias from test results and precluded using more complex statistical models due to missing cells or to losing too many species. To illustrate, in a multivariate model, if a preferred plant species (dependent variable) never occurred on a high deer density island like No Name (factor level), then that species could be excluded, but it would leave an empty cell in the multivariate model for that factor. If a zero were simply added, it would bias the analysis by decreasing the value, which could falsely signify an herbivore effect. If the island (No Name Key) were excluded from the analysis, it would exclude all other test species from that island as well. Therefore, multiple univariate ANOVAs were used to test deer density effects (high, intermediate, low) on densities of plant species that were historically present (no zeros added), thus causing N to fluctuate between each species analysis. Habitats were analyzed separately and analyses included only common plant species found on at least 8 of the 12 islands (> 67%), with at least two islands from the high-density deer treatment. If it was necessary, data were square root or log+1 transformed to satisfy normality/homogeneity assumptions. Multiple comparison Tukey-type tests were used to compare differences between means. If parametric assumptions were not met, Kruskall-Wallace tests for independent samples were employed, and nonparametric multiple-comparison tests with unequal sample sizes (Zar 1999) and tied ranks (Dunn 1964) were then used to test differences between means.

For deer exclosure experiments on No Name, because sphericity assumptions were met, repeated-measures ANOVA (rmANOVA) was used to detect any differences in mean canopy cover between deer treatments (exclosure/open) from August 2001 to January 2004. Plant abundance data (differences between first and last sampling dates) were tested using a split-plot ANOVA with deer treatment and plant species as main effects, and subplots (exclosure/open plot replicates) nested under treatment. The statistical model employed was $Y_{ijk} = u + T_i + S_j + TS_{ij} + P_{k(i)} + P_{k(i)j} + e_{ijkl}$, where Y_{ijk} was the mean

response of difference in abundance for treatment *i* and plant species *j*. Fixed effects included treatment (T_i) and species (S_j) and their interaction term (TS_{ij}). Random effects included subplot ($P_{k(i)}$), the subplot interaction term ($P_{k(i)j}$) and subplot error (e_{ijkl}).

For consumption rate trials, herbivory on each nursery plant species was tested using rmANOVA with deer density (high, intermediate, low) as the main factor. The analyses only included 24-hour samples to satisfy rmANOVA assumptions of sphericity. Differences in deer browsing between plant species were tested for high deer density treatment only (see Results) using an rmANOVA with species as a fixed factor. For the between species analysis, the data were first changed to proportion of leaves remaining by dividing leaf number remaining at each time interval by initial leaf number. The data were arcsine transformed for normality. All statistical analyses were tested for significance at the $\alpha = 0.05$ level.

Results

Habitat characteristics

No trend in total basal area (all species combined) was evident between deer density treatments suggesting that successional stages were similar among the islands (Table 2.2; Figure 2.4). However, mean basal areas (m^2ha^{-1}) ($\pm$1SE) for *B. simaruba* in hammock by deer density treatment (low, medium, high) were as follows: low = 1.50 (0.49), medium = 2.27 (1.35), and high = 19.22 (9.30), suggesting that high deer density islands should have the highest input of *B. simaruba* seedlings. The high variance in basal area for high deer treatment was mainly due to larger *B. simaruba* trees on Big Munson Key. There were no differences in percent canopy cover among deer density treatments, but canopy cover for habitats differed with hammock having the highest percent cover (Table 2.2; Figure 2.4). Therefore, each habitat per island had similar canopy cover and basal area suggesting that deer density would cause any differences in understory composition. Key deer browsing appeared to affect vertical vegetation density in that high deer density islands had the lowest overall vertical obstruction index (VOI) in both the 0-0.6m range and the 0.6-1.2m range. Also, VOI in the 0.6-1.2m range was higher in hammock habitat suggesting it has the highest potential cover, though there was no interaction with deer density (Table 2.2; Figure 2.4).

Key deer preferences

Key deer showed strong preferences (proportion of leaf weight consumed) for certain plant species as measured at the population level (χ^2 of species pooled across sites = 1902.4, df =12, P <0.001; Table 2.3). The overall consumption of plant species differed per site (χ^2 of species pooled within site = 105.5, df =3, P = <0.001) indicating differences in herbivory levels by Key deer at some sites. Total plant consumption at site 4 significantly differed (Tukey-type post hoc test for multiple proportions P < 0.05) from the other 3 sites, caused by higher ingestion of *Morinda royoc* and especially *B. lucida* and *P. rotundata* at site 4 (Table 2.3).

The most preferred species were *B. simaruba*, *E. fruticosa, R. mangle, B. celastrina* and *J. keyensis* and the preference was consistent between sites. Consumption was more variable for moderately preferred species such as *M. royoc*, *P. keyense*, and *R. aculeata*. The remaining plant species were lightly consumed (probably opportunistic), and had higher variation among sites, while *P. piscipula*, *L. racemosa*, *E. axillaris* and *E. foetida* were never eaten. Only two species, *M. royoc* and *P. keyense,* were switched in preference ranking according to the methods used (RPV versus RPI; Table 2.3).

Key deer impacts on plant densities

In hammock habitat, high deer densities negatively influenced the densities of highly preferred plant species in the < 1.2m height class, such as *B. simaruba, E. fruticosa, B. celastrina, J. keyensis,* and *G. discolor* (Table 2.4; Figure 2.5). Key deer browsing did not affect many other woody plant species in the <1.2m height class (Table 2.4). Low-density deer islands had higher densities of *B. simaruba* (nonparametric multiple post hoc, P<0.05) and *G. discolor* (Tukey post hoc P<0.05) than medium or high deer treatments suggesting that Key deer herbivory strongly affected these species. Low and medium deer treatments had higher densities of *E. fruticosa* and *B. celastrina* (Tukey post hoc P<0.05) than high deer treatment. However, the densities of the above mentioned species in the > 1.2m class did not differ between deer treatments, although *E. fruticosa* density was very low on high deer density islands (Figure 2.6; all P > 0.05) indicating that Key deer do not affect plants they cannot reach. This also signifies that

adult tree densities and thus recruitment potential are similar among deer treatments so Key deer browsing is the predominate factor affecting understory species. For many moderately preferred woody species (e.g. *M. royoc, P. keyense, R. aculeata*) there was no effect of deer density, but the trends indicated that most species are at lower densities on the high deer density islands. For some nonpreferred species, such as *P. piscipula* and *C. diversifolia,* there was a positive relationship with increasing deer density in that these two species in the <1.2m height class had higher densities (Tukey post hoc, $P < 0.05$) on the high deer treatment islands (Table 2.5; Figure 2.5). However, *M. toxiferum* density (a nonpreferred species) was higher in both height classes on islands with low deer density (Table 2.5; Figure 2.5). No trends of deer density on plant densities were found for the remaining species (all $P > 0.09$).

Buttonwood habitat showed similar trends to hammock with the most preferred plant species, such as *E. fruticosa, R. mangle* and *J. keyensis*, having low densities on high deer density islands, while there were no differences in densities for moderate or nonpreferred species (Table 2.4, Figure 2.6). *Erithalis fruticosa* and *J. keyensis* densities on low deer treatment islands were higher than medium (marginally for *J. keyensis,* Tukey post hoc $P = 0.056$) and high deer treatments (Tukey post hoc $P < 0.05$). However, *M. phyllanthoides* and *R. acul*eata had higher densities in the >1.2m height class on high deer density islands and were virtually absent at this height from the other two deer treatments (Table 2.5; Figure 2.6). The remaining species densities did not differ between deer densities (all $P > 0.10$).

In mangrove habitat, the preferred species *R. mangle* had a low density in the <1.2m class on high deer treatment keys, although marginally significant (Table 2.4; Figure 2.7) suggesting Key deer herbivory is causing its decline. No trends were detected between the density of *A. germinans* or *L. racemosa* and Key deer density (Table 2.4; Figure 2.7). Moreover, no trends in the >1.2m height class was detected for any mangrove species with deer density further illustrating Key deer do not affect plant species out of their reach (Table 2.5). Overall, it appeared that only highly preferred species in the <1.2m height class were affected by Key deer density in each habitat type, while few differences in density of species >1.2m were detected for all species.

Though multiple univariate tests of the same hypothesis may increase Type I error, several significant results at $\alpha = 0.05$ suggests a non-spurious trend (based on the Bernoulli process) making

Bonferroni adjustments unnecessary because they can decrease power considerably (Moran 2003). For this study, applying less conservative methods (i.e. no Bonferroni adjustments) would forewarn land managers of any significant trends in plant species densities, especially if there is an apparent corollary between high densities of deer and low densities of preferred plant species. Moreover, eliminating bias by excluding plant species that were never present on certain islands and not simply including zeros aided in acquiring real effects.

Deer exclosures

The deer exclosure study on No Name illustrated the strong effect Key deer can have on plant communities as differences for woody species abundance between exclosures and control plots were evident (Table 2.6; Figure 2.8). Percent canopy cover was homogenous (rmANOVA, $P > 0.95$) between exclosures and open plots in pretreatment samples of August 2001 (means (±1SE): open = 95.7% (0.89), exclosure = 95.0% (0.43)) and in January 2004 (open = 97.1% (0.50), exclosure = 97.2% (0.35)). Canopy cover significantly increased over time from 95% to 97% (rmANOVA, $F = 6.07$, $df = 5$, $P = 0.039$).

Split-plot tests for differences in abundance of woody plants (all species combined) between 2001 and 2004 revealed no effect of Key deer herbivory (open vs. exclosure), though differences in abundance were evident between species (Table 2.6). Because the abundance of preferred plant species increased in exclosures and nonpreferred species increased in open plots, changes in mean total plant abundance was not detectable between treatments (open vs. exclosure). Therefore, a separate split-plot ANOVA was used to test the difference in abundance between exclosures and open plots for five selected preferred woody species (*B. simaruba, P. keyense, M. royoc, R. aculeata, G. discolor*) and five nonpreferred woody species (*P. piscipula, E. foetida, E. axillaris, C. diversifolia, R. septentrionalis*). Preferred plant species abundance significantly differed between treatments (Table 2.6) in that preferred species increased inside deer exclosures and decreased in open plots (Figure 2.8) and also grew into taller height classes in exclosures (Figure 2.9) indicating that Key deer browsing is affecting the abundance and stunting the growth of these species. Though the highly preferred *B. simaruba* increased in abundance inside exclosures, it remained in the smallest height class (<5cm), which suggests that recovery time may be long-term for this species to

grow above the browse-tier (>1.2m). All split-plot ANOVA terms were significant for the five selected nonpreferred woody species (Table 2.6) suggesting that Key deer are indirectly affecting these species. The nonpreferred species increased much more in open plots, such as *E. axillaris* and *E. foetida,* and some decreased in exclosures, *P. piscipula* and *M. toxiferum* (Figure 2.8). The large increase of *E. foetida* in open plots and the decrease in *P. piscipula* in both treatment plots were the main cause of the species term being significant (Figure 2.8). Also, the heights of some nonpreferred species (e.g. *E. foetida* and *E. axillaris*) increased in open plots more than in exclosures (Figure 2.9). Analyses for the remaining 12 species not categorized into preference categories showed no difference for change in abundance between open plots and exclosures (all $P > 0.90$). Also one new species, *B. salicifolia*, established in exclosures and one new species, *X. americana*, established in open plots (Figure 2.8), yet neither species ranked very high as food plants (Dooley 1975).

Key deer consumption rates

Key deer browsed preferred nursery plant species significantly more on islands of high-density deer than on intermediate or low-density deer islands (Figure 2.10). In hammock habitat on high-density deer islands, *B. simaruba* received considerably more Key deer damage (Table 2.7) with approximately 70% of leaves eaten in 24 hrs, 99% of leaves eaten after 21 days, and 100% of the *B. simaruba* potted plants were browsed at least once by trial termination. Also, deer significantly affected the heights of *B. simaruba* by browsing the woody stem, which decreased the total height of the plants by 28% on high deer density keys. One *B. simaruba* plant was browsed on day 6 on a medium deer density island (Big Torch Key), which came to ~ 3% of leaves eaten after 21 days for the medium deer density treatment. The number of leaves eaten on *P. keyense* overall differed between deer treatments (marginally); however, there was a much stronger effect over time with 30% of its leaves browsed by day 21 on high-density deer islands (Table 2.7; Figure 2.10). At high densities, Key deer browsed a negligible amount of *C. diversifolia,* with 3% of leaves browsed, while *E. foetida* and *E. axillaris* were uneaten (Table 2.7; Figure 2.10). *Randia aculeata* nursery plants were somewhat denser with leaves, unlike their naturally occurring counterparts, and percent leaf herbivory was less than 25% on the high deer density islands. In mangrove

habitat, *R. mangle* was browsed more on high deer density treatment islands with 72% of the leaves eaten by day 21 (Table 2.7; Figure 2.10). Although *A. germinans* plants on high deer density islands were browsed significantly more than on lower deer density islands, there was not much difference between treatments overall, with less than 10% of leaves browsed on high deer density islands. The difference in consumption rates between deer density treatments implies that preferred plant species (among others) on islands with many deer suffer much more damage, which could lead to limited recruitment.

Because Key deer substantially browsed potted plants mainly on Big Pine and No Name Keys, differences in consumption rates between plant species were analyzed using data from these two islands only. An overall difference in consumption rates between plant species was evident (Table 2.8). *B. simaruba* and *R. mangle* had the least percent leaves remaining, while the remainder of the species had about 75% or more of their leaves remaining after 21 days (Figure 2.11). The results of consumption differences for potted plant species are very similar to those from the cafeteria feeding trials, indicating strong evidence of Key deer preference for certain plant species regardless of the method used.

Table 2.2. ANOVA results for mean basal area, VOI (0-0.6m and 0.6-1.2m), and percent canopy cover for deer density treatments and habitats.

Source	df	SS	MS	F	P
Basal area					
Treatment	2	0.015	0.008	0.287	0.754
Habitat	1	0.019	0.019	0.734	0.403
Treatment x habitat	2	0.215	0.107	4.040	0.056
Error	18	0.478	0.027		
0-0.6m VOI					
Treatment	2	0.083	0.042	3.49	0.045
Habitat	2	0.051	0.025	2.13	0.139
Treatment x habitat	4	0.008	0.002	0.16	0.956
Error	27	0.323	0.012		
0.6-1.2m VOI					
Treatment	2	0.032	0.016	4.06	0.029
Habitat	2	0.179	0.090	22.49	<0.001
Treatment x habitat	4	0.008	0.002	0.51	0.728
Error	27	0.108	0.004		
Canopy cover					
Treatment	2	26.2	13.1	0.22	0.804
Habitat	2	31336.1	15668.1	264.16	<0.001
Treatment x habitat	4	292.7	73.2	1.23	0.320
Error	27	1601.4	59.3		

Table 2.3. Mean percent leaf weight (g) consumed by Key deer of each plant species in feeding trials (7 trials per site).

Species	Site 1	2	3	4	Mean	SE	% F [a]	RPV [b]	RPI [c]
Bursea simaruba	98	96	98	97	97.2	0.56	100.0	197.2	-5.4
Erithala fruticosa	89	92	92	93	91.6	0.87	100.0	191.6	-4.4
Rhizophora mangle	75	93	87	85	85.1	3.83	100.0	185.1	-3.6
Bumelia celastrina	86	86	85	80	84.3	1.57	100.0	184.3	-1.8
Jacquenia keyensis	84	86	84	79	83.1	1.63	100.0	183.1	-1.7
Morinda royoc	53	58	60	98	67.4	10.24	96.5	163.9	-1.5
Pithecellobium keyense	54	45	55	62	54.0	3.53	96.5	150.5	-1.6
Randia aculeata	21	60	51	58	47.7	9.05	96.5	144.2	-1.3
Ardisia escallonioides	12	13	19	23	16.7	2.67	78.6	95.3	1.9
Coccoloba diversifolia	0	20	17	19	13.8	4.64	57.1	70.9	2.3
Avicennia germanins	2	2	8	14	6.3	2.83	53.5	59.8	2.9
Byrsonima lucida	0	0	0	65	16.3	15.52	25.0	41.3	3.3
Pisonia rotundata	0	0	0	54	13.5	12.83	25.0	38.5	3.8
Piscidia piscipula	0	0	0	0	0.0	0.00	0.0	0.0	5.3
Laguncularia racemosa	0	0	0	0	0.0	0.00	0.0	0.0	5.3
Eugenia axillaris	0	0	0	0	0.0	0.00	0.0	0.0	5.3
Eugenia foetida	0	0	0	0	0.0	0.00	0.0	0.0	5.3

[a] % Frequency of each species eaten (at least one bite per trial) out of 28 trials

[b] RPV (Rank Preference Value) = Mean + % Frequency

[c] RPI (Rank Preference Index) - see Methods for calculation

Table 2.4. Univariate ANOVA or Kruskall-Wallace results for mean plant species densities (<1.2m high) for deer density treatments and habitats.

Source	N[a]	df	SS	MS	F or H[b]	P	R^2
Hardwood hammock							
B. simaruba	10	2	---	---	8.37 (H)	0.015	---
E. fruticosa	11	2	1463.8	731.9	4.93	0.050	0.52
B. celastrina	12	2	1205.1	602.6	5.00	0.035	0.53
J. keyensis	10	2	1028.6	514.3	4.79	0.054	0.54
M. royoc	12	2	3609.2	1804.6	2.79	0.114	0.38
P. keyense	12	2	4683967.6	2341983.8	1.00	0.406	0.18
R. aculeata	11	2	6046446.1	3023223.0	0.88	0.452	0.18
A. escallinoides	8	2	543638.7	271819.3	3.26	0.124	0.57
C. diversifolia	11	2	2185456.5	1092728.2	15.21	0.002	0.79
B. lucida	11	2	833.5	416.8	2.85	0.117	0.42
P. piscipula	11	2	729.3	364.6	15.86	0.002	0.80
E. axillaris	12	2	505.6	252.8	0.38	0.693	0.08
E. foetida	12	2	1.65E+07	8226115.858	0.07	0.931	0.02
T. morrissii	12	2	861.5	430.8	4.73	0.039	0.51
M. bahamensis	11	2	458920.7	229460.3	3.29	0.091	0.45
P. longipes	9	2	465.4	232.7	1.50	0.297	0.33
A. elemifera	9	2	746.4	373.2	0.61	0.573	0.17
M. toxiferum	11	2	2.90E+07	1.45E+07	4.99	0.039	0.56
C. erectus	12	2	1795.7	897.9	0.18	0.837	0.04
G. discolor	11	2	759.9	380.0	12.20	0.004	0.75
C. uvifera	10	2	100976.9	50488.5	0.70	0.527	0.17
R. septentrionalis	12	2	2199.1	1099.5	1.99	0.193	0.31
K. ferreum	10	2	140.2	70.1	3.30	0.098	0.49
S. bahamensis	8	2	1002.3	501.1	0.77	0.513	0.23
M. floridana	9	2	89346.1	44673.1	0.16	0.852	0.05
C. rhacoma	12	2	130.3	65.1	1.24	0.334	0.22
Buttonwood transition							
E. fruticosa	10	2	2361.8	1180.9	7.42	0.019	0.68
R. mangle	10	2	302.4	151.2	4.09	0.066	0.54
B. celastrina	12	2	954.1	477.1	1.34	0.310	0.23
J. keyensis	10	2	1545.6	772.8	4.76	0.050	0.57
P. keyense	12	2	71507.5	35753.8	0.23	0.802	0.05
R. aculeata	11	2	---	---	0.08 (H)	0.960	---
A. germanins	12	2	1860.4	930.2	1.66	0.244	0.27
L. racemosa	12	2	---	---	0.38 (H)	0.824	---
E. foetida	12	2	---	---	0.63 (H)	0.438	---
M. bahamensis	11	2	59870.7	29935.4	0.52	0.612	0.12
M. toxiferum	11	2	38.8	19.4	0.14	0.873	0.03
C. erectus	12	2	9632723.9	4816362.0	1.01	0.404	0.18
G. discolor	11	2	---	---	0.60 (H)	0.742	---
C. uvifera	10	2	56.4	28.2	0.15	0.862	0.04
R. septentrionalis	12	2	2.7	1.4	0.05	0.953	0.01
L. carolinianum	11	2	1759.7	879.9	3.07	0.103	0.43
M. phyllanthoides	12	2	19033.8	9516.9	0.08	0.927	0.02

Table 2.4. Continued.

Source	N[a]	df	SS	MS	F or H[b]	P	R^2
Mangrove wetland							
R. mangle	12	2	6328.4	3164.2	4.38	0.053	0.49
A. germanins	12	2	1.26E+08	6.28E+07	1.14	0.361	0.20
L. racemosa	12	2	1.72E+07	8579101.13	0.16	0.853	0.04
C. erectus	12	2	219.4	109.7	1.35	0.308	0.23

[a] N is the number of islands in the analysis (see Methods for explanation)

[b] F statistic is for ANOVA and H statistic is for Kruskall-Wallace tests

Table 2.5. Univariate ANOVA or Kruskall-Wallace results for mean plant species densities (>1.2m high) for deer density treatments and habitats.

Source	N[a]	df	SS	MS	F or H[b]	P	R^2
Hardwood hammock							
B. simaruba	10	2	5578.0	2789.0	0.33	0.730	0.08
E. fruticosa	11	2	2202708.9	1101354.5	4.45	0.057	0.56
B. celastrina	12	2	0.1	0.1	1.13	0.365	0.20
J. keyensis	10	2	0.9	0.4	0.34	0.725	0.09
M. royoc	11	2	251.3	125.6	0.91	0.440	0.19
P. keyense	12	2	625.3	312.6	2.40	0.146	0.35
R. aculeata	11	2	149232.7	74616.3	2.48	0.145	0.38
A. escallinoides	8	2	14555.2	7277.6	5.22	0.060	0.68
C. diversifolia	12	2	53110.5	26555.2	0.36	0.710	0.07
B. lucida	11	2	10850.3	5425.2	1.32	0.319	0.25
P. piscipula	11	2	4513.0	2256.5	0.20	0.824	0.05
E. axillaris	12	2	195.1	97.5	0.36	0.710	0.07
E. foetida	12	2	475.9	237.9	0.92	0.434	0.17
T. morrissii	11	2	49.4	24.7	0.41	0.678	0.09
M. bahamensis	11	2	144.1	72.0	2.78	0.121	0.41
P. longipes	9	2	53513.5	26756.7	0.54	0.610	0.15
A. elemifera	9	2	29.0	14.5	0.16	0.859	0.05
M. toxiferum	11	2	669.8	334.9	9.97	0.007	0.71
C. erectus	12	2	67926.8	33963.4	0.72	0.514	0.14
G. discolor	11	2	63.0	31.5	0.67	0.537	0.14
C. uvifera	10	2	12331.8	6165.9	1.76	0.240	0.34
R. septentrionalis	12	2	180241.5	90120.8	2.36	0.150	0.34
K. ferreum	10	2	6619.0	3309.5	0.77	0.500	0.18
S. bahamensis	8	2	541.5	270.8	0.74	0.522	0.23
M. floridana	9	2	15390.1	7695.1	0.76	0.508	0.20
C. rhacoma	11	2	1233.3	616.7	0.66	0.542	0.14
Buttonwood transition							
E. fruticosa	10	2	127161.8	63580.9	3.03	0.113	0.46
R. mangle	12		---	---	2.01 (H)	0.367	---
B. celastrina	12	2	30602.3	15301.1	0.37	0.700	0.08
J. keyensis	10	2	293.8	146.9	2.27	0.173	0.39
P. keyense	12	2	25795.1	12897.6	0.11	0.896	0.02
R. aculeata	11		---	---	9.90 (H)	0.007	---
A. germinans	12		---	---	2.01 (H)	0.367	---
L. racemosa	12		---	---	1.26 (H)	0.533	---
E. foetida	12	2	312.2	156.1	1.04	0.392	0.19
M. bahamensis	11	2	20154.5	10077.3	0.61	0.569	0.57
M. toxiferum	11	2	78.3	39.2	1.00	0.410	0.20
C. erectus	12	2	1958476.7	979238.4	1.94	0.199	0.30
G. discolor	11	2	22315.6	11157.8	2.68	0.129	0.40
C. uvifera	10		---	---	3.60 (H)	0.166	---
R. septentrionalis	12		---	---	1.94 (H)	0.380	---
M. phyllanthoides	12		---	---	7.86 (H)	0.020	---

Figure 2.5. Continued.

Source	N[a]	df	SS	MS	F or H [b]	P	R^2
Mangrove wetland							
R. mangle	12	2	21898.4	10949.2	0.55	0.597	0.11
A. germinans	12	2	82480.3	41240.2	1.02	0.400	0.18
L. racemosa	12	2	128.5	64.2	1.49	0.276	0.25
C. erectus	12	2	---	---	3.06 (H)	0.217	---

[a] N is the number of islands in the analysis (see Methods for explanation).

[b] F statistic is for ANOVA and H statistic is for Kruskall-Wallace tests

Table 2.6. Split-plot ANOVA results for the difference (between Aug 01and Jan 03) in abundance of plant species in exclosures and open plots (Treatment) in hardwood hammock on No Name.

Source	df	SS	MS	F	P
All species					
Treatment	1,4	27.3	54.2	0.22	0.661
Species	21,84	4702.6	223.9	5.99	<0.001
Treatment x species	21,84	3139.0	37.4	1.65	0.057
Preferred species only [a]					
Treatment	1,4	64.5	64.5	8.20	0.046
Species	4,16	55.5	13.9	1.97	0.147
Treatment x species	4,16	21.1	5.3	0.75	0.572
Nonpreferred species only [b]					
Treatment	1,4	340.0	340.0	10.78	0.030
Species	4,16	3669.0	917.3	16.30	<0.001
Treatment x species	4,16	890.5	222.6	3.96	0.020

[a] Preferred species: *B. simaruba, M. royoc, P. guadalupense,R. aculeata,* and *G. discolor,*

[b] Nonpreferred spp: *C. diversifolia*, *P. piscipula, E. axillaris, E. foetida, and R. septentrionalis*

Table 2.7. Repeated-measures ANOVA results for leaves remaining (counted every day over 21 days) for each nursery plant species between deer density treatments in hammock and mangrove.

		Hammock												Mangrove					
Source	df	*B. simaruba*			*P. keyense*			*R. aculeata*			*C. diversifolia*			*R. mangle*			*A. germinans*		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Between subjects																			
Treatment	2	33760.9	123.9	0.001	8245.9	7.2	0.071	58083.8	23.2	0.041	4.5	6.1	0.141	4142.5	22.7	0.015	122.3	11.3	0.040
Error	3	272.5			1141.9			2505.3			0.7			182.8			10.8		
Within Subjects																			
Time	9	489.2	14.9	<0.001	153.2	4.2	0.002	476.4	5.7	0.001	0.0	0.6	0.819	73.6	16.8	<0.001	4.4	45.9	<0.001
Time x treatment	18	447.1	13.6	<0.001	153.2	4.2	<0.001	1737.7	20.9	<0.001	0.1	2.7	0.270	73.6	16.8	<0.001	4.4	45.9	<0.001
Error	27	32.9			36.4			83.2			0.0			4.4			0.1		

Table 2.8. Repeated-measures ANOVA results for mean percent leaves eaten for nursery plant species[a] on the high deer density islands. Data were arcsine-transformed.

Source	df	SS	MS	F	P
Between Subjects					
Species	5	15.92	3.18	12.46	0.004
Error	6	1.53	0.26		
Within Subjects					
Time	9	5.03	0.56	79.52	<0.001
Time x species	45	12.19	0.05	6.93	0.002
Error	54	0.38	0.01		

[a] plant species: *B. simaruba, P. keyense, R. aculeata, C. diversifolia, R. mangle*, and *A. germinans*

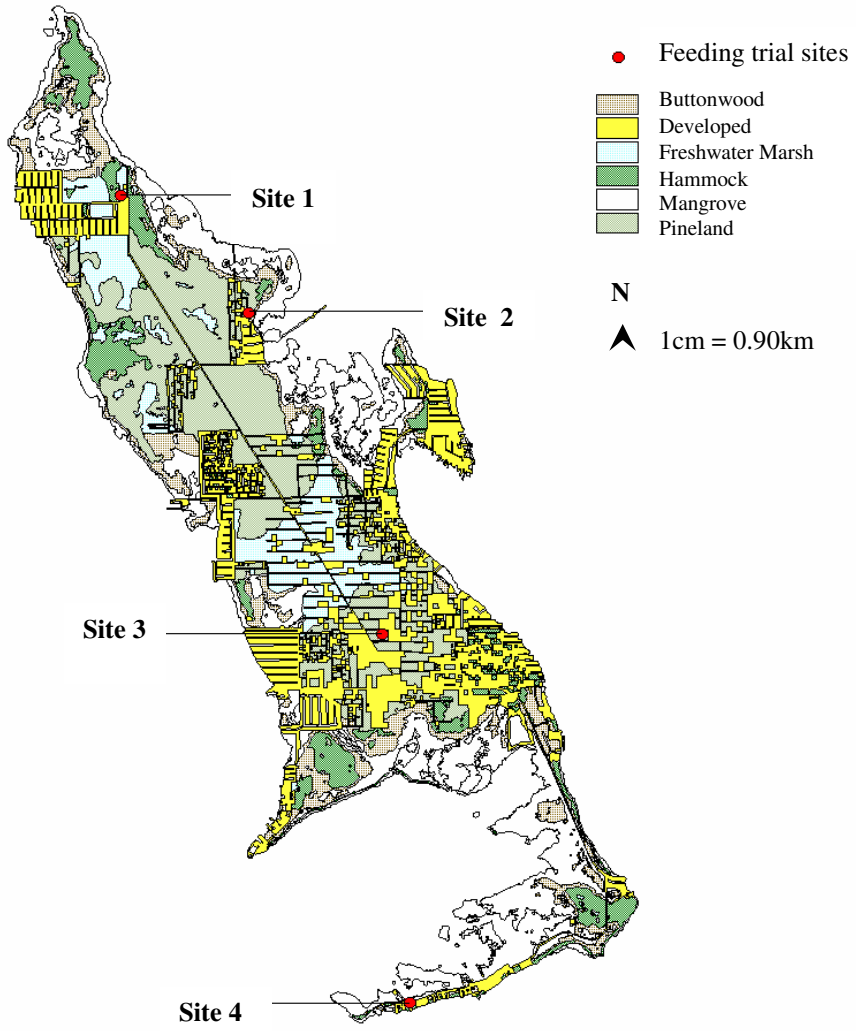

Figure 2.2. Cafeteria feeding trial sites on Big Pine Key.

Figure 2.3. Feeding station used in cafeteria feeding trials on Big Pine Key.

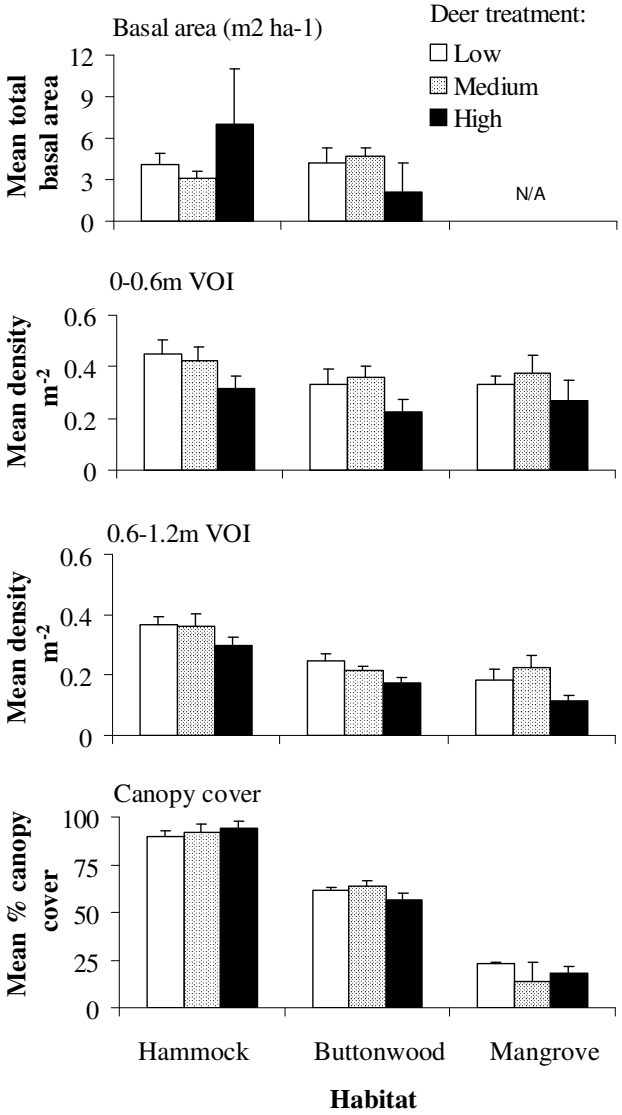

Figure 2.4. Island characteristics (mean ± 1SE) for deer density treatments and habitats. Characteristics include total basal area (all tree species >12.7cm dbh), vertical plant density (VOI) from 0-0.6m and 0.6-1.2m height, and percent canopy cover.

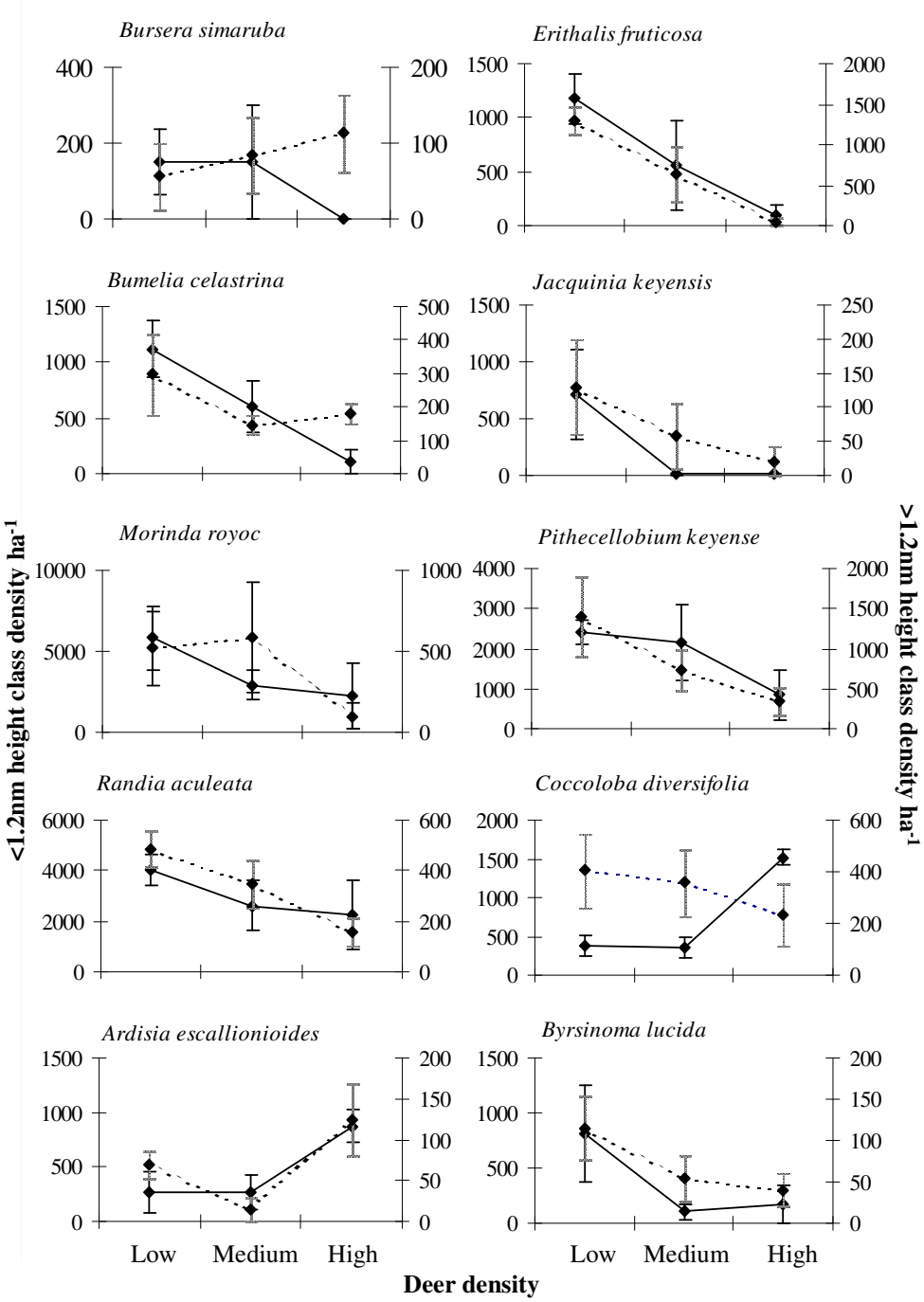

Figure 2.5. Mean plant species densities (± 1SE) in hardwood hammock among deer density treatments. Plant species are categorized in <1.2m (solid lines) and >1.2m (dashed lines) height classes. Right ordinate is <1.2m class and left ordinate is >1.2m class.

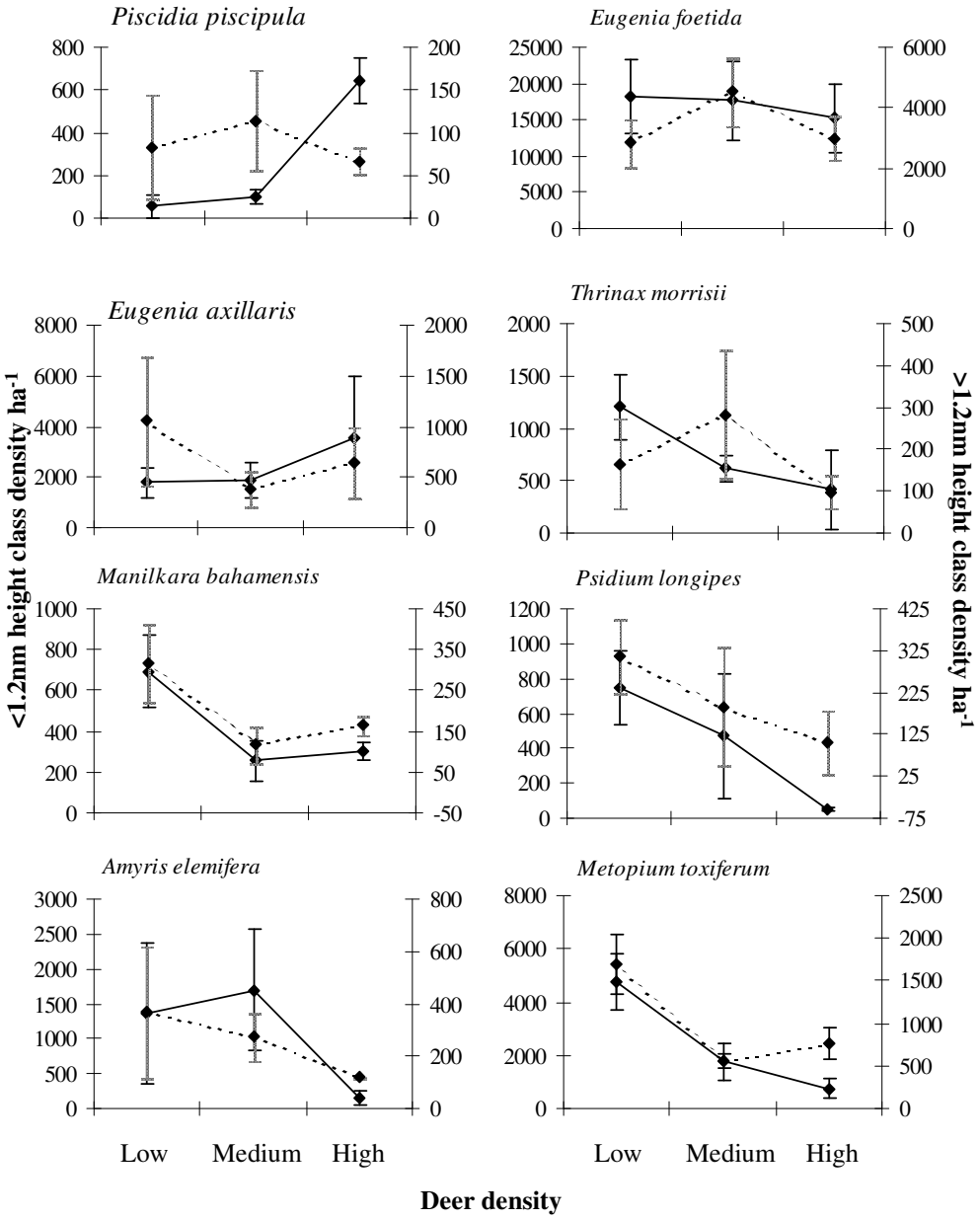

Figure 2.5. Continued.

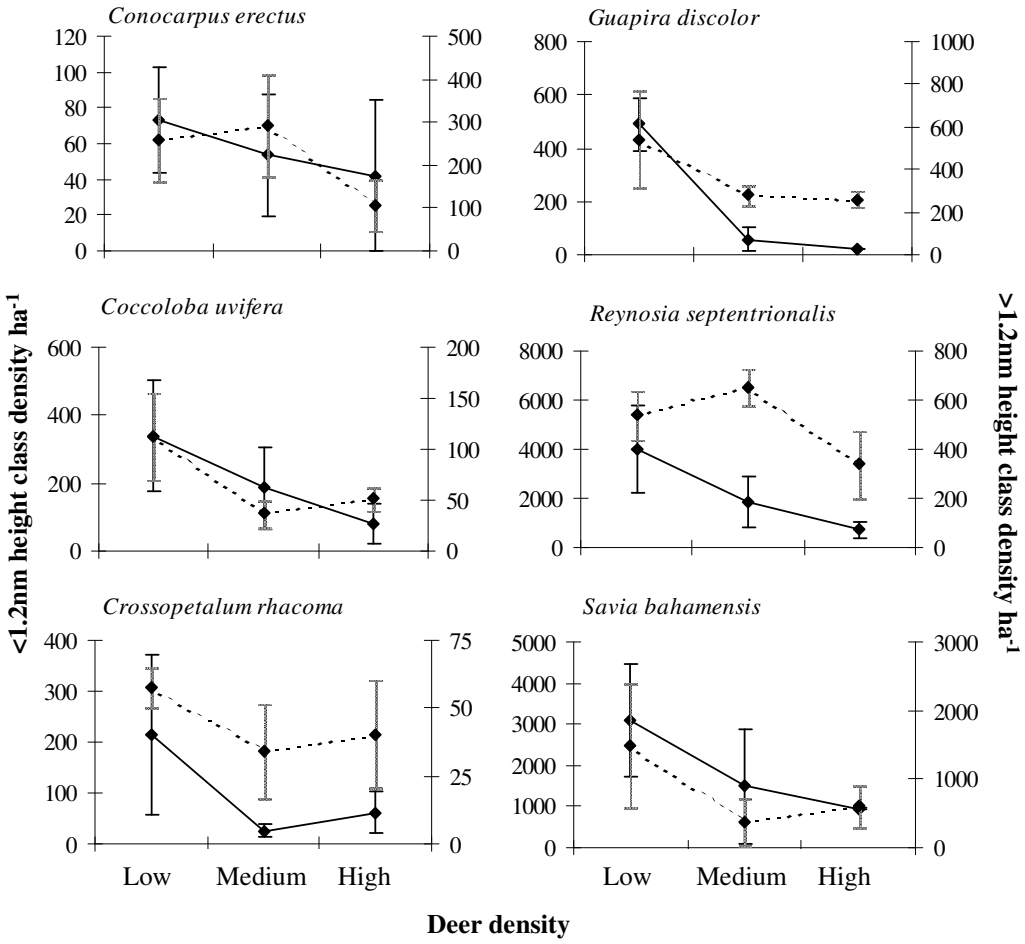

Figure 2.5. Continued.

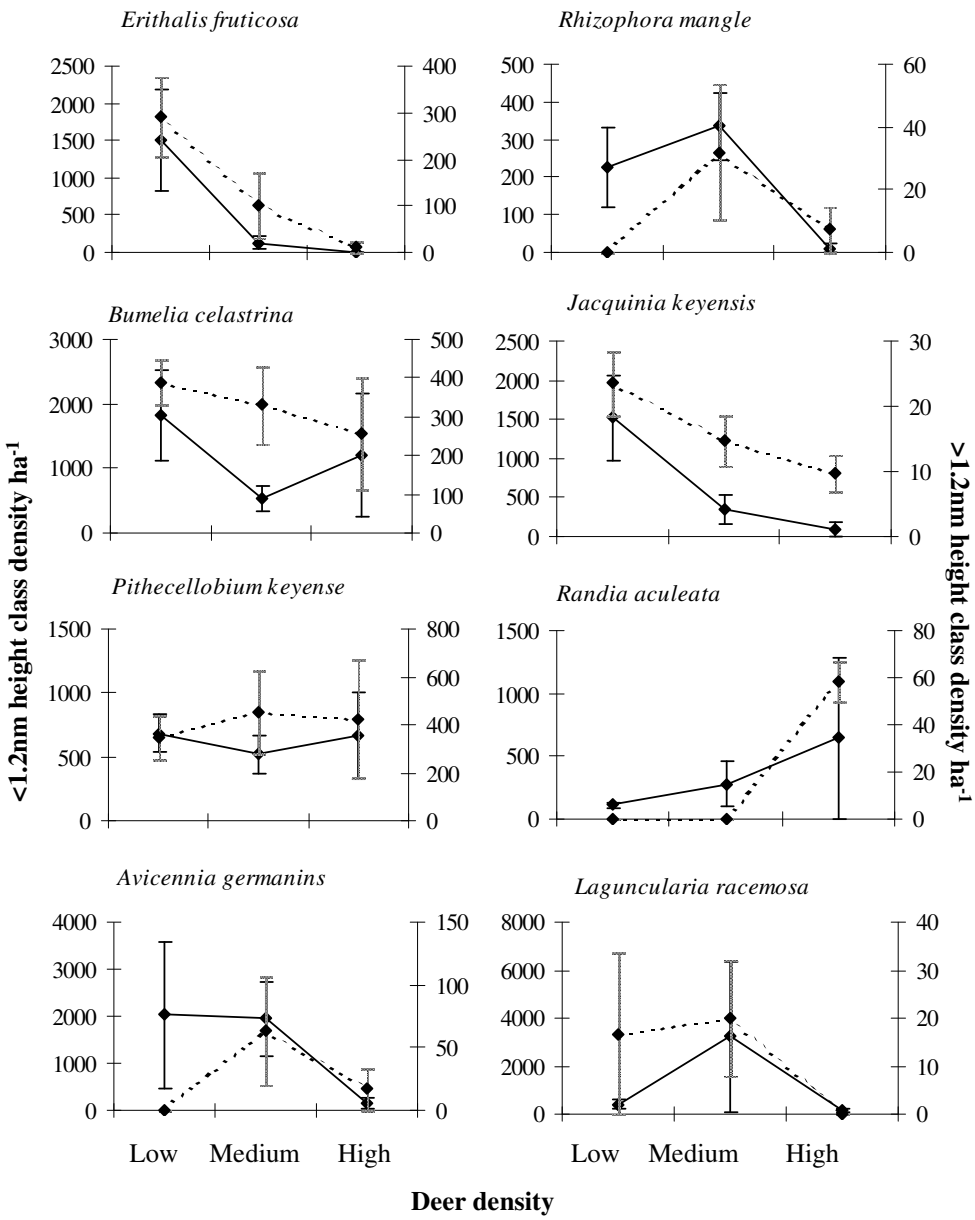

Figure 2.6. Mean plant species densities (± 1SE) in buttonwood transition among deer density treatments. Plant species are categorized in <1.2m (solid lines) and >1.2m (dashed lines) height classes. Right ordinate is <1.2m class and left ordinate is >1.2m class.

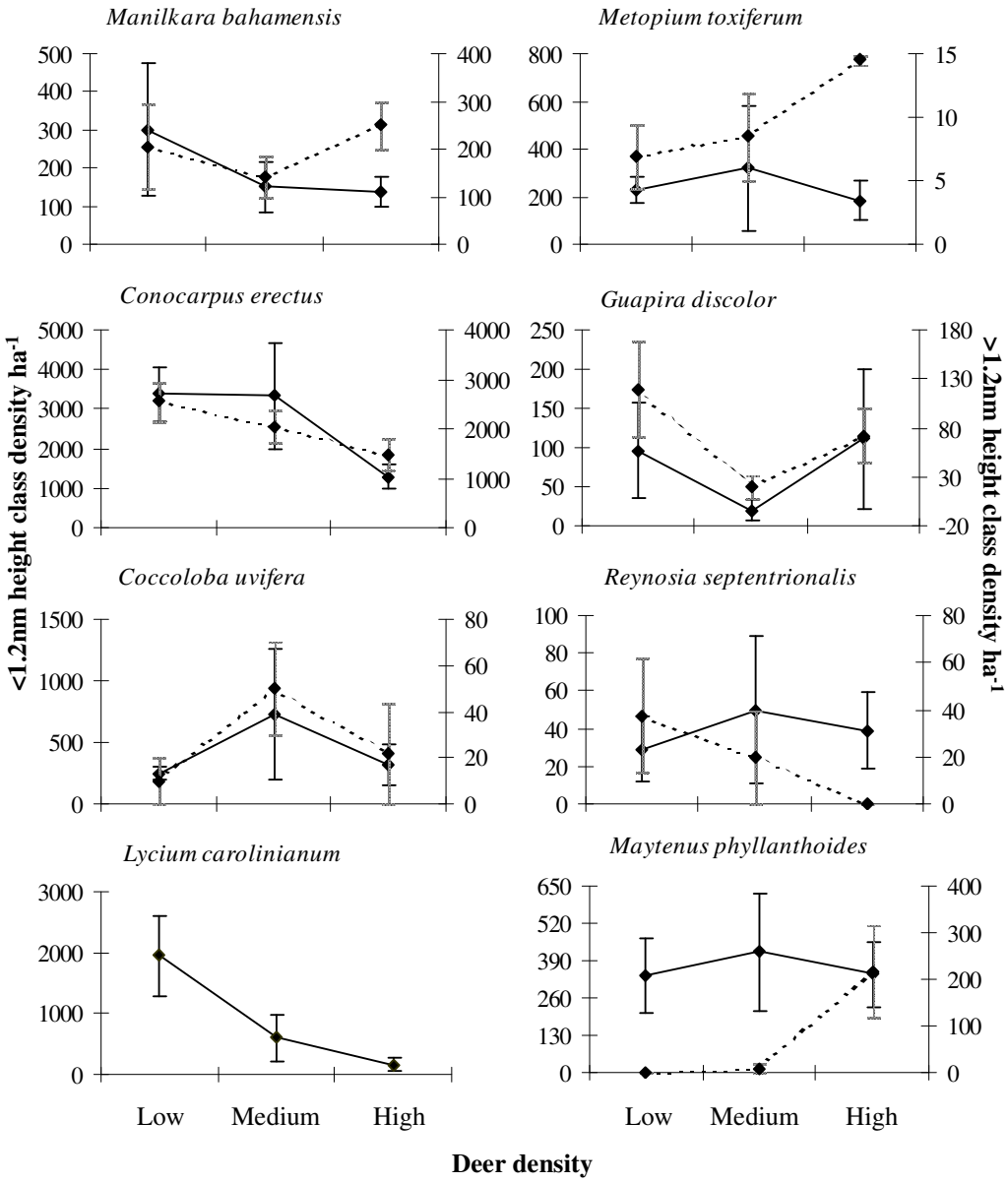

Figure 2.6. Continued

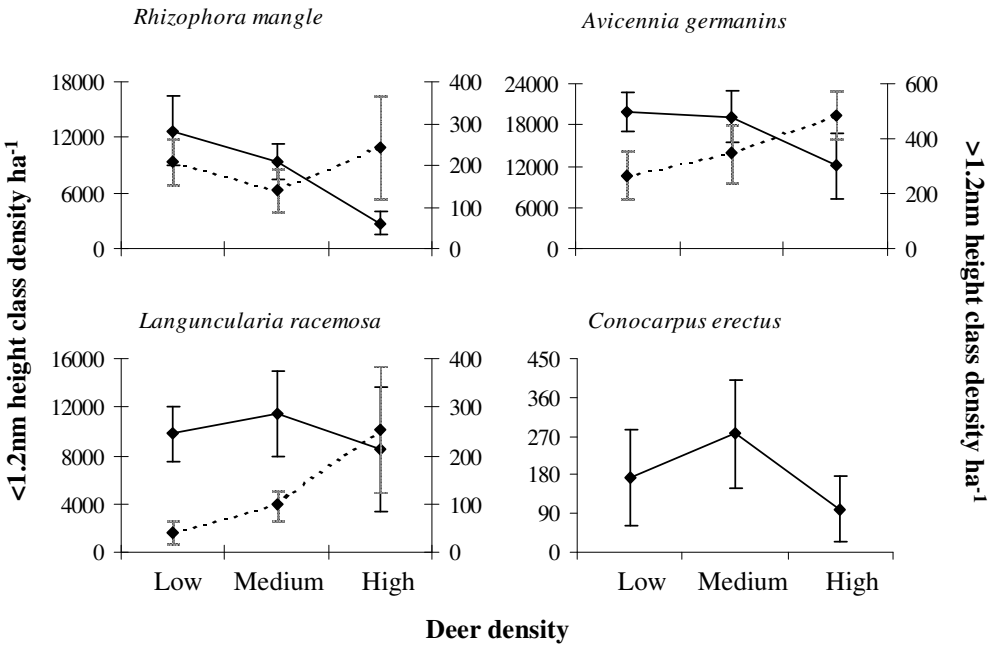

Figure 2.7. Mean plant species densities (± 1SE) in mangrove among deer density treatments. Plant species are categorized in <1.2m (solid lines) and >1.2m (dashed lines) height classes. Right ordinate is <1.2m class and left ordinate is >1.2m class.

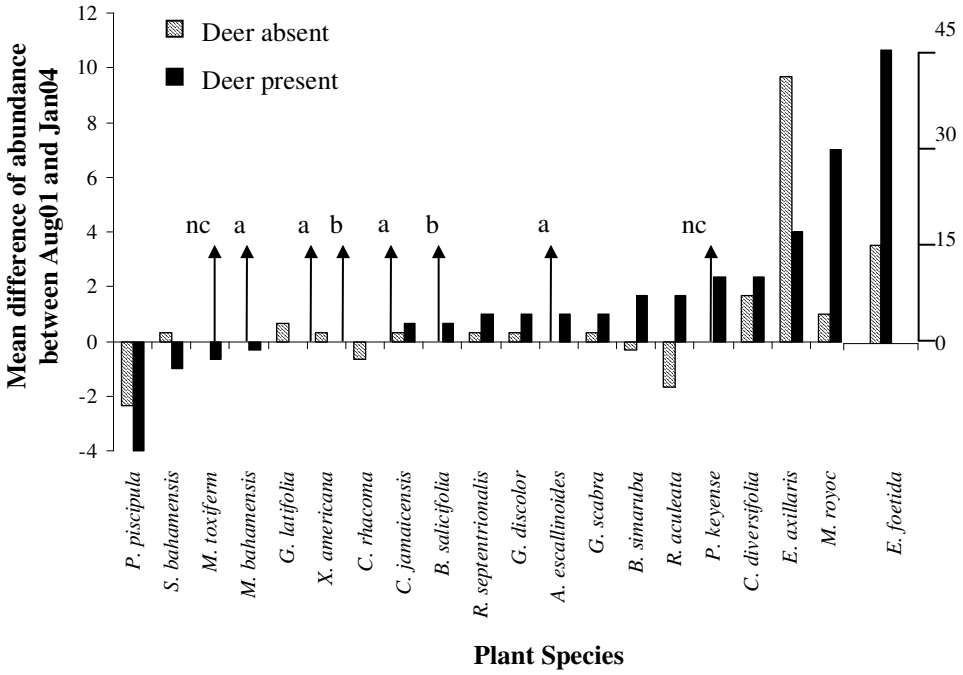

Figure 2.8. Mean difference (between Aug 2001 and Jan 2004) of plant species abundance in exclosures (deer absent) and corresponding open plots (deer present). For visual clarification, the far right abscissa is for *E. foetida* only since it has a much higher abundance. Note: a = species absent from plot, nc = species is present but no change occurred, b = new species appeared. Also, *T. morissii* and *C. argentata* (not shown) are present in both treatment plots but no change in abundance occurred with either

Errata

Figure 2.8. Mean difference (between Aug 2001 and Jan 2004) of plant species abundance in exclosures (deer absent) and corresponding open plots (deer present). For visual clarification, the far right abscissa is for *E. foetida* only since it has a much higher abundance. Note: a = species absent from plot, nc = species is present but no change occurred, b = new species appeared. Also, *T. morissii* and *C. argentata* (not shown) are present in both treatment plots but no change in abundance occurred with either

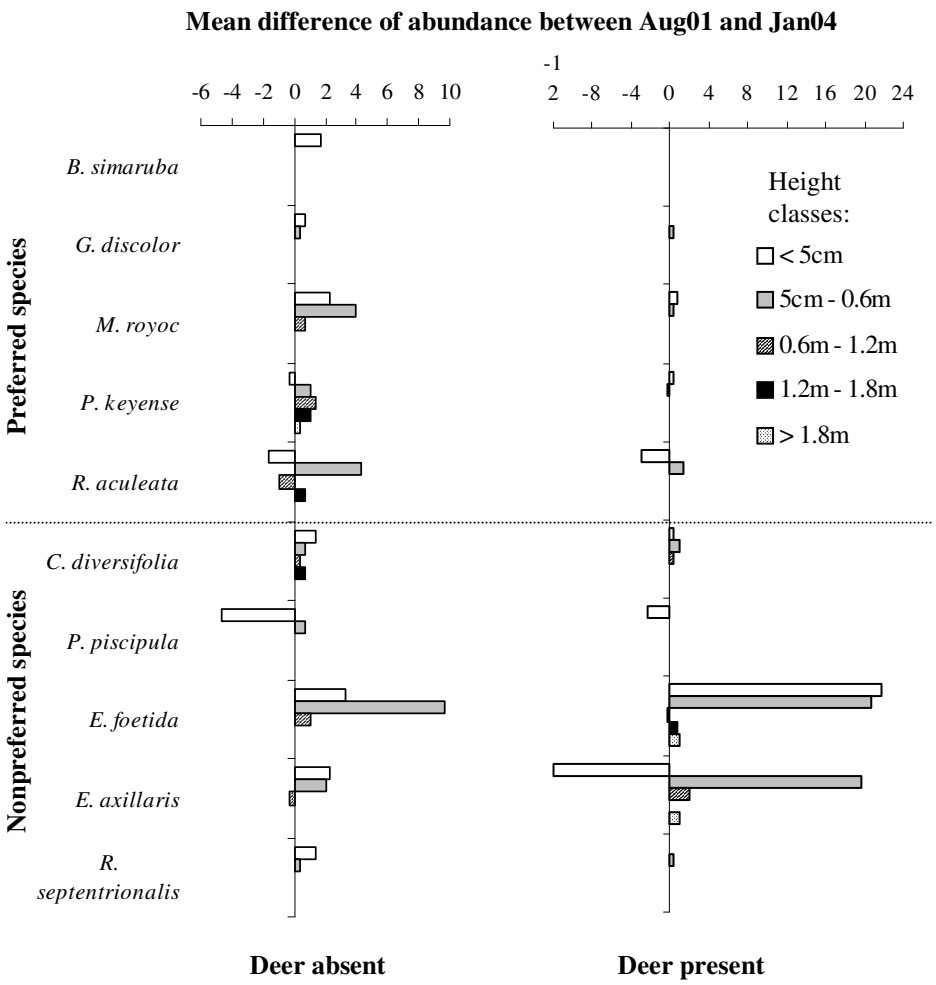

Figure 2.9. Mean difference in abundance between Aug 01 and Jan 04 of preferred and nonpreferred plant species per height class in exclosures (Deer absent) and open plots (Deer present). Note that some species decreasing in one height class may be due to them growing into the next height class , a technicality due to comparing differences between years. For example, *E.axillaris* appears to have lost many individuals in the <5cm class though many of them mainly moved into the 5cm-1.2m height class, which has increased substantially.

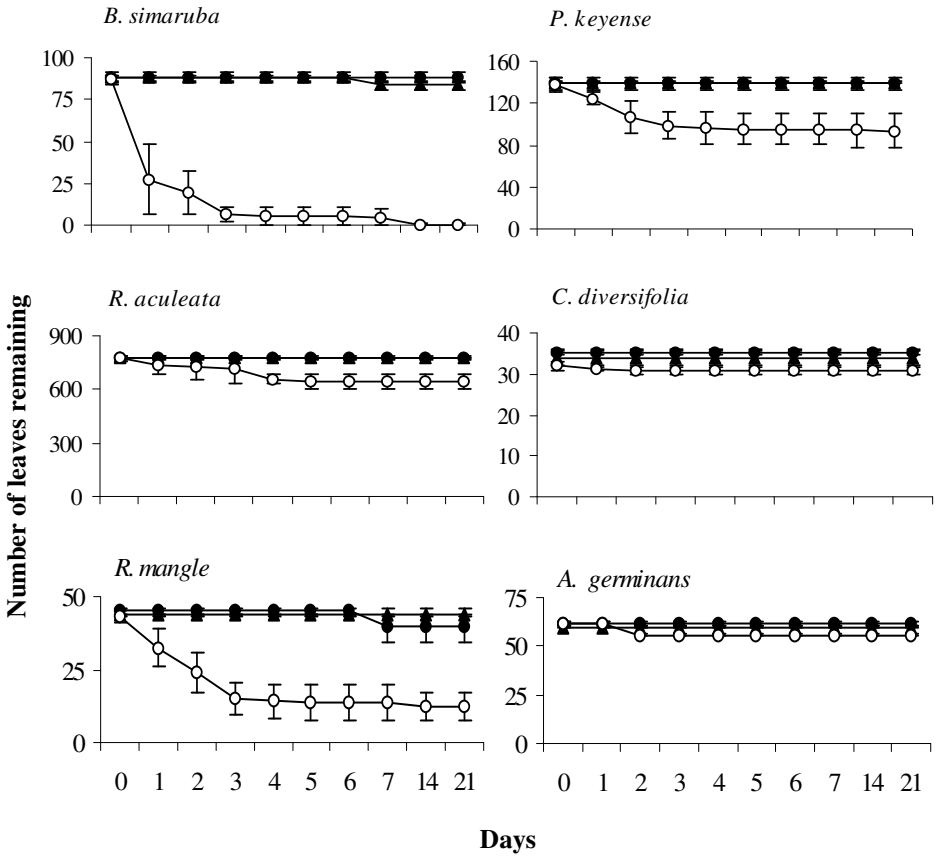

Figure 2.10. Consumption rates for potted plant species. Potted plants were placed on islands of low deer (closed circles), medium deer (closed triangles), and high deer (open circles) densities and the number of leaves remaining were counted over a 21 day period. The top four species above were placed in hardwood hammock and the bottom two species were placed in mangrove habitats. Note that days order 1-7 (1st week), then 14 (2nd week), and 21 (3rd week).

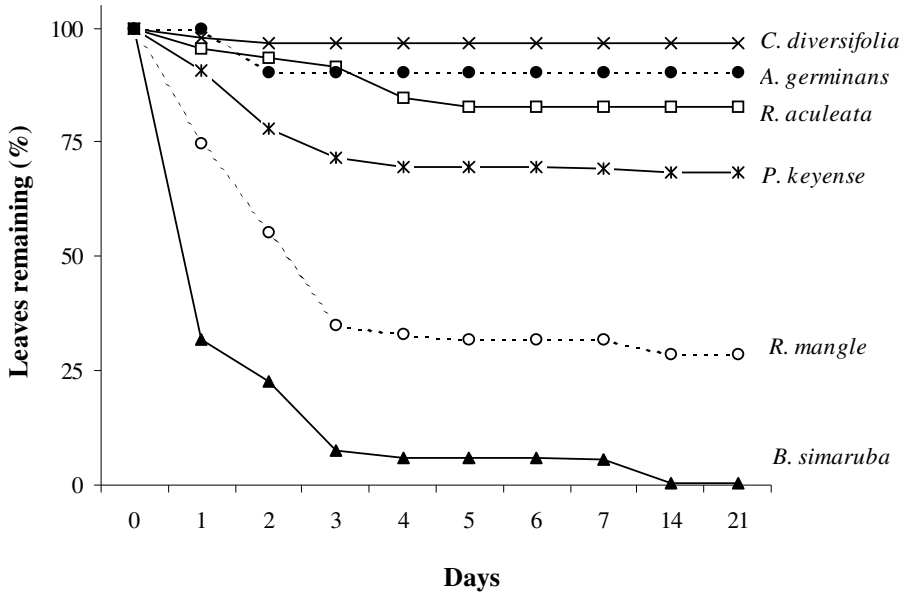

Figure 2.11. The mean percent of leaves remaining per potted plant species on islands of high deer density. Solid lines represent plant species from hammock and dotted lines are species from mangrove habitat.

Discussion

Key deer browsing is negatively affecting highly preferred plant species densities and (indirectly) positively affecting nonpreferred plant species densities suggesting that Key deer are strongly influencing plant community composition on Big Pine, No Name, and Big Munson Keys. The very low densities of seedlings and saplings of *B. simaruba*, *E. fruticosa, R. mangle, B. celsastrina*, *J. keyense,* and *G. discolor* threatens their regeneration by leaving few replacements for senescing or wind-thrown trees on these three islands. High consumption rates on nursery plants of highly preferred plant species indicate that any natural recruitment of these species will be inhibited. Medium deer density islands also had low densities of some preferred species <1.2m high in various habitats, such as *E. fruticosa, J. keyensis*, and *G. discolor*. This is not unusual as some browse-intolerant plant species may respond in a nonlinear fashion and considerably decline in abundance from even moderate browsing pressure (Nugent et al. 2001). Yet, for most plant species, a relatively substantial amount of adult trees still remain on each island indicating that impacts of heavy browsing on plant species regeneration may not become apparent for many years. Yet, preferred plant species that have grown above the browse-tier may provide minor supplemental nutrition while they persist. For example, though many tree species in the lower Keys self-prune lower branches causing browse to be out of Key deer reach (Alexander and Dickson 1970), Key deer may still consume leaf litter as found in other deer studies (McInnes et al. 1992; Takahashi and Kaji 2001; Harrison 2003). In urban areas, Key deer were observed eating fallen leaves and fruits from ornamental trees, such as *Hibiscus rosa-sinensis*, *Ficus elastica*, and other species (personal observation), and may consume litter from native tree species as well.

On islands with many deer, hammock habitat appears most affected by Key deer browsing, probably due to greater plant diversity (Monroe County Growth Management Division 1992), higher productivity (Ross et al. 2003) and substantial use (Lopez 2001). Key deer herbivory is negatively affecting highly preferred plant species densities in buttonwood transition and mangrove wetlands as well. Browsing impacts may not be as strong in buttonwood transition, however, which is notably influenced by tidal inundation and associated factors (Klimstra et al. 1990; Ross et al. 1992) that may cause irregularity in plant distribution and composition (Dickson 1955; Folk 1992). Contrarily, in mangrove wetlands,

reductions in *R. mangle* density on high deer density islands can have substantial negative community effects. *Rhizophora mangle* is a stabilizing species for marginal and coastal areas (Davis 1940), and anecdotal evidence suggests it may be a pioneer species for upland habitats in south Florida (Alexander 1955). Moreover, mangroves are the main primary food source for many secondary consumers (Rodriguez 1987) and may serve as an extensive energy base for food webs in coastal Florida (Odum and Heald 1971). Thus, heavy Key deer browsing could result in localized trophic cascades on islands with many Key deer. Also, regeneration pathways of *R. mangle* communities could become destabilized following extensive deer herbivory. For example, *Rhizophora* usually have very high densities of seedlings (advanced recruits) that, in turn, can survive hurricanes and replace adults that were damaged or killed (Baldwin et al. 2001). *Rhizophora mangle* trees lost to hurricanes will not be efficiently replaced if Key deer browsing depletes seedling resources because epicormic regrowth is not a common regeneration mechanism of *R. mangle* (Baldwin et al. 2001). This has serious implications for islands with high deer densities as most islands in the Keys are preserved by *R. mangle,* which is already considered a species of special concern in the Keys due to habitat loss from human development.

Effects of Key deer browsing were only severe on about 7 out of 40 (~18%) woody species observed in this study, some of which were anticipated while others were not. For example, *E. foetida* is highly preferred by *O. virginianus* in nearby Cuba (Martinez et al. 2001), yet is avoided by Key deer. *Bursera simaruba* is moderately preferred by *O. virginianus* in Cuba (Martinez et al. 2001), but has never been documented as a Key deer food, though it experienced the highest levels of herbivory. Possibly, previously low relative densities of *B. simaruba*, relatively low Key deer densities, digestive factors, and/or recent diet switching (Webster and Parker 2000) may explain the species absence from rumen samples in the 1970s (Dooley 1975). Key deer were not deterred by the spinescent *B. celastrina*, though spines may be used for mechanical defense against mammalian herbivores (e.g. Takada et al. 2003; Young et al. 2003). The low densities of *J. keyensis*, *G. discolor*, and *E. fruticosa* on high deer treatment islands were not unexpected since they were considerably browsed by Key deer in the early 1970s (Klimstra et al. 1974), when deer numbers were relatively lower. However, moderately preferred species *P. keyense, M. royoc* and *R. aculeata* were noticeably browsed in the past (Klimstra et al. 1974), but their extant densities were

unaffected by high deer densities. Yet, deer may not notably browse less preferred species until preferred species become scarce (Westoby 1974; Nugent et al. 2001) or these moderately preferred species might be browse tolerant given that *M. royoc* (though it still decreased outside exclosures) is a very weedy species and may recover quickly from browsing pressure. Also, moderately preferred plant species might experience much higher variation in herbivory levels (Diaz 2000; Forsyth et al. 2003), which could make deer browsing effects undetectable.

Certain nonpreferred plant species showed a positive relationship with high deer density. Though the nonpreferred *P. piscipula* decreased inside and outside exclosures (microsite), both *P. piscipula* and *C. diversifolia* (nonpreferred species) were at significantly higher densities on islands with many deer (macrosite), which may indicate a competitive release from declining browse-intolerant species. Shifts in plant species composition toward less-browsed species can be a common occurrence following heavy deer herbivory (Dyksterhuis 1949; Tilghman 1989; Seagle and Liang 1997; Augustine and McNaughton 1998; Cornett et al. 2000; Horsley et al. 2003), which could lead to alternate stable states in plant communities (Stromayer and Warren 1997), or hinder heavily browsed species from establishing, even after release from browsing pressure, because environmental conditions are no longer favorable (Stromayer and Warren 1997). Unfavorable conditions could be slowing the growth of the highly preferred *B. simaruba* inside the deer exclosures, or herbivory pressures from other local species could be present. However, insect damage is very infrequent on *B. simaruba* (personal observation), the marsh rabbit is generally not found near the exclosure sites or in uplands (Faulhaber 2003), and consumption of *B. simaruba* by the introduced *Iguana iguana* is dubious. It appears that amelioration of Key deer browsing pressure may allow highly susceptible plant species to reestablish and grow above the browse-tier, albeit over a long time frame for *B. simaruba*.

Relatively high local densities (exceeding 15 deer km^{-2}) of the federally endangered Key deer on No Name, Big Pine, and Big Munson keys have several possible ramifications on natural communities. Browsing effects on plant species composition and structure could decrease the availability of nutritional forage leading deer to malnutrition and disease (Davidson and Doster 1997), indirectly affect other species (e.g. birds, MacArthur and MacArthur 1971), change Key deer behavior (e.g. use of vegetative cover for

parturition sites, Silvy 1975), and namely affect forest species regeneration (e.g Leopold et al. 1947; Alverson et al. 1988; Tilghman 1989; Veblen et al. 1989; Waller and Alverson 1997; Rooney 2001; Russel et al. 2001; Schabel 2001; Vourc'h et al. 2001; Zamora et al. 2001). The present study provides important implications for conservation biology in that relative densities of endangered species must be accounted for to deter them from attaining 'destructive' densities. Nonetheless, preferred adult tree species remain relatively abundant, and Key deer have only recently reached relatively high densities on certain islands (Lopez 2001), thus extensive browsing effects on plant communities may be at incipient stages on islands with high densities of Key deer, allowing time for management actions.

CHAPTER 3

LONG-TERM CHANGES IN PLANT COMMUNITIES INFLUENCED BY KEY DEER HERBIVORY

Synopsis

The aim of the present study was to estimate changes in plant species composition in several habitat types that might be influenced by changes in Key deer (*Odocoileus virginianus clavium*) densities over a decade in the National Key Deer Refuge (NKDR) in the lower Florida Keys. Baseline vegetation data from a 1990 study were compared to vegetation data in 2002 (the present study) in buttonwood, hammock, and mangrove habitats on 12 islands with Key deer density categories of low, medium, and high. On islands with high Key deer densities, the relative densities of preferred plant species <1.2m tall significantly decreased over time, while nonpreferred species <1.2m tall significantly increased in all habitat types. Few noticeable changes were observed in the relative densities of plant species <1.2m tall on islands with low and medium Key deer densities. Relative densities of preferred plant species >1.2m tall (midstory/canopy) also decreased in hammock habitat on islands with high Key deer densities suggesting that heavy browsing is stunting plant growth and could effect long-term regeneration of certain plant species. Plant species richness did not vary between 1990 and 2002 for islands with high deer densities, but tended to increase slightly on islands with low deer densities. Although other factors could affect plant communities over time (e.g. succession, anthropogenic factors, etc.), evidence from this study suggests that impacts from relatively high Key deer densities are a strong causal factor influencing plant species composition.

Introduction

It can take many years or even decades before the wide-ranging effects of intensive deer herbivory appear in forest communities. Long-lived canopy species that grow above the browse-tier can survive high deer density levels for extensive periods, barring other factors. Consequently, browsing effects may not wholly unfold until regeneration takes place in canopy composition (Frelich and Lorimer 1985). Monitoring long-term changes in the understory of plant communities, however, should expedite observable responses that can be directly related to deer browsing pressures. Unfortunately, effectual baseline vegetation data is lacking in many natural areas, so few long-term studies on deer herbivory have been done (e.g. Hough 1965; Whitney 1984; Van Deelen et al. 1996; Rooney et al. 2004).

The present study explored the long-term effects of deer herbivory on plant community structure in the lower Florida Keys within the range of the federally endangered Key deer (*Odocoileus virginianus clavium*). Historically, habitat loss and over-hunting lowered Key deer numbers resulting in their enlistment as an endangered species in 1967 and their protection under the Endangered Species Act in 1973 (USFWS 1999). The establishment of the National Key Deer Refuge (NKDR) in 1957, and active management by the United States Fish and Wildlife Service (USFWS), permitted an increase in the Key deer population from approximately 25-80 animals in the 1950s (Dickson 1955) to 350-400 by the 1990s (Klimstra 1990) and over 500-700 animals by 2000 (Lopez 2001). A lack of natural predators helps sustain the higher Key deer numbers, although automobile collisions are a major mortality factor (Lopez 2001). Although Key deer abundance has increased, a skewed distribution developed with over two-thirds of the population predominately residing on two islands, Big Pine Key and No Name Key (Folk 1992; Lopez 2001). To maintain long-term survival and genetic diversity of an endangered species, much impetus is placed on increasing their absolute population size. However, if this action results in high relative densities of the protected species, especially a large herbivore like Key deer, it could be detrimental to other components of the ecosystem, particularly local plant species.

The increase in Key deer densities was expected to affect plant species composition in the understory (plants <1.2m tall) and perhaps the midstory/canopy plant species composition (plants >1.2m tall), especially on islands where Key deer densities have been relatively high compared to other islands.

Key deer are selective browsers (Dooley 1975); therefore, preferred plant species were expected to decrease over time, while nonpreferred species increase on islands with many deer, a pattern commonly observed in deer herbivory studies (e.g. Hough 1965; Tilghman 1989; Van Deelen et al. 1996; Augustine and McNaughton 1998; Cornett et al. 2000; Horsley et al. 2003; but see Belsky 1985). Also, plant species richness was expected to decrease with increasing Key deer densities. Because Key deer utilize a variety of habitats to varying degrees (Klimstra et al. 1974; Folk 1992; Lopez 2001), and their diet includes over 160 plant species that range from lowlands to uplands (Klimstra and Dooley 1990), effects of Key deer herbivory on plant species were anticipated for all sampled habitat types on islands with increasingly high densities of deer.

Study Area

The study was conducted in the lower Florida Keys within the boundaries (24° 36´ N – 81° 18´ W to 81° 34´ W) of the National Key Deer Refuge (NKDR). The climate is subtropical with evident wet (~May-October) and dry (~November-April) seasons. In the lower Keys, the mean annual temperature is ~ 25.2°C and mean annual rainfall is ~ 100cm. Soils vary from blue-grey 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 1955).

A number of islands within the NKDR contain several habitat types from lowlands to uplands and from saline to freshwater environments. Most plant species are adapted to relatively xeric conditions due to rapid runoff of rainfall (Dooley 1975). Vegetation is primarily of West Indian origin (Stern and Brizicky 1957) and subsequent plant nomenclature followed Scurlock (1987).

[See Chapter 1 for full descriptions of the islands, habitats, Key deer characteristics, etc.]

Methods

Study islands

Although the Key deer range includes around 26 islands, many are transiently used, mainly during the wet season (Folk 1992; Lopez 2001). Accordingly, 12 frequently used islands were selected for study

representing a Key deer density gradient: low (Sugarloaf, Cudjoe, Summerland, Ramrod), medium (Little Torch, Middle Torch, Big Torch, Howe, Little Pine), and high (Big Pine, No Name, Big Munson) (see Figure 2.1). For the 12 islands, baseline vegetation data was available from the early 1990s (Folk 1992) in hammock, buttonwood and mangrove habitats. Pineland was not included here due to confounding effects of fire history (see Chapter 5 for pineland). Beach dune hammock, cactus hammock and buttonwood prairie were also not included because they are only found on certain islands.

Key deer density estimates

Deer densities were estimated by various methods for each sampling period. Folk (1992) used deer pellet counts, track counts, and sightings (census) to provide a quantitative index [in Klimstra (1990)] consisting of a range of deer abundance per island from which the midpoint was used to calculate deer density per island in the present study. Lopez used infrared-triggered cameras placed near water holes and other frequently used areas to estimate Key deer numbers on most islands (R.R. Lopez unpublished data), except on Big Pine and No Name keys where census and radio-telemetry were used to estimate deer densities (Lopez 2001). Deer estimates from Folk and Lopez were conservatively converted to densities (deer/km^2) by dividing the estimated number of deer by island size km^2 (Table 3.1).

Vegetation sampling

To evaluate impacts of herbivory as the Key deer herd increased, vegetation sampled from April 1988 through April 1990 (Folk 1992) was compared to vegetation sampled from January to May 2001and 2002 in the present study. Throughout the text, sampling dates will be referred to as 1990 and 2002, respectively. Densities (ha^{-1}) of woody plant species were estimated using nested quadrats in the 1990 study, which employed 1 x 30.5m quadrats for buttonwood and mangrove, and used 1 x 15.3m quadrats for hammock. The 2002 study used 1 x 50m quadrats for all habitats. Woody seedlings less than 30.5cm tall were sampled in 1m^2 quadrats nested in the larger quadrat in the 1990 study, while the 2002 study quantified woody seedlings in the entire larger quadrat. The 1990 and 2002 studies used the same number of larger quadrats per habitat/island; the total quadrats (n) of all 12 islands combined were: hammock = 85,

buttonwood = 36, and mangrove = 72. Densities of woody plant species were summarized to a <1.2m height class (within Key deer reach) and a >1.2m height class. The former height class was used to estimate changes in understory vegetation that can be directly related to browsing effects, while the latter height class was used to examine any changes in midstory/canopy plant species composition that may have occurred over the last 12 years due to deer herbivory (i.e. lack of regeneration or plant growth).

Quadrats from the 1990 were located on aerial photographs (91.4 cm x 91.4 cm) stored at the NKDR. Using available digital maps of the lower Florida Keys (MacAulay et al. 1994), quadrats from 1990 were digitized to Global Information System (GIS) via ArcView 3.2 and were projected to latitude-longitude. In the field, a handheld Garmin 45™ GPS (Global Positioning System) was used to locate the quadrat sites from 1990, and the 2002 quadrats were laid out in the same directional heading as the 1990 study. If quadrats from 1990 were positioned in recently disturbed areas in 2002, they were relocated to similar habitat in another area of the island to keep sample sizes equal, though this happened infrequently (n = 6).

Because Key deer are selective browsers, woody plant species were dichotomized into preference categories: preferred and nonpreferred. The preferred category consisted of plant species that: 1) Key deer commonly browsed throughout a given year (Klimstra and Dooley 1990), 2) other researchers previously noted as highly browsed (Klimstra et al. 1974), 3) ranked high in cafeteria feeding trials (Chapter 2), or 4) were in the top 28 plant species (75% of the total volume) out of >164 species found in Key deer rumen samples (Dooley 1975). Examples of preferred woody species were *B. simaruba, E. fruticosa, R. mangle, B. celastrina, J. keyensis, G. discolor, P. keyense,* and *R. aculeata.* Nonpreferred species are those that ranked low in feeding trials and/or ranked below the top 28 species in rumen analyses. Categorization was dubious for a few plant species, which were excluded from analyses, as they might erroneously influence results. For example, discrepancies occurred in preference ratings between Dooley (1975) and feeding trials (Chapter 2) for two species, *A. germinans* and *B. lucida,* most likely because plant species ranking in rumen sample analysis was mainly based on proportions of seed or fruit materials consumed for these two species, whereas feeding trials measured proportions of foliage consumed. Furthermore, Key deer

primarily utilized the fruits of some palm species, e.g. *T. morrissii* and *C. argentata*, and the effects of fruit consumption on plant species recruitment were unknown due to untested mechanisms, such as endozoochory.

Data Analysis

Differences in quadrat sizes among studies could influence the results. Therefore, using a method similar to Rooney et al. (2004), plant species richness was passively sampled, which balanced sampling effort by equilibrating vegetation quadrat area between studies. The passive sampling technique employed followed the formula (Gotelli and Graves 1996):

$$E(S_j) = \sum_{i=1}^{S} 1 - (1 - a_j / A_T) n_i$$

where

a_j	=	area of the *j*th subsample (i.e. the smaller quadrat)
A_T	=	area of the larger sample (i.e. the larger quadrat)
N_i	=	abundance of species *i* per island
$E(S_j)$	=	the expected number of species in the subsample

Plant species richness from the 2002 passive subsample was compared to the species richness from 1990 data using a paired *t*-test for islands within deer density treatments (low, medium, or high). Furthermore, for each island, similarity of plant species composition between sampling dates (1990 and 2002) was measured with Jaccard index (C_j).

Many plant samples from the 1990 study were taken during the wet season, causing plant samples to be saturated with seedlings; also, sampling effort (quadrat size) differed between studies, both of which could affect absolute plant densities. This was problematic when testing for temporal effects of herbivory, as the sampling effects could not be factored out effectively. Therefore, relative densities (rather than absolute densities) of plant species were statistically evaluated. Relative density per sampling period per habitat was calculated as: species density / $\sum$ all species densities. The relative densities of plant species – dichotomized by preferred and nonpreferred species - were compared between 1990 and 2002 for each deer density category (low, medium, high) and tested for significance using replicated G-tests (Sokal and Rohlf

1969). Tests determined any differences between relative plant densities for each deer preference category for individual sites (islands) and sites pooled per deer density category. Heterogeneity tested if shifts in direction and/or magnitude of relative plant densities were equal among sites within each deer density category (Sokal and Rohlf 1969).

Results

Deer effects on plant species richness

For woody plant species, no trends in species richness between 1990 and 2002 (passive samples) were evident for high or medium deer density islands in any habitat (Table 3.2; Figure 3.1). Woody species richness tended to increase slightly in hammock and buttonwood habitats on low deer density islands (Table 3.2; Figure 3.1). However, Jaccard similarity indices were relatively low averaging from 50% - 62% for buttonwood and hammock habitats for each deer density category. This was due to losses/gains of plant species in plant samples on each island regardless of deer density. Jaccard similarity indices for mangrove habitat were all > 95% on all islands. This was not surprising due to the limited number of halophytic woody plant species present in or acclimated to mangrove wetlands.

Deer effects on relative plant densities

Differences in the relative densities of preferred and nonpreferred woody plant species were observed between 1990 and 2002 for islands grouped by deer densities (low, medium, high) (Figure 3.2). For plant species <1.2m tall on high deer density islands, the relative densities of preferred species significantly declined by 10%, 10%, and 25% in buttonwood, hammock, and mangrove habitats respectively, while nonpreferred species significantly increased by 18% and 28% in hammock and mangrove habitats respectively (Table 3.3; Figure 3.2) suggesting that increasing Key deer densities influenced plant composition. For plant species <1.2m tall on low deer density islands, relative densities of preferred species increased by < 6% in all habitats and nonpreferred species decreased by 12% and 5% in buttonwood and hammock habitats respectively, but increased by 5% in mangrove habitat (Figure 3.2), though none of the trends were significant (Table 3.3). For plant species <1.2m tall on medium deer

density islands, relative densities of preferred species significantly increased in buttonwood habitat (Table 3.3; Figure 3.2) while relative densities of nonpreferred plant species remained relatively unchanged between years.

For plant species > 1.2 tall on high deer density islands, relative densities of preferred species significantly declined by 6% in hammock habitat (Table 3.4; Figure 3.2) suggesting that growth and or/ density of preferred plant species is being impeded by increased deer browsing pressure. No significant trends were detected for preferred or nonpreferred plant species in buttonwood or hammock habitats for low or medium deer density islands. Preferred species >1.2m tall significantly declined by 30% on high deer density islands and by 36% on medium deer density islands in mangrove habitat (Figure 3.2). However, the magnitude and direction of relative densities per island differed between years within each deer density treatment indicated by a significant heterogeneity effect (Table 3.4); thus results for mangrove species >1.2m tall might be spurious and should be viewed with caution.

Table 3.1. Key deer densities on 12 islands of frequent deer use in 1990 and 2002. Key deer densities were calculated by dividing the number of deer estimated by island size.

Island Name	Island size km^2	Key deer km^{-2}	
		1990	2002
Big Pine Key	25.03	7.39	17.74
No Name Key	4.91	13.75	21.59
Big Munson Key	0.48	36.46	31.25
Big Torch Key	6.32	0.63	7.91
Howe Key	3.92	3.19	3.83
Middle Torch Key	3.44	1.89	7.27
Little Torch Key	3.35	0.45	4.48
Little Pine Key	3.17	2.05	4.73
Cudjoe Key	14.35	0.21	0.35
Sugarloaf Key	8.06	0.50	0.62
Summerland Key	4.75	0.21	0.42
Ramrod Key	4.33	0.12	0.46
Estimated population size		300-400	500-700

Table 3.2. Paired t-test results for woody plant species richness between 1990 and 2002 for deer density treatments (high, medium, low) in each habitat.

Deer density	df	*t*	P
Hammock			
High	2	0.479	0.679
Medium	4	0.518	0.532
Low	3	3.267	0.047
Buttonwood			
High	2	0.231	0.839
Medium	4	0.863	0.437
Low	3	3.16	0.051
Mangrove			
High	2	3.742	0.065
Medium	4	1.849	0.138
Low	3	1.623	0.203

Table 3.3. Replicated G-tests for relative densities of woody plant species <1.2m tall. Separate tests compared relative densities of preferred (Pref) or nonpreferred (Nonpref) plant species between 1990 and 2002 by deer density island groups.

Deer density	Test	df	*G* Pref	Nonpref
Buttonwood				
High	pooled	1	5.47 *	0.39
	heterogeneity	2	4.12	1.07
	total	3	9.59 *	1.47
Medium	pooled	1	7.50 *	0.64
	heterogeneity	4	45.88 *	3.31
	total	5	53.38 *	3.95
Low	pooled	1	1.98	4.91
	heterogeneity	3	6.15	10.26 *
	total	4	8.13	15.18 *
Hammock				
High	pooled	1	6.14 *	6.31 *
	heterogeneity	2	0.49	0.96
	total	3	8.63 *	7.93 *
Medium	pooled	1	0.43	51.52 *
	heterogeneity	4	3.00	6.21
	total	5	3.43	57.73 *
Low	pooled	1	2.54	0.62
	heterogeneity	3	3.40	2.56
	total	4	5.95	3.18
Mangrove				
High	pooled	1	11.65 *	27.30 *
	heterogeneity	2	3.71	5.89
	total	3	15.36 *	33.29 *
Medium	pooled	1	3.25	2.08
	heterogeneity	4	6.74	12.09 *
	total	5	10.00	14.17 *
Low	pooled	1	0.55	1.79
	heterogeneity	3	8.14 *	1.29
	total	4	8.69	3.08

* Asterisks indicate significance (P <0.05).

Table 3.4. Replicated G-tests for relative densities of woody plant species >1.2m tall. Separate tests compared relative densities of preferred (Pref) or nonpreferred (Nonpref) plant species between 1990 and 2002 by deer density island groups.

Deer density	Test	df	*G* Pref	*G* Nonpref
Buttonwood				
High	pooled	1	0.01	0.21
	heterogeneity	2	0.49	0.42
	total	3	0.50	0.62
Medium	pooled	1	0.01	0.02
	heterogeneity	4	3.62	3.04
	total	5	3.63	3.05
Low	pooled	1	0.02	0.40
	heterogeneity	3	3.10	1.69
	total	4	3.12	2.10
Hammock				
High	pooled	1	4.81 *	0.20
	heterogeneity	2	0.73	0.02
	total	3	5.54	0.22
Medium	pooled	1	0.02	0.98
	heterogeneity	4	0.94	0.67
	total	5	0.96	1.65
Low	pooled	1	0.70	0.23
	heterogeneity	3	0.84	0.23
	total	4	1.54	0.46
Mangrove				
High	pooled	1	27.72 *	25.81 *
	heterogeneity	2	23.31 *	1.38
	total	3	51.03 *	27.19 *
Medium	pooled	1	63.32 *	0.07
	heterogeneity	4	32.32 *	56.04 *
	total	5	95.64 *	56.11 *
Low	pooled	1	4.06 *	0.45
	heterogeneity	3	54.06 *	7.84 *
	total	4	58.13 *	8.28

* Asterisks indicate significance ($P < 0.05$).

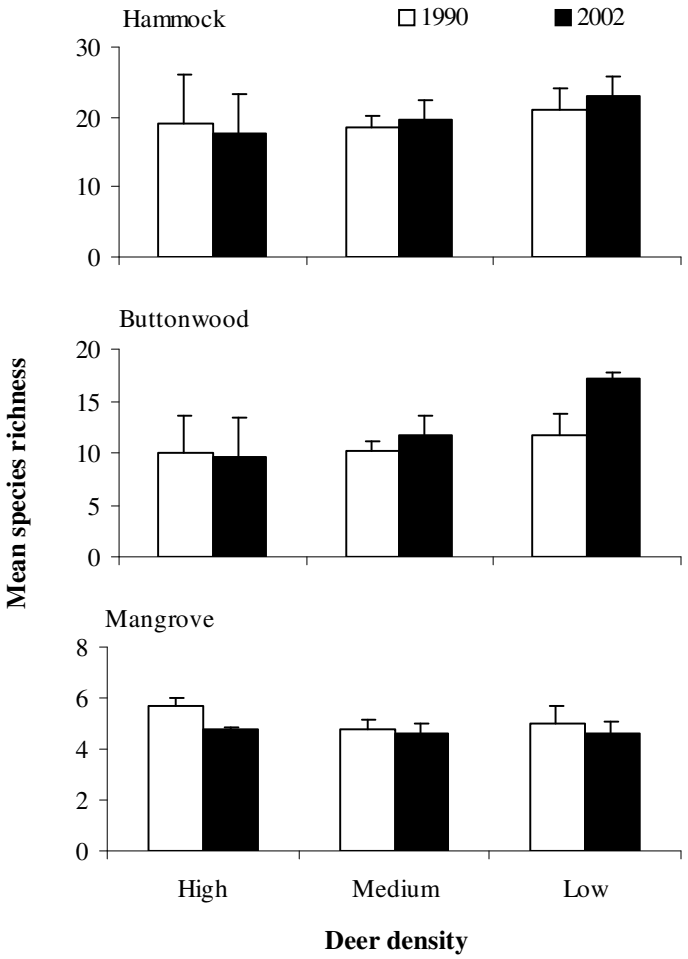

Figure 3.1. Woody plant species richness per Key deer density (high, medium, low) and habitat for 1990 and 2002. Species richness data from 2002 was passively sampled from a larger sampl area (see Methods for a complete explanation).

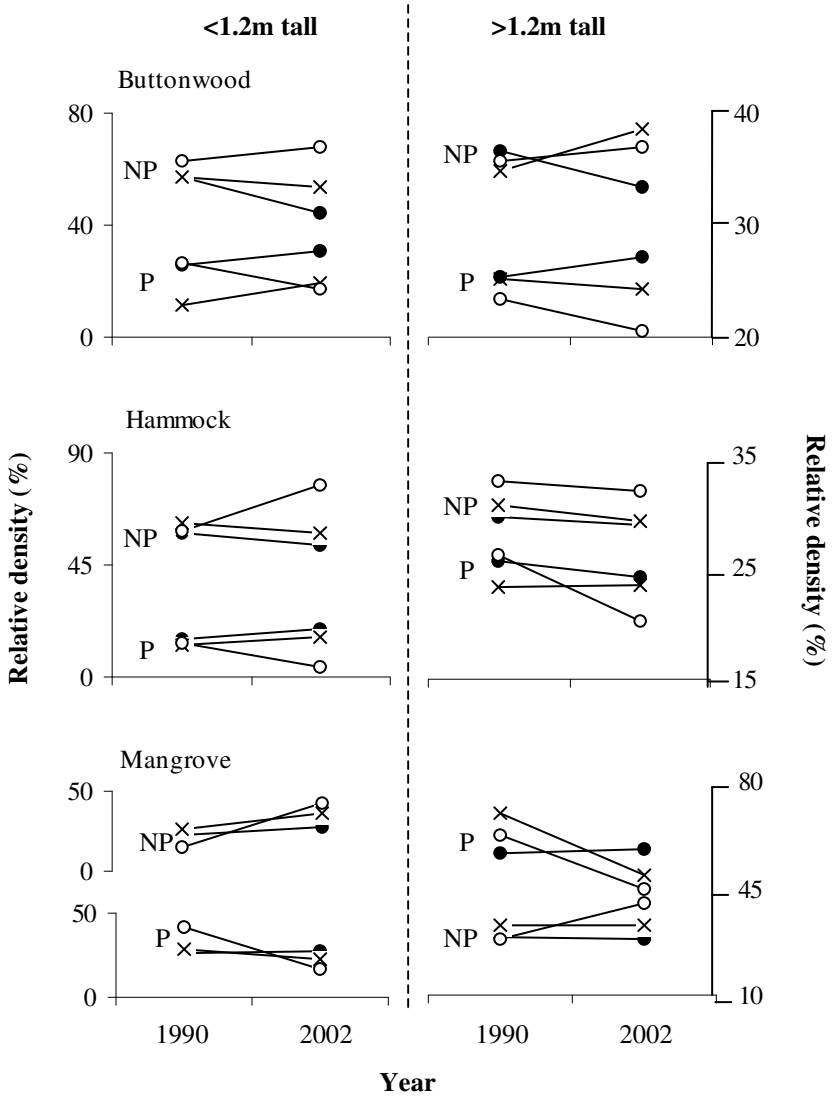

Figure 3.2. Relative densities of woody plant species in 1990 and 2002. Treatments are low (●), medium (×), and high (○) Key deer densities. Plant species are dichotomized by nonpreferred (NP) and preferred (P) categories and height classes (<1.2m tall and >1.2m tall).

Discussion

Though compositional shifts in plant species were observed to some extent on all 12 study islands, there appears to be low impacts of increased browsing pressure on low and medium Key deer density islands. Contrarily, the relative densities of preferred and nonpreferred plant species <1.2m tall within all habitat types were negatively and positively associated, respectively, with increasing Key deer densities on Big Pine, No Name, and Big Munson Keys where Key deer densities have remained relatively high during 1990 and 2002 compared to other islands. Preferred plant species >1.2m tall exhibited a decreasing trend on high deer density islands as well. This indicates that in a relatively short time period (approximately 12 years) heavy Key deer herbivory can impede the growth or diminish the densities of certain plant species enough to influence midstory (and possibly canopy) composition, which could limit regeneration and eventually lead to local extinctions of affected species. Most negative browsing impacts on high deer density keys were apparent for preferred plant species <1.2m tall (e.g. *B. simaruba*, *G. discolor, J. keyensis*, and *B. celastr*ina) that had initially low relative densities in 1990 samples. Trends in the data indicate that the magnitude of Key deer impacts may be dependent on initial plant densities (of preferred species), as found elsewhere in deer herbivory studies (Rooney and Dress 1997; Augustine et al. 1998). If deer densities are very high (e.g. > 30 Key deer/km^2 on Big Munson), however, substantial declines - and ultimate local extinctions - of preferred plant species will occur regardless of initial plant densities.

Woody plant species richness appeared unaffected by high deer densities, which contrasts with findings from other studies regarding diversity and deer herbivory (e.g. Balgooyen and Waller 1995; Rooney and Dress 1997; Horsley et al. 2003). Because preferred and nonpreferred plant species exhibit counteracting responses to deer herbivory, indicator species (mainly highly preferred plant species) provide more valuable information for browsing effects (e.g. Balgooyen and Waller 1995) than measures of diversity (i.e. species richness).

Besides direct browsing effects on declines in preferred plant densities, other indirect effects of deer herbivory likely contribute to the process (Rooney and Waller 2003). For example, on high Key deer density islands the colonization and expansion by some nonpreferred woody species, such as the broad-leaved species *P. piscipula* (Chapter 2), and dominance of the nonpreferred species *Eugenia foetida* and *E.*

axillaries (Appendix 1) in the understory of hammock communities could deter the establishment of preferred plant species via interspecific competition and decreased microsite availability. Yet, in spite of increasing Key deer densities, forest interiors have not exhibited increases in either exotic plant or fern species as observed in other deer herbivory studies (e.g. Rooney and Dress 1997; Stromayer and Warren 1997; Rooney et al. 2004). Likely active management of exotics on public lands deterred any indirect benefits from deer effects.

Ample evidence from the present study shows that shifts in relative densities of preferred and nonpreferred plant species in forest communities are associated with relatively high increases in Key deer densities on Big Pine, No Name, and Big Munson keys. Yet, shifts in plant species composition among the islands cannot be attributed solely to Key deer browsing. Anthropogenic factors can have strong negative effects on forest composition (Drayton and Primack 1996; McCollin et al. 2000). Large areas of habitat were lost to development within the NKDR that directly affected plant communities; also development resulted in indirect effects on plant communities from increases in local Key deer densities as a function of available useable space (Lopez 2001) and/or a function of urbanization (Folk and Klimstra 1990; Chapter 4). Therefore, islands with both high deer densities and urban sprawl (e.g. Big pine) have a high risk of losing plant species at an accelerated rate (Stromayer and Warren 1997).

Management implications

Comparing plant density samples from different seasons (wet/dry) may cause changes in plant composition to be more apparent than real. For, example, sampling during the wet season could overestimate potential plant availability for Key deer in that tree and shrub seedling densities are saturated but ephemeral and may die off before deer can utilize them, also making it difficult to disentangle browsing effects. A larger quadrat size (1 x 50m) provided a more adequate sample of plant species than smaller quadrats. The $50m^2$ quadrat size should be used in future studies so less common plant species will not be under-sampled. Limiting urban expansion on islands already heavily developed (e.g. Big Pine) and practicing sustainable development (or no further development) on other islands in the NKDR is recommended to decrease habitat loss and discourage unmanageable increases in local Key deer densities and subsequent browsing

pressure. Monitoring of vegetation among islands frequented by Key deer should continue, and critical objectives of evaluating habitat condition (e.g. high plant diversity vs. availability of food plant species for Key deer) should be developed.

CHAPTER 4

KEY DEER IMPACTS ON HARDWOOD HAMMOCK HABITAT ADJACENT TO URBAN AREAS

Synopsis

In the National Key Deer Refuge, Key deer (*Odocoileus virginianus clavium*) aggregation has become prevalent in urban areas on islands with relatively high deer densities, such as Big Pine and No Name Keys. As a result, browsing impacts might affect plant species communities in habitats adjacent to urban areas of high Key deer use more than habitats distant from urban areas. To test this hypothesis, vegetation structure (e.g. all woody species combined <1.2 m tall, diversity, and preferred species only <1.2m tall) from hardwood hammock habitats adjacent to and distant from urban areas was compared on islands of high (> 18 deer/ km^2) and low (< 1 deer/ km^2) Key deer densities. No differences between hammocks adjacent to or distant from urban areas for total plant densities or diversity were observed on either low or high deer density islands. On low deer density islands, analyses of the densities of woody preferred plant species <1.2m tall showed no trends between hammock habitats adjacent to and distant from urban areas. On islands with high deer densities, however, hammock habitats adjacent to urban areas had lower densities of woody preferred plant species <1.2m tall compared to hammock habitats distant from urban areas. Even though preferred woody plant species are already depleted on islands with high deer densities, urbanization appears to increase negative impacts on these species via increased browsing pressure. Favored ornamentals and human handouts stimulate Key deer to aggregate in urban locales. These stimuli should be controlled and further development stemmed to prevent negative changes in Key deer feeding behaviors, and to prevent degradation of rare hardwood hammock habitats.

Introduction

Large mammalian herbivores, such as deer, usually move between habitats to forage (Bowers 1997), and a patchy food distribution may influence deer to develop close social units by gathering in areas with greater resources (Peterle 1975). Urban areas usually provide supplementary resources for deer (e.g. ornamentals, hand-outs, plant cuttings, etc.) thus encouraging deer to aggregate in or near urban environments. Urbanization has altered the social behavior (e.g. aggregation) of the endangered Florida Key deer (*Odocoileus virginianus clavium*) (Folk and Klimstra 1991), which could modify their feeding behavior as well.

Key deer exhibit solitary habits and weak family bonds (Hardin et al. 1976). Utilization of several habitat types (Dickson 1955; Silvy 1975; Klimstra and Dooley 1990; Folk 1992; Lopez 2001), ample food sources (Klimstra and Dooley 1990) and a lack of natural predators should discourage large Key deer group sizes. From 1968-73, Hardin et al. (1976) found that observations of single Key deer were very common while groups of six or more deer were extremely rare and were considered 'random associations' on Big Pine Key – a relatively high deer density island –when Key deer (300-400) and human populations (~800) were relatively low. In contrast, after large-scale conversion of lands to subdivisions created an urban mosaic on Big Pine in the 1980s, mean group size per observation period in residential areas during 1989-1990 was about six Key deer, with maximum group sizes of up to 21 deer (Folk and Klimstra 1991) though the Key deer population was still around 300-400 animals (Klimstra 1990). The drastic change in Key deer group sizes in urban areas was likely due to resultant uplands produced from fill that provided favored browse such as ornamental plants and mowed clearings (Kilmstra and Dooley 1990), and from human handouts (food and water) causing Key deer to aggregate in the locality (Folk and Klimstra 1991; Folk 1992; USFWS 1999).

Because Key deer aggregate in urban locales, natural habitats adjacent to urban areas could be more susceptible to browsing impacts from a 'spill-over' effect. Indeed, browse lines were evident in native vegetation surrounding residential areas (Folk and Klimstra 1991; personal observation). Lopez (2003) found that Key deer spent more time feeding (> 50% of observations) on natural vegetation adjacent to residential areas rather than feeding on ornamentals, handouts or garbage (each between 10% - 20% of

observations). However, the amount of damage to natural vegetation in habitats adjacent to urban areas has not been quantified, which is the aim of the present study.

Browsing damage to ornamental or crop species is higher during the winter for northern white-tailed deer when natural food is scarce (Decker and Brown 1982; Conover 1984). However, the absence of harsh winters, year-round natural food availability, and Key deer dietary requirements (Dooley 1975), likely cause ornamentals and handouts to be opportunistic food sources for Key deer while native vegetation is persistently consumed (Lopez 2003), similar to findings for supplementally-fed captive white-tailed deer (Hubert et al. 1980). Therefore, it was hypothesized that natural habitats (i.e. hardwood hammock) near urban sites frequented by Key deer should experience higher browsing pressure than habitats more distant from urban areas; subsequently, the densities and diversity of plant species should decrease in habitats near urban areas. More remote habitats located farther from development - where deer aggregation is not prevalent - should have higher densities and diversity of plant species. It is important to understand any increases of Key deer browsing pressure, due to urbanization, on hardwood hammock because it is a rare habitat considered imperiled in the state of Florida (Florida Natural Areas Inventory 1990).

Study Area

The study was conducted in the lower Florida Keys within the boundaries (24° 36´ N – 81° 18´ W to 81° 34´ W) of the National Key Deer Refuge (NKDR). The climate is subtropical with evident wet (~May-October) and dry (~November-April) seasons. In the lower Keys, the mean annual temperature is ~ 25.2°C and mean annual rainfall is ~ 100cm. Soils vary from blue-grey 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 1955).

Study sites were located in hardwood hammock habitat, a climax successional community in the lower Florida Keys formed by tropical hardwood plant species that occur in uplands (Folk 1992). Hardwoods produce litter, which accumulates organic matter that can eventually develop into substantial soil. Soil acclimatizes hammock flora to mesic conditions along with a closed canopy that reduces the loss

of soil moisture and moderates thermal extremes (Monroe County Department of Planning and Zoning 1986). Common plant species include: canopy species - *Metopium toxiferum*, *Piscidia piscipula*, *Busera simaruba*; sub-canopy species - *Coccoloba diversifolia*, *Bumelia salicifolia*; small tree/shrub species – *Pithecellobium keyense*, *Eugenia spp.*, *Capparis spp.*, *Savia bahamensis*; and a sparse herbaceous layer - *Chiococca alba*, *Smilax havanensis*, and various grasses and ferns. Plant nomenclature followed Scurlock (1987).

Key deer urbanization occurs on Big Pine Key (Folk and Klimstra 1991; Folk 1992; Lopez 2003; personal observation) and to an extent on No Name Key (Folk and Klimstra 1991; Folk 1992; personal observation). Sites considered urban, where deer aggregation occurs, are mainly residential areas, except on No Name where Key deer also congregate near the main road due to human handouts and availability of herbaceous cover along the right-of-way (Folk 1992; personal observation). Although a variety of habitats may be found near urban areas, hammock habitat was chosen for study because (1) it is seldom influenced by confounding factors such as fire or tidal inundation, (2) isolated stands adjacent to and distant from urban areas are available on islands with low and high densities of deer, and (3) it is highly utilized by Key deer (USFWS 1999; Lopez 2001) thus strong browsing impacts were expected (see Chapters 2 & 3).

Methods

Four islands were sampled in the study that had either high deer densities [No Name = 22 deer/km^2 and Big Pine = 18 deer/km^2 (Lopez 2001)] or low deer densities [Cudjoe = 0.35 deer/km^2 and Sugarloaf = 0.62 deer/km^2 (R.R. Lopez unpublished data)]. The distribution (% of total island area) of hammock habitats (H) and developed areas (D) for each island were as follows: Big Pine (H = 9%, D = 24%), No Name (H = 34%, D =7%), Cudjoe (H = 8%, D = 16%), Sugarloaf (H = 19%, D= 7%) (Figures 4.1 and 4.2). Key deer distribution throughout Big Pine and No Name Keys were obtained by radio-telemetry studies where mean (± SE) annual home range size of Key deer females was 42 ± 4 ha with mean (± SE) daily movements of 302 ± 13 m (Lopez 2001). Most Key deer observations from radio-telemetry were located near urban areas. Considering Key deer home range and daily movements, vegetation was sampled on each island within hammock stands that were <500m (adjacent) and >500m (distant) from

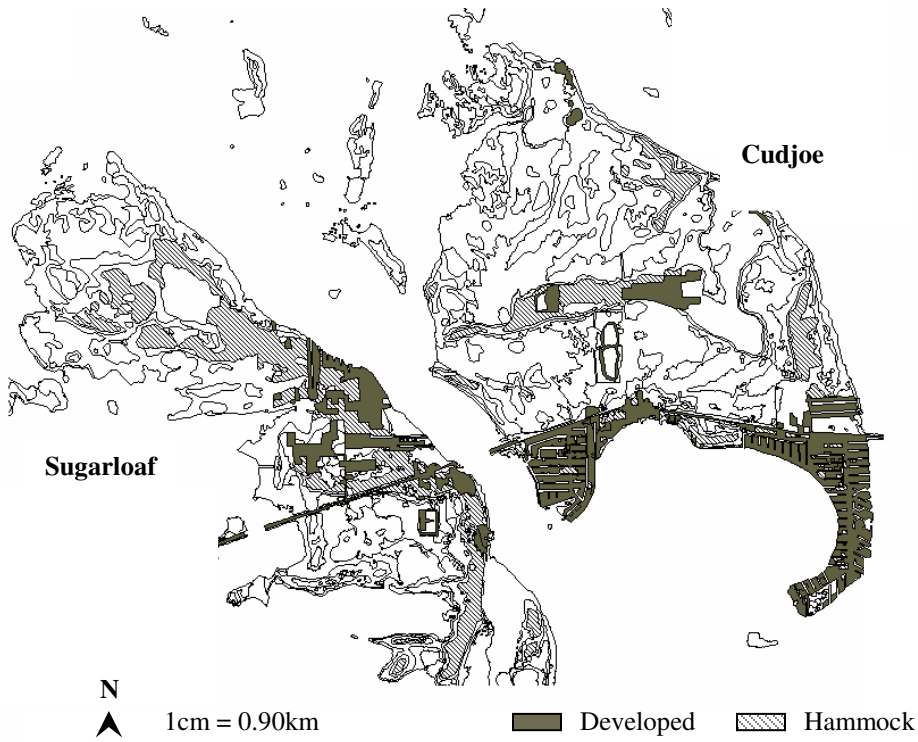

Figure 4.1. Low deer density islands (Cudjoe and Sugarloaf) indicating urban areas (solid color) and hammock habitats (hatched).

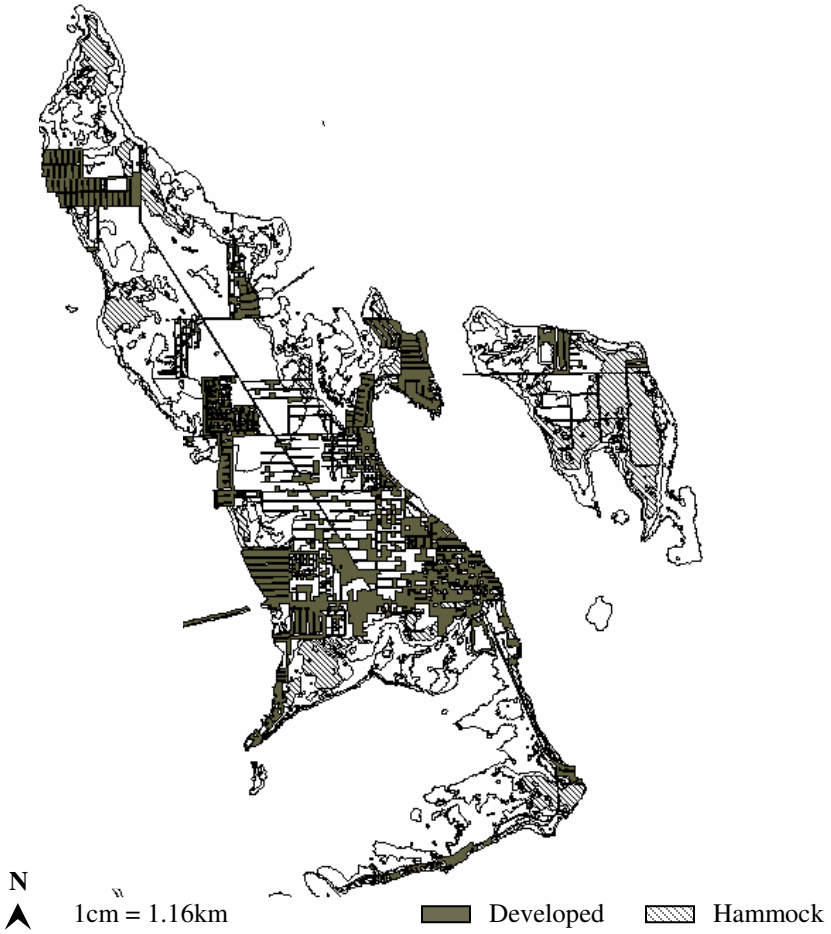

Figure 4.2. High deer density islands (Big Pine and No Name) indicating urban areas (solid color) and hammock habitats (hatched).

developed/residential areas (hereafter called urban). Using available digital habitat maps of the lower Florida Keys (MacAulay et al. 1994) in ArcView GIS 3.2, urban areas within islands were buffered by a 500m radius, and then random points (representing vegetation quadrats) were selected in hammock habitats that were within the buffer (adjacent) or outside the buffer (distant). Distances between adjacent and distant hammock stands were > 600m within each island, and vegetation quadrats for adjacent sites were at least 50m from urban areas to limit possible edge effects. Boundaries such as roads, development, and other habitats isolated many hammock stands, thus stands served as replicates (3-5 stands site^{-1} island^{-1}). If large tracts of hammock habitat were contiguous (i.e. not isolated), then groups of quadrats demarcated stands, where groups were separated by at least 250m within each site (adjacent/distant), but remained within the 500m buffers for adjacent sites.

Vegetation sampling

In hammock stands, woody plant densities (ha^{-1}) were found for each species to examine any impacts of Key deer herbivory between sites (adjacent/distant) and deer density (low/high). In the field, vegetation quadrats were located from the digitized (GIS) points using a handheld Garmin 45™ GPS (Global Positioning System). Depending on stand size, three to five quadrats were used to collect plant density data that were averaged for each hammock stand.

Vegetation sampling was conducted during the dry season from January to May of 2002 using nested quadrats. Rectangular quadrats (1 x 50m) were used to estimate densities (ha^{-1}) of woody plant species with a diameter at breast height (dbh) < 12.7cm. Plant species were assigned to two height classes: <1.2m (within Key deer reach) and >1.2m. A 10 x 50m quadrat, bisected by the 1 x 50m quadrat, was used to count large tree species with a dbh >12.7 cm from which basal area was calculated.

Plant species diversity

To see if Key deer browsing affected the plant community between sites on islands of different deer densities, plant species diversity was measured for each hammock stand for woody species. The measures of diversity used were Fisher's α and species richness. Fisher's α was chosen because it has high

discriminant ability and is not influenced by sample size (Magurran 1988). Mean woody plant densities <1.2m tall, summarized from quadrat data, were used to calculate Fisher's α. Species richness, which is influenced by sample size, was only used for qualitative comparisons and was not statistically analyzed.

Data Analysis

Statistical analyses follow protocol similar to Takada et al. (2002). First, an analysis was performed to see if deer density affected the plant community in hammock habitats by testing for differences in woody plant density (all species combined <1.2m tall) and woody plant diversity (Fisher's α). A split-plot ANOVA was used to test each variable (plant density/ α diversity) with deer density (low/high) and site (distant/adjacent) as fixed factors, and island (Big Pine, No Name, Cudjoe, Sugarloaf) nested under deer density. If the interaction term of the model was significant, then the differences in plant densities or diversity between sites would likely be explained by differences in deer density. Second, to test whether plant density (all species combined <1.2m tall) and Fisher's α differed among sites on high deer density islands, a two-way ANOVA was used for each variable with island and site as fixed factors. The same analysis (i.e. two-way ANOVA) was then performed for the two variables for islands of low deer density. Because many woody plant species in hammock habitat may not be affected by deer densities (see Chapter 2), it was thought that preferred plant species (*Bursera simaruba, Erithalis fruticosa, Bumelia celastrina, Jacquinia keyensis*, and *Guapira discolor*) would be better indicators of differential browsing pressures if no deer density effects were found for all plant species combined. Therefore, densities of preferred plant species <1.2m tall were summarized for each hammock stand and analyzed separately. The same statistical protocol used above for all plant species combined was followed for preferred plant species. Preferred species data was square root transformed for normality.

Intrinsic habitat characteristics not directly related to deer browsing might also affect understory species. Therefore, density of plant species >1.2m tall (out of Key deer reach), total basal area of trees (all species combined) with a dbh >12.7cm, and percent canopy cover were compared within deer density categories (low/high) and each was tested using a two-way ANOVA with island and site (adjacent/distant) as fixed factors. Plant density (>1.2m tall) data were square root transformed, basal area data were log +1

transformed and percent canopy cover data were arcsine transformed to meet normality or homogeneity of variance assumptions. Canopy cover was measured with a concave densiometer on a tripod (45cm high) placed every 10m along the 1m x 50m quadrat. Procedures for the densiometer recordings followed Lemmon (1957) (see Chapter 2). All statistical analyses were tested at the $\alpha = 0.05$ significance level.

Results

Habitat characteristics

Densities of plant species >1.2m tall, percent canopy cover, and total basal area (m^2ha^{-1}) were similar between sites (adjacent/distant) for both high and low deer density islands (Tables 4.1 and 4.2; Figure 4.3). This suggests that hammock habitats had comparable characteristics between site types on islands of similar deer densities.

Browsing effects on vegetation structure

Browsing effects between sites distant from and adjacent to urban areas were first tested at the plant community level, and data indicated that Key deer herbivory was not affecting the plant community level between sites on islands of either high or low deer densities. For the split-plot ANOVA model, interactions between Key deer densities and densities of all woody plant species combined <1.2m tall were not significant, nor were interactions for Fisher's α diversity (Table 4.3: Figures 4.4 & 4.5). When islands with different Key deer densities were analyzed separately, the densities of all woody species combined <1.2m tall and Fisher's α did not differ between sites within islands of either low or high densities of Key deer (Table 4.4) indicating no trends with deer density (high/low) or site (adjacent/distant) for total plant species or diversity. However, No Name Key had a lower Fisher's α than Big Pine (Table 4.4, Figure 4.5) likely due to the higher deer density on No Name. Islands with low deer densities had similar Fisher's α diversity among sites and keys (Table 4.4; Figure 4.5).

Since browsing effects were not evident for all plant species combined, preferred plant species, being better indicators of browsing pressure, were analyzed separately. The interaction term from the split-plot model indicated a marginal effect of deer density on densities of preferred plant species <1.2m tall

between sites (Table 4.3; Figure 4.4). On islands with high densities of deer, further analysis revealed lower densities of preferred plant species <1.2m tall in hammock stands adjacent to urban areas compared to distant hammock stands (Table 4.5; Figure 4.4), and lower densities of preferred plant species <1.2m tall on No Name compared to Big Pine (Table 4.5). No trend in the densities of preferred species <1.2m tall was evident between sites for low deer density islands (Table 4.5; Figure 4.4). Preferred plant species densities >1.2m tall were similar among sites on islands with both high and low deer densities (Table 5; Figure 4), again suggesting that deer density affected preferred species <1.2m tall rather than intrinsic differences between habitats.

Table 4.1. Two-way ANOVA results for hammock characteristics. Results were for canopy cover (%), basal area (m2ha-1), and plant density >1.2m (all species combined) by site (adjacent/distant) and by keys: high deer density (Big Pine and No Name), low deer density (Cudjoe and Sugarloaf). Canopy cover was arcsine; basal area was log+1; and plant density was square root - transformed.

	Source	df	SS	MS	F	P	R^2
Canopy cover (%)							
High deer density	Key	1	0.003	0.003	1.389	0.260	0.251
	Site	1	0.000	0.000	0.202	0.661	
	Key x Site	1	0.006	0.006	2.939	0.110	
	Error	13	0.026	0.002			
Low deer density	Key	1	0.017	0.017	2.385	0.154	0.253
	Site	1	0.007	0.007	1.005	0.340	
	Key x Site	1	0.000	0.000	0.009	0.927	
	Error	10	0.073	0.007			
Basal area (m^2ha^{-1})							
High deer density	Key	1	0.026	0.026	0.278	0.607	0.055
	Site	1	0.013	0.013	0.138	0.717	
	Key x Site	1	0.033	0.033	0.348	0.565	
	Error	13	1.233	0.095			
Low deer density	Key	1	0.001	0.001	0.020	0.891	0.126
	Site	1	0.000	0.000	0.007	0.935	
	Key x Site	1	0.043	0.043	1.415	0.262	
	Error	10	0.300	0.030			
Plant species >1.2m							
High deer density	Key	1	328.4	328.4	0.974	0.342	0.092
	Site	1	75.5	75.5	0.224	0.644	
	Key x Site	1	47.9	47.9	0.142	0.712	
	Error	13	4383.9	337.2			
Low deer density	Key	1	789.2	789.2	2.805	0.125	0.322
	Site	1	360.9	360.9	1.283	0.284	
	Key x Site	1	118.4	118.4	0.421	0.531	
	Error	10	2813.8	281.4			

Table 4.2. Mean (±1 SE) percent canopy cover and basal area (m^2h^{-1}). Islands are high deer densities (Big Pine and No Name) and low deer densities (Cudjoe and Sugarloaf) with sites distant (D) from and adjacent (A) to urban areas.

	Big Pine		No Name		Cudjoe		Sugarloaf	
Attribute	D	A	D	A	D	A	D	A
Mean Canopy cover (%)	95.6	93.2	94.2	93.3	90.1	94.2	91.8	95.6
SE	1.6	3.5	4.7	2.4	6.4	3.1	1.7	4.0
Mean Basal area (m^2ha^{-1})	4.6	6.0	6.2	4.4	4.3	3.1	3.4	4.5
SE	1.5	3.0	2.9	1.3	1.1	1.2	1.1	1.1

Table 4.3. Split-plot ANOVA results for densities of plant species <1.2m tall (all species and preferred species only[1]) and Fisher's alpha diversity by deer density (low/high) and site (adjacent/distant). Preferred species data were square root-transformed.

Source	df	SS	MS	F	P
All plant species					
Deer	1	7.37E+07	7.37E+07	0.213	0.690
Error	2	6.93E+08	3.47E+08		
Site	1	2.30E+07	2.30E+07	0.708	0.489
Error	2	6.51E+07	3.25E+07		
Deer x Site	1	2.03E+07	2.03E+07	0.623	0.513
Error	2	6.51E+07	3.25E+07		
Preferred plant species only					
Deer	1	6482.2	6482.2	28.92	0.033
Error	2	448.4	224.2		
Site	1	26.8	26.8	1.05	0.414
Error	2	51.3	25.7		
Deer x Site	1	352.5	352.5	13.74	0.066
Error	2	51.3	25.7		
Fisher's alpha diversity					
Deer	1	0.168	0.168	0.341	0.618
Error	2	0.988	0.494		
Site	1	0.083	0.083	9.888	0.098
Error	2	0.017	0.008		
Der x Site	1	0.032	0.032	3.814	0.190
Error	2	0.017	0.008		

Table 4.4. Two-way ANOVA results for density of all woody plant species combined <1.2m and Fisher's alpha by site (adjacent/distant) and by islands. Islands were high deer density (Big Pine and No Name), low deer density (Cudjoe and Sugarloaf). Plant density data were square root-transformed.

	Source	df	SS	MS	F	P
plant species <1.2m						
High deer density	Key	1	8905.8	8905.8	7.928	0.015
	Site	1	868.0	868.0	0.773	0.395
	Key x Site	1	88.7	88.7	0.079	0.783
	Error	13	14603.3	1123.3		
Low deer density	Key	1	1686.3	1686.3	2.231	0.166
	Site	1	3.3	3.3	0.004	0.949
	Key x Site	1	0.4	0.4	0.001	0.982
	Error	10	7559.8	756.0		
Fisher's alpha diversity						
High deer density	Key	1	4.06	4.06	39.4	<.001
	Site	1	0.03	0.03	0.24	0.629
	Key x Site	1	0.01	0.01	0.10	0.759
	Error	13	1.34	0.10		
Low deer density	Key	1	0.08	0.08	0.52	0.486
	Site	1	0.38	0.38	2.46	0.148
	Key x Site	1	0.05	0.05	0.33	0.581
	Error	10	1.52	0.15		

Table 4.5. Two-way ANOVA results for preferred[1] plant species <1.2m and >1.2m tall by site (adjacent/distant) and by islands. Islands were high deer density (Big Pine and No Name), and low deer density (Cudjoe and Sugarloaf). All data were square root-transformed.

	Source	df	SS	MS	F	P
plant species densities <1.2m tall						
High deer density	Key	1	1121.5	1121.5	40.981	<0.001
	Site	1	1100.9	1100.9	40.230	<0.001
	Key x Site	1	52.1	52.1	1.906	0.191
	Error	13	355.8	27.4		
Low deer density	Key	1	72.5	72.5	0.423	0.530
	Site	1	273.8	273.8	1.600	0.235
	Key x Site	1	1.9	1.9	0.011	0.919
	Error	10	1711.9	171.2		
plant species densities >1.2m tall						
High deer density	Key	1	85.6	85.6	1.440	0.252
	Site	1	3.2	3.2	0.054	0.820
	Key x Site	1	100.6	100.6	1.693	0.216
	Error	13	772.7	59.4		
Low deer density	Key	1	37.9	37.9	0.430	0.527
	Site	1	70.7	70.7	0.802	0.391
	Key x Site	1	55.4	55.4	0.629	0.446
	Error	10	880.7	88.1		

[1] preferred species: *Bursera simaruba, Erithalis fruticosa, Bumelia celastrina*, *Jacquinia keyensis* and *Guapira discolor*

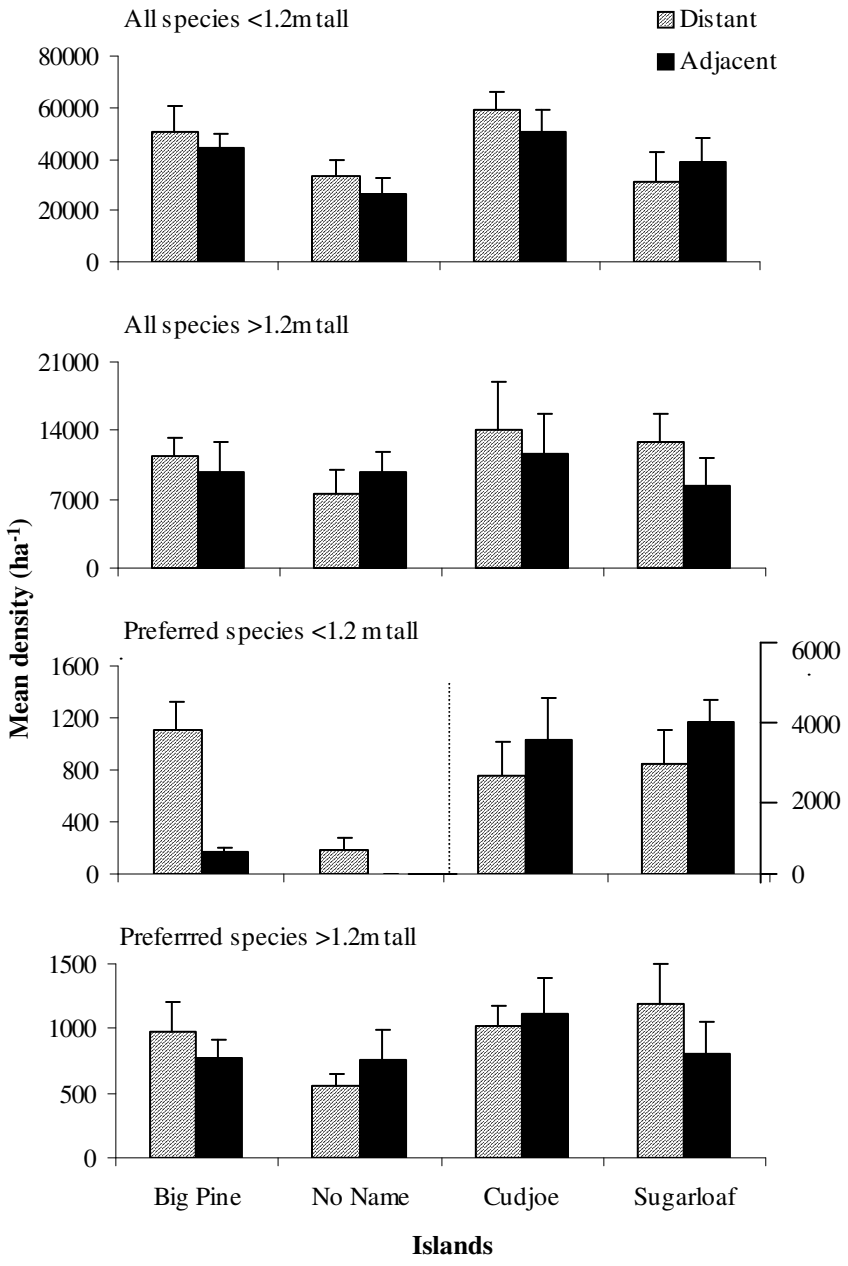

Figure 4.3. Mean densities of woody plant species in hammock habitats. Habitats are distant from and adjacent to urban areas on islands with high deer densities (Big Pine and No Name) and islands with low deer densities (Cudjoe and Sugarloaf). For clarity, preferred plant species <1.2m tall have two ordinates: left - Big Pine and No Name; right - Cudjoe and Sugarloaf

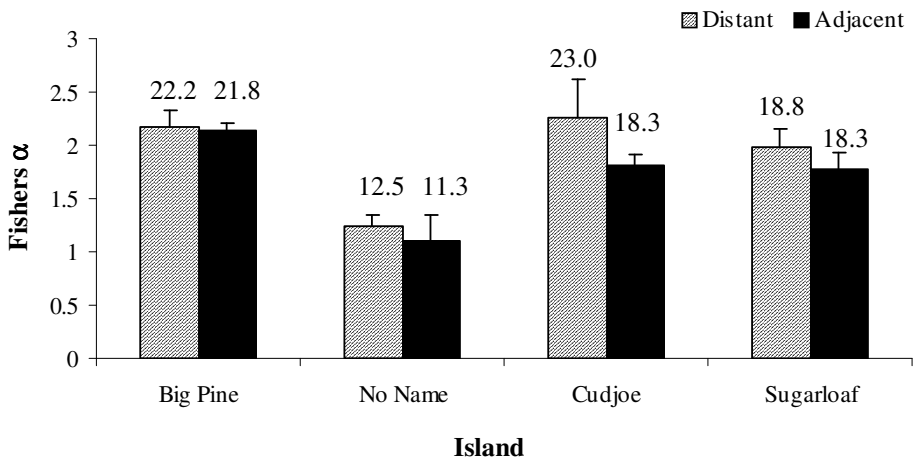

Figure 4.4. Mean Fisher's alpha diversity (+1SE) for woody species in hammock habitats. Habitats are arranged by site (adjacent/distant) on islands of high deer density (Big Pine and No Name) and low deer density (Cudjoe and Sugarloaf). Numbers above the bars are mean plant species richness per site per island.

Discussion

Because habitat characteristics (e.g. basal area, canopy cover) were similar among sites, Key deer browsing predominately caused the declines in the densities of preferred plant species, such as *B. simaruba, E. fruticosa, B. celastrina, J. keyensis, and G. discolor*, in hammock understories adjacent to urban areas on Big Pine and No Name where Key deer densities are relatively high. Preferred plant species are already depleted on islands with many Key deer compared to islands with fewer deer (Figure 4.4; see Chapter 2) implicating that Key deer urbanization is further increasing browsing pressure and accelerating negative effects on these preferred plant species in hardwood hammocks. Effects of Key deer herbivory were not apparent in hardwood hammock for all woody species combined, α diversity or species richness on islands with low or high Key deer densities. Increases of nonpreferred plant species, such as *Piscidia piscipulum* and *Coccoloba diversifolia* among others, likely replaced diminished densities of preferred species on high deer density keys thus negating observable deer effects on diversity in habitats adjacent to urban areas. Unobserved browsing effects on total plant density or diversity, therefore, should be viewed with caution because plant population extinctions can still result from "cryptic degradation" in habitats that seem intact (Rooney et al. 2004) where shifts in plant species composition cause a misleading healthy appearance of the habitat (Webster and Parker 2000) in which preferred plant species are declining.

The preferred native plant species in hardwood hammocks suffer from 'associational susceptibility' [habitat-habitat associations rather than the conventional plant-plant associations (e.g. Brown and Ewel 1987; White and Whitham 2000)], being more prone to Key deer depredation in habitats associated with urban environments. The degree of associational susceptibility, however, might be a function of island size or deer density. For example, compared to Big Pine, No Name is relatively smaller and has a relatively higher Key deer density (>20 deer/km^2). Very low densities of preferred plant species were observed on No Name in hammock habitats that were distant (as well as adjacent) from urban areas (Figure 4). Augustine and Jordan (1998) found a similar trend in that the distance from alfalfa fields explained white-tailed deer herbivory levels on forest plant species except where deer densities exceeded 20 deer/km^2.

Mowed clearings, increased edge and open areas encourage Key deer to gather in urban areas, as does illegally feeding Key deer. Lopez (2003) found that illegal feedings of Key deer in urban areas increased 25% during the tourist season (Oct - Mar), which provides an allochthonous input and encourages Key deer to remain in or disperse into urban areas. These seasonal supplemental resources (perhaps similar to pulsed resources in Ostfeld and Keesing 2000) are subsidiary causal agents of increased browsing pressure and subsequent depletion of local preferred plant species in hammock habitats surrounding urban areas.

Urbanization has caused human-induced browse lines by altering the landscape and by modifying Key deer feeding and social behaviors. Future development of lands in the NKDR should be stemmed because an urban-deer interface could further increase browsing impacts due to associated 'edge effects' (Alverson et al. 1988) or habitat fragmentation (Augustine and Frelich 1998), and prevent natural reinvasion by browse-sensitive plant species into habitats adjacent to urban areas that are isolated from other natural sources (Anderson and Katz 1993). All of these factors would be detrimental to the protection of the rare hardwood hammock plant community in the Florida Keys.

Management implications

Measures should be taken to deter Key deer aggregation in urban environments, such as the continued education of tourists (and residents) on the ramifications of illegally feeding wildlife. Because white-tailed deer have preferences among ornamental species (Conover and Kania 1988), residents can protect landscape plants that Key deer favor (e.g. *Hibiscus spp*., *Schefflera spp*., and others) via localized fencing, or plant native species that Key deer avoid (e.g. *Eugenia spp*., *Piscida piscipula*, etc.). Also, state (F.A.C. 39-27.002(5)) and federal (16 U.S.C. 1531) laws prohibiting the feeding of Key deer (USFWS 1999) should be strictly enforced in urban areas. An effort to safeguard public lands outside of the urban mosaic is also advisable. Land acquisition may not only reduce habitat loss, but will help preserve relatively remote habitats that are less susceptible to excessive Key deer impacts. Other habitats including mangrove and buttonwood wetlands and endangered rock pinelands should be tested for urban-deer effects to better focus management efforts. This study suggests that Key deer densities must be evaluated among

and within islands at the landscape level to understand browsing impacts. However, management evaluations will have to consider the 'social carrying capacity' of Key deer because public interests may desire large deer herds to increase the probability of encounters with Key deer.

CHAPTER 5

THE ROLE OF FIRE AND KEY DEER HERBIVORY ON PINE ROCKLAND PLANT COMMUNITIES

Synopsis

Fire plays an important role in maintaining pine rockland plant communities in the lower Florida Keys. Key deer (*Odocoileus virginianus clavium*) herbivory also shapes the pineland vegetation. In the present study, burned and unburned pineland plant communities were compared between Big Pine (high Key deer density) and Sugarloaf (low Key deer density) islands. Pinelands burned 10 years and 14 years prior to sampling, and control (unburned) areas were compared to elicit effects of fire and deer herbivory on woody and herbaceous vegetation. In addition, fenced deer exclosures built on No Name Key (high Key deer density) in August 2001 were burned along with adjacent open plots in July 2003, and plant data were analyzed for fire/deer effects. Results suggested that fire and Key deer herbivory reduced both hardwood plant densities and growth. Though fire and deer herbivory may interact, they also can differentially affect plant species due to species-specific response to fire or selective deer herbivory. Preferred woody plant species densities were higher in all height classes on Sugarloaf than Big Pine regardless of burn treatment. Overall, the reduction of hardwoods slows succession of pinelands to hammock, reduces canopy cover, and aids in sustaining herbaceous species. Herbaceous species cover and richness was higher overall on Big Pine than Sugarloaf, likely due to lower canopy cover and decreased hardwood densities. Herbaceous cover was also higher in unburned pinelands on Big Pine as previously burned areas recovering from fire experienced higher browsing pressure. Preferred woody species tended to increase in deer exclosures before and after fire, while preferred species decreased in adjacent open plots mainly after fire. Percent cover of preferred herbaceous species increased inside exclosures especially after fire, while preferred herb species remained low in open plots even after fire. Controlled burns should be maintained in pine

rocklands in the lower Keys to prevent hardwood invasion and to sustain pineland plant species. Frequency of fire should take into account time for succession to hammock, fuel build-up, and effects (i.e. potential increases) on Key deer herds due to increased plant quality from fire.

Introduction

Fire is an important component in many Florida ecosystems (Abrahamson 1984*b*), and can increase, decrease, or even stabilize community succession (Abrahamson 1984*a*). Succession of pine rockland to hardwood hammock may occur within 2 to 3 decades in the absence of fire on the Florida mainland (Alexander 1967) but may take longer (>100 years) in pinelands in the lower Keys (Carlson et al. 1993). In the lower Keys, there are generally more hardwood species in pinelands that are subject to less-frequent burns (Folk 1992). Fire in pinelands benefits Key deer (*Odocoileus virginianus clavium*) by releasing nutrients, stimulating new plant growth, increasing forage production and availability, improving palatability of food plants, and increasing nutritive plant value (Carlson et al 1993). Key deer browse more frequently in recently burned pinelands and will feed extensively on new woody and herbaceous growth for 6-9 months after fire (USFWS 1999). White-tailed deer herbivory can influence plant species composition and affect successional pathways (Connel and Slayter 1977; Ball et al. 2000; Coomes et al. 2003). Therefore, both fire and deer herbivory can be causal factors in shaping pineland plant communities.

Pineland is highly utilized by Key deer (Klimstra et al. 1974; Silvy 1975; Lopez 2001) and is an important habitat for foraging Key deer (Dickson 1955; Klimstra and Dooley 1990; Carlson et al. 1993). Key deer were federally listed as an endangered species in 1967 because approximately 50-80 animals remained in the 1950s (Dickson 1955). Federal protection and the establishment of the Key Deer National Wildlife Refuge (KDNWR) in 1957 (USFWS 1999) allowed the Key deer population to increase to over 700 animals in 2000 (Lopez 2001). Of a potential range of 26 islands, over two-thirds of the Key deer population reside on only two islands, Big Pine Key and No Name Key (Lopez 2001) resulting in a skewed distribution and high Key deer densities on these islands. This provided grounds for considering the effects of the endangered Key deer on an endangered plant community, pine rockland (Florida Natural Areas

Inventory 1990). There has been much impetus in protecting both of the endangered entities (Key deer and pine rocklands) in the lower Keys.

This project investigated the effects of Key deer herbivory and fire on plant communities in pine rocklands. By comparing vegetation in burned and unburned pinelands and on islands with high and low deer densities, the interactions of Key deer herbivory and fire could be examined. White-tailed deer browsing can affect plant species regeneration in pinelands (Ross et al. 1970) and reduce the growth of plant species in relatively short-time periods (< 2 years) after fire (Davis 1967). Though new growth of woody species and herbaceous species is maximized in burned habitats in the Keys and pinelands that have been burned frequently support more herbaceous species, Key deer browse burned areas more frequently (Carlson et al 1993). Thus, cover and richness of herb species should be lowest in burned-high deer density pinelands, higher for unburned-low/high deer density pinelands, and highest in burned-low deer density pinelands. Whereas densities of woody species should be lowest in burned-high deer density pinelands, higher for unburned-high deer density / burned-low deer density pinelands, highest in unburned-low deer density pinelands. Furthermore, herbaceous cover and richness and preferred woody species densities should increase inside deer exclosures in burned pinelands, and decrease in adjacent burned open plots due to strong browsing pressure by Key deer.

Study Area

The study was conducted in the lower Florida Keys within the boundaries (24° 36´ N – 81° 18´ W to 81° 34´ W) of the National Key Deer Refuge (NKDR). The climate is subtropical with evident wet (~May-October) and dry (~November-April) seasons. In the lower Keys, the mean annual temperature is ~ 25.2°C and mean annual rainfall is ~ 100cm. Soils vary from blue-grey 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 1955).

Pineland is mainly found on five islands in the NKDR. Of all the habitats on each island, percent pineland was as follows: Big Pine (28%), Sugarloaf (5%), Cudjoe (5%), Little Pine (17%), No Name (11%) with relic stands on Howe (1%) and Knockemdowns (1%). The only pine species in the lower Keys is

Pinus elliottii var. *densa*. Vegetation is primarily of West Indian origin (Stern and Brizicky 1957) and subsequent plant nomenclature follows Scurlock (1987) for woody species and Wunderlin (1998) for herbaceous species. [Refer to Chapter 1 for more detailed descriptions of the islands, habitats, Key deer characteristics, etc.]

Fire history

Though records of fire are not well established in the lower Keys, a fire history of controlled burns and wildfires was mapped within the NKDR (Bergh and Wisby 1996) on available digital habitat maps (MacAuley et al. 1994). Big Pine had the most frequently burned areas in 1966, 1977, 1987, 1990, 1991, and 1994 where some areas were burned in more than 1 year. Big Pine also contains areas that have not been burned in at least 50 years. Although fire history before the 1950s is vague, it was suggested that frequent fires occurred on Big Pine before the 1950s (Alexander and Dickson 1973). Sugarloaf was burned in 1987, 1990, and 1991 and also contains areas that have not been burned in at least 50 years. All pineland areas were burned on Little Pine, Cudjoe, and No Name in various years between 1960 and 1996, whereas Howe has not been burned within the last 50 years. For the present study Key deer effects were examined for Big Pine and Sugarloaf only, as they contained pinelands burned in similar years and pinelands that have not been burned for > 50 years.

Methods

Experimental design

Existing Key deer density treatments and burn treatments were utilized to understand their effects on pine rockland plant communities. Deer treatments were high deer density [Big Pine = 18 deer/ km^2 (Lopez 2001)] and low deer density [Sugarloaf = 0.6 deer/ km^2 (R.R. Lopez unpublished data)]. Burn treatments for each island consisted of pineland areas sampled 10 years after fire (YAF) (1991), 14 YAF (1987), and Control areas (unburned within the last 50 years).

Vegetation sampling

To examine fire and deer herbivory effects, 43 randomly located vegetation quadrats were sampled in pine rockland habitat on Big Pine and Sugarloaf keys in areas of the above burn treatments (n = 5 -12 quadrats per burn treatment per island). Vegetation sampling was conducted during the dry season from January to May of 2001. A 1m x 50m quadrat was used to sample woody plant species with a diameter at breast height (DBH) < 12.7cm. Woody plant species were assigned to height classes: <0.6m, 0.6m-1.2m, 1.2m-1.8m, and >1.8m. The former two height classes are within the Key deer browse tier. Herbaceous ground cover was estimated at five circular plots ($1m^2$) placed every 10m along the 1 x 50m quadrat. Plant species that exhibited root suckering were recorded as individuals if they branched underground and the protruding stems were separated.

Canopy cover can be affected by fire and can influence understory (e.g. woody seedlings and herbaceous species) composition due to varying levels of light penetration. To examine differences between islands and/or burn treatments, canopy cover was measured with a concave densiometer on a tripod (45cm high) placed every 10m along the 1m x 50m quadrat. Methodology for recording densiometer readings was according to Lemmon (1957). Data were averaged for the quadrat, and for the burn treatment per island.

Deer exclosures

In August 2001, three square $37m^2$ fenced deer exclosures were constructed on No Name Key [22 deer/km^2 (Lopez 2001)] in pine rockland habitat with corresponding open (control) plots. Although plots were randomly located, they were selected near roads (between 15m - 100m) to facilitate construction and decrease cost. Galvanized chain-linked fencing 1.8m high was erected to exclude Key deer, but was raised 15cm above the ground to allow access by other potential herbivores including the lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), raccoon (*Procyon lotor*) and the Florida box turtle (*Terrapene carolina bauri*), a seed disperser (Liu et al. 2003).

Data were collected every 6 months from August 2001 to July 2004. In June 2003 a fire burned >95% of the vegetation in the exclosures (n = 2) and their adjacent open plots (n = 2). The plots were

sampled after the burn, then in August 2003, January 2004 and July 2004 (1year post-burn) to examine the effects of fire and deer herbivory on plant composition and structure. Woody shrubs were quantified over the entire plot in the following height classes: < 5cm, 5cm – 0.6m, 0.6m – 1.2m, 1.2m – 1.8m, and > 1.8m. Mean percent cover of herbaceous species was quantified in nine circular subplots ($1m^2$) in each exclosure/open plot. Herb percent frequency was quantified from the 18 ($1m^2$) subplots from the treatment (exclosure/open plots) replicates. To limit edge effects, data were not recorded in a buffer zone (0.3m W x 2.1m H) within the plot perimeters, where effects of fence construction and/or where Key deer may be able to reach under the raised fence could influence vegetation.

Data Analysis

For some analyses, plant species were analyzed by Key deer preference categories. Key deer preferences for plant species were established from feeding trials (Chapter 2), rumen analyses (Klimstra and Dooley 1990), and direct or indirect observations of Key deer browse (Dickson 1955: Klimstra et al. 1974; personal observations). Examples of preferred plant species include: woody - *Bursera simaruba, Erithalis fruticosa, Bumelia celastrina, Jacquinia keyensis, Guapira discolor, Pithecellobium keyense*, and *Morinda royoc*; herbaceous – *Chiococca pinetorum, Smilax havanensis, Chamaecrista aspera*. Nonpreferred species are those found below the top 28 species in rumen samples (Klimstra and Dooley 1990). Other species such as palm species, *Byrsonima lucida* (woody), and grass species that Key deer mainly consume for the fruits/seeds, are placed in a separate category since the effects of deer browsing on species recruitment (e.g. endozoochory) are unknown.

For vegetation quadrat data, total woody plant density (all species and height classes combined), herbaceous % cover, and canopy % cover were each analyzed separately using a two-way ANOVA with deer density (low/high) and burn year (10YAF, 14YAF, Control) as fixed factors. Woody plant data were square root transformed to meet normality assumptions.

Because deer exclosures were burned years after they were erected, statistics were employed for data collected from June 2003 (when the fire occurred) to July 2004. Repeated-measures ANOVA (rmANOVA) were employed to test for significant differences between plant data for treatments

(exclosure/open) and years (Jun 03 – Jul 04). A separate rmANOVA was used for preferred species, nonpreferred species and other species for each mean woody abundance and mean herb percent cover. Sphericity was met for each rmANOVA and results did not qualitatively differ from Greenhouse-Geisser estimates (Zar 1999). All statistical analyses were tested at the $\alpha = 0.05$ significance level.

Results

Canopy cover

Percent canopy cover significantly differed in pinelands between Big Pine (high deer density) and Sugarloaf (low deer density) (Table 5.1; Figure 5.1). No significant differences for percent canopy cover were evident between pinelands burned 10YAF, 14YAF, and Control, or for deer density by burn treatment interactions (Table 5.1). In the burned pineland treatments, likely canopy cover increased to levels near Control pineland canopy cover due to the times since fire ($\geq$ 10yrs), though slightly higher canopy cover in Control areas was evident for both islands (Figure 5.1).

Fire-deer effects on vegetation

Mean woody plant species densities (all species and height classes combined) were significantly greater on Sugarloaf than on Big Pine (Table 5.2; Figure 5.2). The differences between Sugarloaf and Big Pine plant densities also differed between burn treatments given the significant interaction term (Table 5.2). This is likely due to the lower densities of preferred woody plant species on Big Pine (Figure 5.3). All height classes of preferred species are represented on Sugarloaf regardless of burn treatment, but a trend of lower densities of preferred species >1.2m in burn treatments on Big Pine suggests that the effects of fire and browsing are impeding the growth of these species (Figure 5.3). On Sugarloaf, species richness of woody plant species was higher in 10YAF, 14YAF, and Control plots with 15, 17, and 16 species respectively, compared to Big Pine's 8, 12 and 15 species respectively. Mainly, the species absent on Big Pine were *Bursera simaruba, Jacquinia keyensis, Erithalis fruticosa, and Bumelia celastrina*, which are all preferred species (though mainly associated with hardwood hammock habitat). *Pinus elliotti* var. *densa*

was represented in the >1.8m height class for all burn treatments on both islands, and had the highest mean densities (ha^{-1}) in the 14 YAF plots (Big Pine = 1000; Sugarloaf = 800) and lowest mean densities in the 10 YAF plots (Big Pine = 400; Sugarloaf = 80). In the Control plot on Sugarloaf, *P. elliotti* var. *densa* also had a low mean density of 160 individuals/ha in the >1.8m height class and was absent from all lower height classes.

Mean percent cover of herbaceous species was significantly higher on Big Pine than Sugarloaf (Table 5.3; Figure 5.4). However, no differences between burn treatments or deer density and burn treatment interactions were evident (Table 5.3) though control plots tended to have the lowest cover values on both islands. *Cladium jamaicense* was the dominant herb on both islands. Three grass species and *Ernodea littoralis* (nonpreferred species) had the next highest percent cover on Big Pine, while a grass species, *Chiococca pinetorum* (preferred species), *E. littoralis*, and *Cassytha filiformis* had the next highest cover on Sugarloaf. Herb species richness on Big Pine was 15, 16, and 25 for 10YAF, 14YAF, and Control areas respectively and Sugarloaf herb richness was 6, 9, and 7 for 10YAF, 14YAF, and Control areas respectively. The highest herb richness in control plots on Big Pine was likely due to stronger browsing pressures in burn plots.

Effects of fire and deer exclosures on vegetation

Woody plant abundance (all species and height classes combined) remained above zero when the fire occurred because approximately 5% of each plot was not burned and no tree species >1.8m tall were killed. Some woody stems that appeared dead re-flushed after the fire. Nonetheless, trends in plant abundance were evident before and after the fire. The abundance of nonpreferred woody plant species marginally differed between exclosure and open plots (Table 5.4) being higher in open plots. Nonpreferred species abundance increased after fire in open plots (Table 5.4), being slightly higher (2%) in July 2004 than August 2001 (Figure 5.5), while nonpreferred species remained relatively unchanged inside exclosures returning to a similar abundance after the fire as before (Figure 5.5). Preferred plant species abundance significantly differed between exclosure and open plots (Table 5.4), being higher in exclosures after fire (Figure 5.5). Preferred species abundance increased somewhat in open plots before the fire then

continually decreased after August 2003 (> 2 months after the fire), while preferred species inside exclosures showed a steady increase before the fire, then increased again and stabilized after the fire (Figure 5.5). Palm species and *Byrsonima lucida* did not differ between treatments (Table 5.4) as they increased in both open and exclosure plots though their abundances remained higher inside exclosures (Figure 5.5). These species spiked 2 months after the fire and then declined in open plots by January 2004 (Figure 5.5) causing the significant time x deer effect (Table 5.4). Inside exclosures, woody species richness increased from 15 before the fire to 18 after the fire adding *Cassia bahamensis, Reynosia septentrionalis*, and *Coccoloba diversifolia*. In open plots, species richness declined from 14 before the fire to 12 after the fire due to losses of *Randia aculeata* (preferred species) and *Coccoloba uvifera,* which were in height classes <1.2m tall.

The percent cover of nonpreferred herbaceous species was similar for exclosure and open plots (Table 5.4) in that both increased two months after the fire (August 2003), and then declined to levels similar to August 2001 by July 2004 (Figure 5.6). Percent cover of grass species did not differ between exclosure and open plots after the fire (Table 5.4) though grasses increased inside exclosures causing the significant time x deer interaction (Table 5.4). Preferred species differed between treatments (Table 5.4) being higher in exclosures after the fire (Figure 5.6). Inside exclosures, percent cover of preferred species increased slightly before the fire, and then after the fire increased higher (>8%) than the pre-burn level (Figure 5.6) while in open plots, preferred species remained low after the fire (Figure 5.6). Inside exclosures, the percent cover of the herb *Chamaecrista aspera* continually increased and responded positively to fire (Figure 5.6) and the percent frequency of *C. aspera* increased from 22% in August 2001 to 83% by July 2004. Though the percent frequency of *C. aspera* increased slightly in open plots from 11% in August 2001 to 22% in July 2004, percent cover remained very low (<1%) even after fire due to heavy browsing (Figure 5.6). Herb species richness increased slightly inside exclosures where 2 new species were added (an unidentified grass and vine species) while two grass species were lost in open plots after the fire. Though not quantified, *C. aspera*, *Flavaria linearis*, *Chamaesyce* sp., and grass species flowered inside exclosures, while only two grass species flowered in open plots. *Flavaria linearis* was also taller (>0.5m) inside exclosures.

Table 5.1. Two-way ANOVA results for percent canopy cover in pine rocklands on Big Pine and Sugarloaf keys. Deer treatments were high density (Big Pine) and low density (Sugarloaf) and burn year treatments were 10 YAF, 14 YAF, and Control (unburned).

Source	df	SS	MS	F	P
Deer	1	6228.4	6228.4	26.21	<0.001
Year	2	1020.7	510.4	2.15	0.131
Deer x Year	2	226.0	113.0	0.48	0.625
Error	37	8791.2	237.6		

Table 5.2. Two-way ANOVA results comparing total woody plant density between Big Pine and Sugarloaf keys. Plant densities were summarized for all species and height classes. Deer treatments were high density (Big Pine) and low density (Sugarloaf) and burn year treatments were 10 YAF 14YAF, and Control (unburned). Data were square root transformed.

Source	df	SS	MS	F	P
Deer	1	36886.4	36886.4	44.11	<0.001
Year	2	4858.0	2429.0	2.91	0.067
Deer x Year	2	7035.8	3517.9	4.21	0.023
Error	37	30941.2	836.2		

Table 5.3. Two-way ANOVA results for herbaceous % cover in pine rocklands between Big Pine and Sugarloaf keys. Deer treatments were high (Big Pine) and low (Sugarloaf) and burn year treatments were 10YAF, 14 YAF, and Control (unburned).

Source	df	SS	MS	F	P
Deer	1	509.4	509.4	9.852	0.003
Year	2	34.0	17.0	0.329	0.722
Deer x Year	2	61.8	30.9	0.598	0.555
Error	37	1913.2	51.7		

Table 5.4. Repeated-measures ANOVA results for the exclosure study on No Name. Significant results indicate differences for woody abundance or herbaceous % cover between Deer treatment (exclosure vs. open plots) for sample dates that occurred from June 2003 (when a fire occurred) to July 2004 (approximately 1 year post-burn).

		Preferred			Nonpreferred			Other [1]		
Source	df	MS	F	P	MS	F	P	MS	F	P
Woody species										
Between Subjects										
Deer	1	191.5	19.2	0.048	11.0	16.6	0.055	3.4	1.4	0.358
Error	2	10.0			0.66			2.4		
Within Subjects										
Time	3	146.8	224.0	<0.001	9.5	9.4	0.011	39.1	387.9	<0.001
Time x Deer	3	31.2	47.7	<0.001	2.6	2.6	0.147	1.5	15.2	0.019
Error	6				1.0			0.10		
Herbaceous species										
Between Subjects										
Deer	1	109.0	2287.2	<0.001	17.3	0.50	0.552	13.3	4.4	0.171
Error	2	0.05			34.5			3.0		
Within Subjects										
Time	3	11.5	18.7	0.002	129.5	39.2	0.02	4.6	16.0	0.056
Time x Deer	3	11.2	18.2	0.002	5.0	1.5	0.344	2.9	10.4	0.083
Error	6	0.62			3.3			0.28		

[1] Other = Palm species and *B. lucida* for woody spp., and grasses for herb spp.

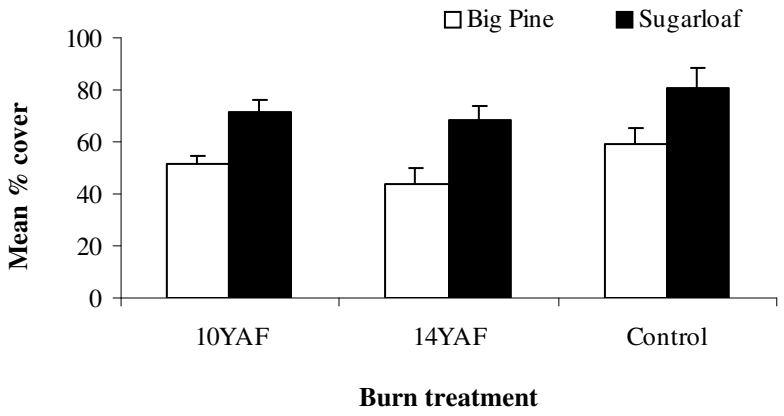

Figure 5.1. Mean percent canopy cover (±SE) for pine rockland habitats on Big Pine and Sugarloaf. Deer treatments were high density (Big Pine) and low density (Sugarloaf) and burn year treatments were 10 YAF, 14 YAF, and Control (unburned).

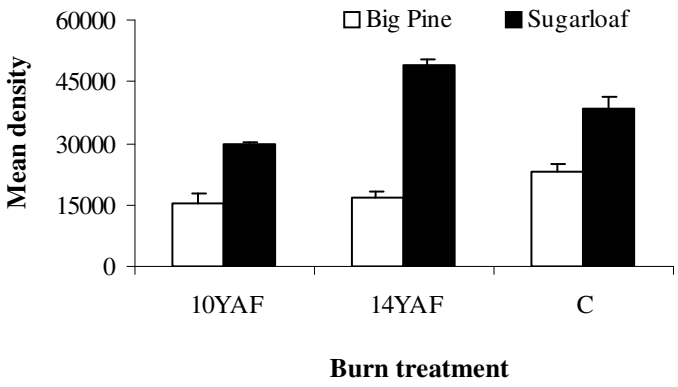

Figure 5.2. Mean (±SE) total woody plant densities for Big Pine and Sugarloaf. Plant densities were summarized for all species and height classes. Deer treatments were high density (Big Pine) and low density (Sugarloaf) and burn year treatments were 10 YAF, 14 YAF, and Control (unburned).

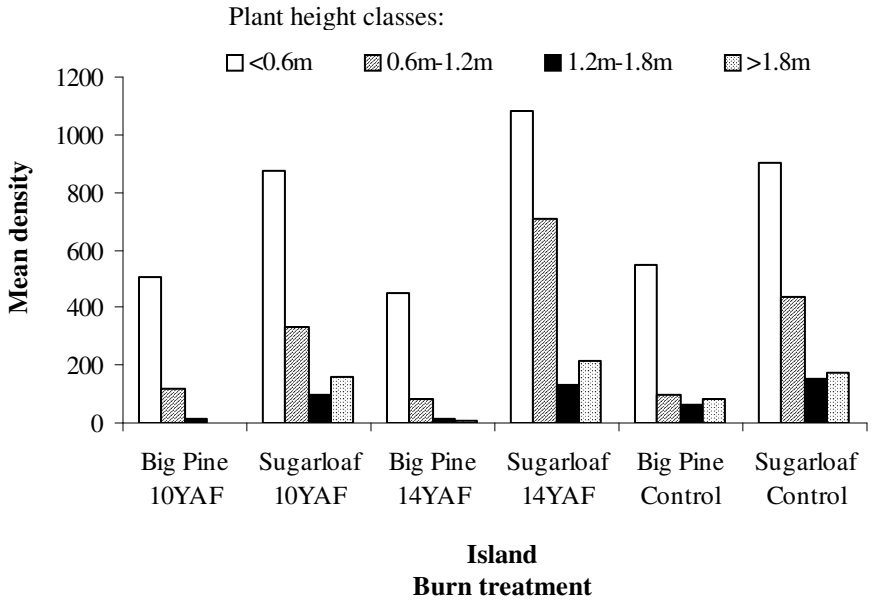

Figure 5.3. Mean densities of preferred woody plant species in pinelands on Big Pine and Sugarloaf. Deer treatments were high density (Big Pine) and low density (Sugarloaf) and burn year treatments 10 YAF, 14 YAF, and Control (unburned).

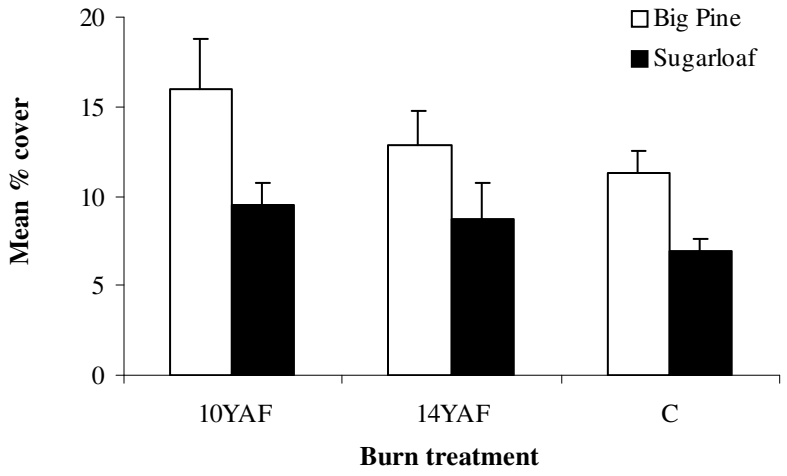

Figure 5.4. Mean (±SE) percent cover of herbaceous species on Big Pine and Sugarloaf. Deer treatments were high (Big Pine) and low (Sugarloaf) and burn year treatments were 10YAF, 14 YAF, and Control (unburned).

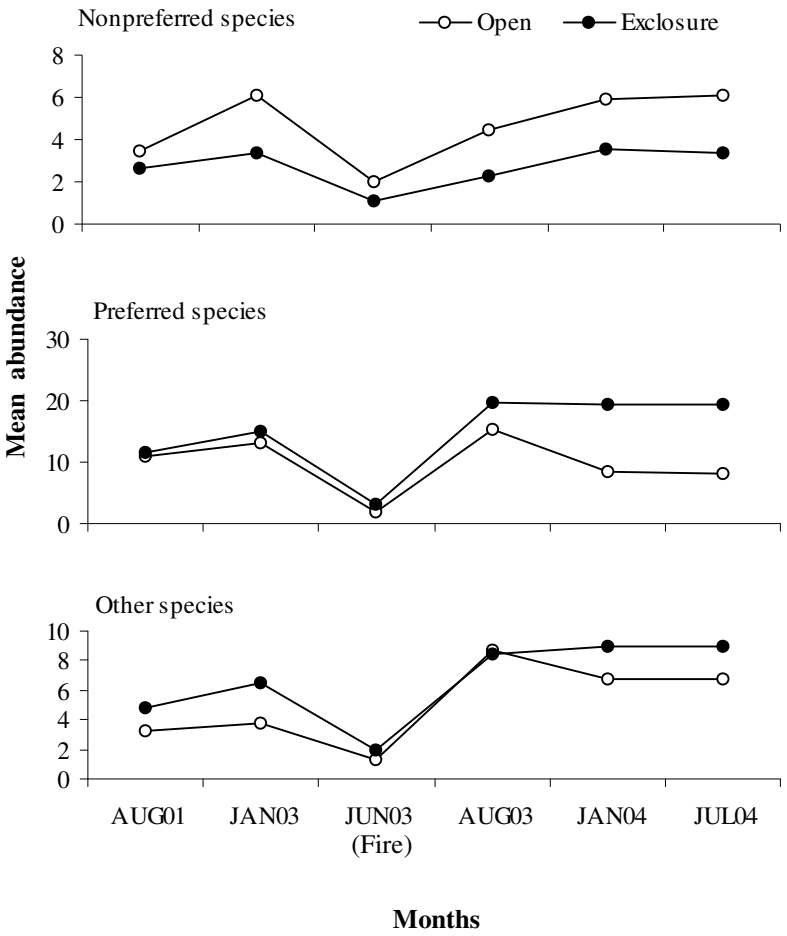

Figure 5.5. Mean woody plant species abundance in exclosure and open plots in pine rocklands on No Name. A fire occurred in June 2003. Plant abundances were all height classes combined for each deer preference category. Plant species are categorized as nonpreferred, preferred, and other (Palm spp. and *Byrsonima lucida*).

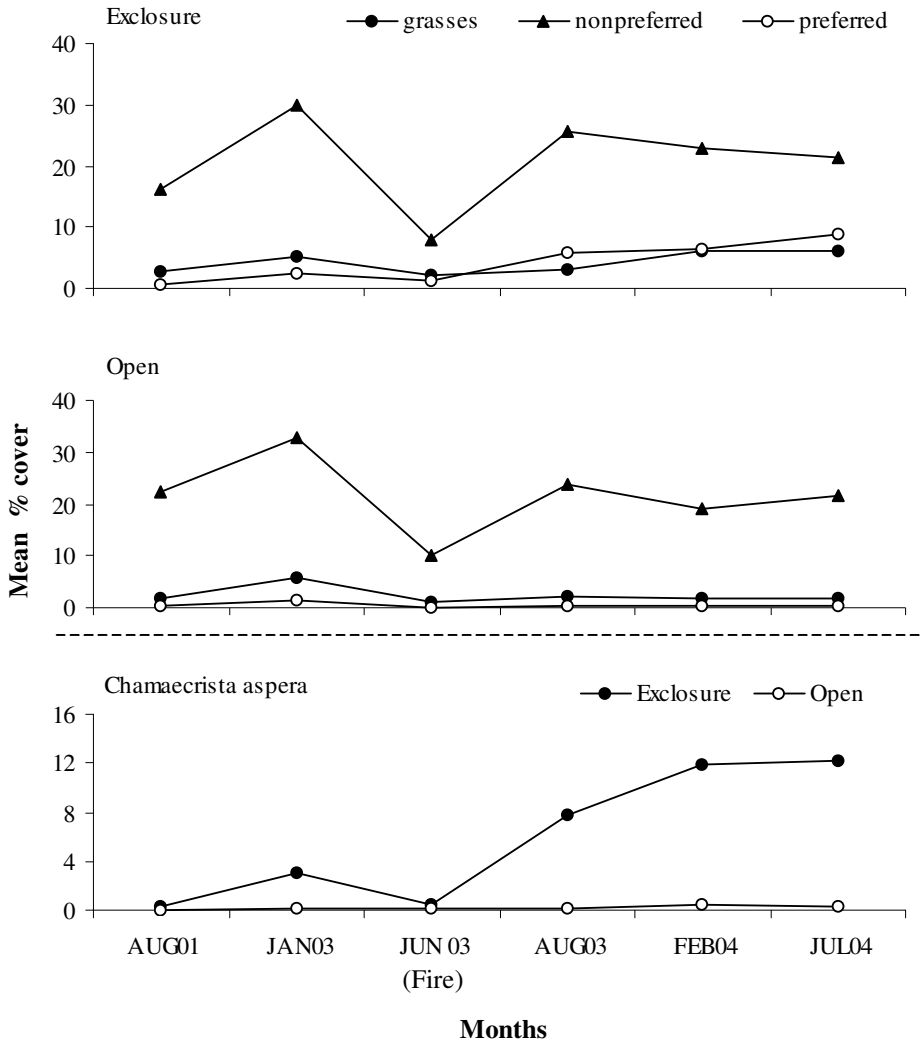

Figure 5.6. Mean percent cover of herbaceous species in exclosure and control plots in pine rocklands on No Name. A fire occurred in June 2003. Herbaceous species are categorized as preferred, nonpreferred and grasses. *C. aspera* is shown as an example of a preferred species.

Discussion

In pine rocklands, both fire and Key deer herbivory affect plant species richness and inhibit the growth of many woody species. Key deer herbivory deters the establishment of preferred hardwood species such as *Bursera simaruba, Erithalis fruticosa, Jacquinia keyensis*, and *Bumelia celastrina*, all of which are facultative hammock species and are absent from pinelands on Big Pine but present in pinelands on Sugarloaf regardless of burn treatments. Evidence from this study suggests that Key deer herbivory affects woody plant species composition more than fire. Lack of a fire effect on plant species composition is not unusual (e.g. Dix 1960; Daubenmire 1969; Abrahamson 1984*a*), though it is not the rule. Interestingly, fire and deer herbivory also interact as indicated by lower densities of taller preferred woody species in previously burned areas on Big Pine compared to unburned areas. Fire and deer herbivory also (additively) affect *Pinus elliotti* var. *densa* densities because no regeneration is found in unburned pinelands on Sugarloaf where lack of fire and deer herbivory fail to reduce hardwood encroachment which likely shade-out or out-compete *P. elliotti* var. *densa* recruits. Therefore, while fire effects alone (depending on frequency) may not wholly deter hardwood invasion into pinelands, the addition of Key deer herbivory aids in retarding succession of pine rocklands into hardwood hammock. However, excessive browsing by Key deer could be detrimental to certain plant species as observed in other habitats on Big Pine (Chapter 2).

Some preferred herbaceous species especially suffer from heavy Key deer browsing after fire as evidenced from the deer exclosure study on No Name. Herbaceous species tend to recover slowly after release from white-tailed deer browsing (Balgooyen and Waller 1995), yet fire often aids in the recovery (Lay 1956; Snyder 1986). For example, mean cover of *Chamaecrista aspera* increased by < 2% inside exclosures over a 2-year period. After a fire occurred in the deer exclosures mean cover of *C. aspera* increased to 8% by 2 months post-burn and >10% by 1 year post-burn. Though fire can have positive effects on herbaceous species, heavy deer browsing pressure can be detrimental for herb species in burned areas (McCulloch 1969). Fire can increase browsing pressure via increased plant quality (e.g. nutrient levels, Carlson et al. 1993) in that mean % cover of *C. aspera* remained very low outside exclosures on No Name even after fire. Therefore, a complex interaction of fire and Key deer herbivory determine

herbaceous community composition. Further evidence for fire-deer effects on herb species was observed in unburned pinelands on Big Pine that had the highest herb species richness. Unburned pinelands might offer a 'refuge' for some (possibly shade-tolerant) herb species where Key deer browsing is not prevalent. Though on Sugarloaf, high canopy cover likely limits herb establishment in pinelands.

Though the fire-deer effects between Big Pine and Sugarloaf are limited due to fires occurring $\geq$ 10 years ago, the exclosure study on No Name illustrates the strong effects of fire-deer interactions. Fire and Key deer browsing each play an important role in shaping pine rockland plant communities. Counteracting positive and negative influences of browsing pressure and fire on pineland plant species can complicate management efforts. However, a balance of controlled burn regimes and deer management is required to maintain viable pineland plant communities in the lower Florida Keys.

Management implications

Pinelands should be burned in small tracts (< 20 acres) allowing for unburned areas to act as a refuge from heavy deer herbivory on islands with high Key deer densities. Burning smaller areas would allow for a greater variety of successional stages and may increase plant diversity. Fire frequency should occur at least within a 10-year period to prevent hardwood invasion on islands with many Key deer, but perhaps more frequently on other islands with lower Key deer densities. Mechanical thinning of hardwoods may also be required to preventexcessive fuel buildup. Because fire maintains plant species within Key deer reach and increases herb cover, caution should be exercised as burning large areas might increase food availability and further increase Key deer densities and browsing impacts on Big Pine. However, browsing could also aid in thinning hardwood plant densities, stunting hardwood plant heights, and decreasing fuel-buildup, all of which could deter detrimental high-intensity or canopy fires. Future studies examining fire-deer interactions should employ an experimental design on high Key deer density islands containing recently burned vs. unburned plots, each with deer exclosure/control plots, and recently burned vs. unburned plots among islands with different Key deer densities. The design should incorporate a long-term component involving multiple burns (at a selected frequency) to establish guidelines for future prescribed burn regimes.

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APPENDICES

Appendix 1. Woody species common and scientific names. Names are ranked in descending order of relative density summarized (from quadrat data 2001-02) over all 12 islands in the study.

Rank	Common Name	Scientific Name	Relative density[a]
1	Spanish stopper	*Eugenia foetida*	18.90
2	Black mangrove	*Avicennia germinans*	15.55
3	White mangrove	*Laguncularia racemosa*	9.60
4	Red mangrove	*Rhizophora mangle*	6.92
5	Indian mulberry	*Morinda royoc*	4.94
6	Blackbead	*Pithecellobium keyense*	4.53
7	Buttonwood	*Conocarpus erectus*	4.45
8	Poisonwood	*Metopium toxiferum*	4.10
9	White stopper	*Eugenia axillaris*	3.90
10	White indigo-berry	*Randia aculeata*	3.76
11	Darling plum	*Reynosia septentrionalis*	2.54
12	Maiden bush	*Savia bahamensis*	1.98
13	Saffron plum	*Bumelia celastrina*	1.71
14	Black torch	*Erithala fruticosa*	1.62
15	Keys thatch palm	*Thrinax morrissii*	1.46
16	Long stalked stopper	*Psidium longipes*	1.24
17	Pigeon plum	*Coccoloba diversifolia*	1.04
18	Joewood	*Jacquinia keyensis*	1.01
19	Myrsine	*Myrsine floridana*	0.96
20	Wild dilly	*Manilkara bahamensis*	0.88
21	Torchwood	*Amyris elemifera*	0.83
22	Locust berry	*Byrsinoma lucida*	0.74
23	Christmas berry	*Lycium carolinianum*	0.70
24	Long leaf blolly	*Guapira discolor*	0.61
25	Sea grape	*Coccoloba uvifera*	0.60
26	Silver palm	*Coccothrinax argentata*	0.53
27	Limber caper	*Capparis flexuosa*	0.48
28	Marlberry	*Ardisia escallinoides*	0.37
29	Mayten	*Maytenus phyllanthoides*	0.33
30	Slash pine	*Pinus elliottii var. densa*	0.32
31	Jamaica dogwood	*Piscidia piscipula*	0.31
32	Wax myrtle	*Myrica cerifera*	0.29
33	Gumbo-limbo	*Bursera simaruba*	0.25
34	Saw palmetto	*Serenoa repens*	0.25
35	Rough velvet seed	*Guettarda scabra*	0.22
36	Cabbage palm	*Sabal palmetto*	0.18
37	Willow bustic	*Bumelia salicifolia*	0.17
38	Bahama nightshade	*Solanum bahamense*	0.16
39	Rhacoma	*Crossopetalum rhacoma*	0.15

Appendix 1. Continued

Rank	Common Name	Scientific Name	Relative density[a]
40	Black ironwood	Krugiodensdrom ferreum	0.14
41	Pisonia	Pisonia rotundata	0.13
42	Spicewood	Calypranthes pallens	0.12
43	Crabwood	Ateramnus lucidus	0.12
44	Milkbark	*Drypetes diversifolia*	0.11
45	Necklace pod	*Sophora tomentosa*	0.11
46	False boxwood	*Gyminda latifolia*	0.09
47	Tallow wood	*Ximennia americana*	0.08
48	Varnish leaf	*Dodonaea viscosa*	0.08
49	Bay cedar	*Suriana maritima*	0.04
50	Paradise tree	*Simarouba glauca*	0.04
51	Wild lime	*Zanthoxlum fagara*	0.04
52	Inkwood	*Exothea paniculata*	0.04
53	Brazilian pepper	*Schinus terebenthifolia*	0.03
54	Pineland croton	*Croton linearis*	0.03
55	Sapodilla	*Manilkara zapota*	0.02
56	Jamaican caper	*Capparis cynophallophora*	0.02
57	Caesalpinia	*Caesalpinia pauciflora*	0.02
58	Ficus	*Ficus sp.*	0.02
59	Bahama senna	*Cassia bahamensis*	0.02
60	Pond apple	*Annona glabra*	0.02
61	Silver buttonwood	*C. erectus var. sericeus*	0.01
62	Cocoplum	*Chrysobalanus icaco*	0.01
63	Satinleaf	*Chrysophyllum oliviforme*	0.01
64	Pine acacia	*Acacia pinetorum*	0.01
66	Manchineel	*Hippomane mancinella*	0.01
69	False sisal	*Agave decipiens*	<0.01
70	Strongbark	*Bourreria ovata*	<0.01
71	Guava	*Psidium guajava*	<0.01

[a] Relative density = $\frac{\text{total plant species density on all islands}}{\text{total of all plant species densities on all islands}} \times 100$

ABOUT THE AUTHOR

Mark Allen Barrett, son of David and Patsy Barrett, was born on 5 October 1972 in Austin, Texas. In Florida between 1998 and 2004, he assisted in several research projects involving seagrass restoration in Tampa Bay, live-rock bed construction in Tampa Bay, NASA aquaculture, effects of elevated CO_2 on plant-insect interactions at Cape Kennedy, monitoring/transplanting endangered cacti in the Florida Keys, and an OPS position at the Florida Department of Environmental Protection in Tampa. Mark received a National Pell Grant from 1998-2000, and he completed a bachelor's degree in biology at the University of South Florida in 2000. In 2000, he began a Ph.D. program in Ecology under the supervision of Peter Stiling, Ph.D. at the University of South Florida. During the program, Mark was a Research Assistant and a Teacher's Assistant for biology and ecology labs. In 2004, Mark is expected to complete his doctoral degree.