ELSEVIER

BIOLOGICAL CONSERVATION

Effects of Key deer herbivory on forest communities in the lower Florida Keys

Mark A. Barrett*, Peter Stiling

Department of Biology, University of South Florida, 4202 E Fowler Ave, SCA110 Tampa, FL 33620, USA

ARTICLE INFO

ABSTRACT

Ungulate herbivory can have strong impacts on plant communities, but these impacts are rarely considered in recovery plans of endangered species. This study examined the effects of the endangered Key deer (*Odocoileus virginianus clavium*) on its environment in the lower Florida Keys. The Key deer population has increased to over 700 deer from approximately 50 deer in the 1950s; however, approximately 75% of the population resides on only a few islands (Big Pine, No Name, Big Munson) where Key deer herbivory on forest communities may be substantial. Effects of deer herbivory on plant densities were estimated on these islands using vegetation quadrats in hardwood hammock, buttonwood transition, and mangrove wetlands and compared to nine other islands with intermediate or low deer densities. On islands with high deer density, densities of preferred woody plant species <1.2 m tall (within Key deer reach) were significantly lower than islands with lower deer densities, while densities of some nonpreferred species were significantly higher. Deer exclosures established in hardwood hammock on a high-density deer island revealed a mean increase in abundance/height of preferred woody species inside exclosures, while nonpreferred species significantly increased in open plots. We conclude that on high deer density islands, highly preferred plant species might eventually fail to regenerate and unpalatable plant species may become dominant. Careful criteria need to be developed to maintain Key deer numbers above an endangered species status yet below levels that are destructive to local forest species.

© 2005 Elsevier Ltd. All rights reserved.

1. Introduction

Ungulates, such as deer, can have strong effects on plant mortality and plant community composition, and can modify successional pathways and alter nutrient cycles at numerous spatial scales (McNaughton, 1976; Seagle et al., 1992; Inouye et al., 1994; Hobbs, 1996; McLaren, 1996; Frank and Groffman, 1998; Ball et al., 2000; Coomes et al., 2003; Rooney and Waller, 2003). Browsing effects by white-tailed deer (*Odocoileus virginianus*) are well documented in the northern United States, but studies are generally lacking in the southeastern United States, including Florida (Russell et al., 2001).

The present study investigated the effects of Florida Key deer (*Odocoileus virginianus clavium*) herbivory on local plant species following a substantial increase in the population over a 30-year period (Silvy, 1975; Lopez, 2001). Key deer, a diminutive subspecies of the white-tailed deer, are endemic to the lower Florida Keys. Habitat loss and over-hunting significantly lowered Key deer numbers resulting in the establishment of the National Key Deer Refuge (NKDR) in 1957 and federal listing as an endangered species in 1967 (USFWS, 1999). Consequently, the Key deer population increased from approximately 50 animals in the 1950s to 300–400 in the 1970s to over 700 animals by 2000 (Lopez, 2001). Approximately 75%

---

of the population resides on only two islands (out of 26), Big Pine and No Name Keys (Lopez et al., 2004a), resulting in a skewed distribution and relatively high Key deer densities on these two islands with lesser densities on various other islands. The magnitude of deer effects on local vegetation can best be determined when a sufficient contrast exists among deer densities (e.g., Tilghman, 1989; Horsley et al., 2003). Consequently, disproportionate Key deer densities allowed for a distinctive study that considers the effects of an endangered species on its habitat, including unique plant communities, such as rare tropical hardwood hammock, considered imperiled in the state of Florida (Florida Natural Areas Inventory, 1990).

Observational and manipulative studies were conducted to understand plant-Key deer density dynamics. Because Key deer use several habitats (Klimstra et al., 1974; Folk, 1991; Lopez et al., 2004b), and their diet includes lowland and upland plant species (Klimstra and Dooley, 1990), impacts of Key deer were anticipated for all sampled plant communities on islands with high deer densities. Specific predictions were as follows: (1) Key deer should show a distinct preference for some plant species over others, i.e., nonrandom selection, (2) Densities of woody plant species <1.2 m tall (within Key deer reach) that are preferred by deer should be lower on islands with high Key deer densities than on islands with fewer deer, whereas woody plant species not preferred by deer should have higher densities on islands with high deer densities, and (3) Deer exclosures established on an island with a high deer density will cause an increase in abundance and height of woody plant species preferred by deer, whereas woody species not preferred by deer will increase in open (no exclosure) plots.

2. Study area

The study was conducted in the lower Florida Keys within the boundaries of the NKDR (24°36′N–81°18′W to 81°34′W). The climate is subtropical with evident wet (May–October) and dry (November–April) seasons. The mean annual temperature is ~25.2 °C and mean annual rainfall is ~100 cm.

The NKDR archipelago contains lowlands, uplands, saline and freshwater environments. Three general habitat types – hardwood hammock, buttonwood transition, and mangrove wetlands – were utilized in this study with habitat descriptions based on Folk (1991). Hardwood hammock is a climax successional community formed by tropical hardwood plant species that occur in uplands. Common woody tree and shrub species include: Jamaica dogwood (*Piscidia piscipula*), Gumbo-limbo (*Bursera simaruba*), Pigeon plum (*Coccoloba diversifolia*), Willow bustic (*Bumelia salicifolia*), White stopper (*Eugenia axillaris*), Spanish stopper (*Eugenia foetida*), and Maiden bush (*Savia bahamensis*). Buttonwood transition is composed of salt tolerant plant species that inhabit areas adjacent to upland habitats composed of (woody species): Buttonwood (*Conocarpus erectus*), Joewood (*Jacquinia keyensis*), Wild dilly (*Manilkara bahamensis*), Saffron plum (*Bumelia celastrina*), Mayten (*Maytenus phyllanthoides*), and Blacktorch (*Erithalis fruticosa*). Extended periods of saltwater inundation and poor nutrient exchange in mangrove wetlands produces mostly stunted woody plant species including: Black mangrove (*Avicennia germinans*), Red mangrove (*Rhizophora mangle*), White mangrove (*Laguncularia racemosa*), and Buttonwood.

3. Methods

3.1. Study islands

Key deer transiently use (mainly during the wet season) many islands within the NKDR archipelago (Folk, 1991; Lopez, 2001). Therefore, 12 islands frequently used year-round by Key deer that exhibit a deer density gradient were used to assign treatments: *low* deer density (Sugarloaf, Cudjoe, Summerland, Ramrod); *medium* deer density (Little Torch, Middle Torch, Big Torch, Howe, Little Pine); and *high* deer density (Big Pine, No Name, Big Munson) (Table 1). Islands at or near carrying capacity were defined as high-density islands (>17 deer km^{-2}) as reported by Lopez et al. (2004a). Islands at half of the estimated carrying capacity were defined as medium-density islands (3–8 deer km^{-2}, Lopez, 2001), and islands well below the estimated carrying capacity (<1 deer km^{-2}, Lopez, 2001) were defined as low-density islands. Each of the 12 islands contained the three habitats described above. Pine rockland, beach dune and cactus hammocks, freshwater marsh, and buttonwood prairie were not included due to their limited distribution among the islands.

3.2. Cafeteria feeding trials

Cafeteria-feeding trials were conducted to understand plant selection by Key deer, which can aid in predicting herbivore effects on natural vegetation (Diaz, 2000). Feeding trials were conducted on Big Pine Key at four urban-residential sites. Preliminary trials (5 per site) were conducted in March 2002 to allow Key deer to acclimate to the feeding station. Thereafter, 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 individual Key deer were not tested, deer-plant species preference was

Table 1 – Key deer densities (high, medium, low) on 12 islands of frequent deer use within the NKDR

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

assessed at the population level. Trials were not conducted on days with excessive wind, as Key deer were apprehensive to feed on these days.

Sixteen woody plant species (Table 2) were selected for feeding trials by their frequency of occurrence in the NKDR (Dickson, 1955; Folk, 1991; personal observation) and by their incidence in Key deer rumen samples (Klimstra and Dooley, 1990). Stems of the 16 plant species were clipped from branches >1.2 m from the ground when possible. Stems collected from Big Pine, Middle Torch, and Sugarloaf Keys were used in preliminary test trials (acclimation period), which revealed no differences in deer-plant species selection due to island source (Friedman χ^2, for each species $P > 0.236$), so subsequent data were pooled for the trials. The stems (clipped ends) were secured to the feeding station in a circular array of PVC slots, 60 cm from the ground, so deer could "pull" off leaves simulating natural herbivory. To control for plant species associations, stems of each species were randomly placed in the slots numbered 1–16 (slot number 1 always faced north) for each trial. Separate cut stems were also set aside to account for weight loss due to evaporation; however, during the mean period of 1.5 h between clipping stems and trial termination, mean weight loss per species (<1.3 g) was negligible.

Trials commenced at 6 pm once per day and deer were allowed 7 min to feed. The stems were weighed to the nearest gram immediately before and after each trial and the leaves were counted. Because leaf number and leaf weight were highly correlated (Spearman's $r_s = 0.982$, $P < 0.001$), only weight was analyzed. Leaves remaining on a stem after the trial were clipped and the bare stem was weighed. The following equation determined the percent leaf (wet) weight browsed by Key deer: [(Pretrial stem (g) − post trial stem (g))/(Pretrial stem (g) − stem weight (g))] × 100. For example, if a cut stem weighed 50 g pretrial and 15 g post trial (stem plus remaining leaves), the remaining leaves were clipped, and the stem alone weighed 10 g, then [(50 g − 15 g)/(50 g − 10 g)] × 100 = 87.5% leaf weight consumed. A Relative Preference Value (RPV) was established by summing the mean percentage of leaf weight consumed per plant species plus the percent frequency of the plant species being eaten (at least one bite) throughout the 28 trials.

Although similar amounts of each plant species are ideal for preference testing (Johnson, 1980), the methodology only allowed a crude estimate of leaf weights. The average bulk leaf weight was ∼42 g (±7 g) species^{-1} trial^{-1}. Using relative proportions consumed per plant species likely caused the minor differences in leaf weights to be inconsequential. 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 (g) consumed per species per site. RPI values of each plant species were summarized over sites, and the lowest RPI value designated the most relatively preferred species. RPI values were qualitatively compared to RPV values to calibrate deer-plant preference.

3.3. Vegetation sampling

To examine the effects of Key deer herbivory on plant densities (ha^{-1}) among islands, vegetation was sampled on each island during the dry season from January to May of 2001 and 2002. A total of 200 nested quadrats were sampled throughout the 12 islands in the three habitat types (per island): hammock ($n = 5$–10), buttonwood ($n = 4$), and mangrove ($n = 6$). A 1×50 m quadrat was used to sample woody plant species with a diameter at breast height (dbh) < 12.7 cm. Plant species that exhibited root suckering were recorded as individuals if they branched underground and the protruding stems were

Table 2 – Mean percent leaf weight (g) consumed by Key deer of each plant species in feeding trials

Species	Site				Total (across sites)				
	1	2	3	4	Mean	SE %	F[a]	RPV[b]	RPI[c]
Bursera simaruba	98	96	98	97	97.2	0.56	100	197.2	−5.4
Erithalis fruticosa	89	92	92	93	91.6	0.87	100	191.6	−4.4
Rhizophora mangle	75	93	87	85	85.1	3.83	100	185.1	−3.6
Bumelia celastrina	86	86	85	80	84.3	1.57	100	184.3	−1.8
Jacquinia keyensis	84	86	84	79	83.1	1.63	100	183.1	−1.7
Morinda royoc	53	58	60	98	67.4	10.2	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 germinans	2	2	8	14	6.3	2.83	53.5	59.8	2.9
Byrsinoma lucida	0	0	0	65	16.3	15.5	25.0	41.3	3.3
Piscidia piscipula	0	0	0	0	0.0	0.0	0.0	0.0	5.3
Laguncularia racemosa	0	0	0	0	0.0	0.0	0.0	0.0	5.3
Eugenia axillaris	0	0	0	0	0.0	0.0	0.0	0.0	5.3
Eugenia foetida	0	0	0	0	0.0	0.0	0.0	0.0	5.3

a % Frequency eaten per species (>one bite per trial) out of 28 trials.
b Rank preference value (RPV) = mean % + % frequency.
c Rank preference index (RPI) – see Methods for calculation.

separated. Woody plant species were assigned to height classes: <1.2 m tall (seedlings/saplings within Key deer reach) and >1.2 m tall. Though Key deer browsing can directly affect plant species <1.2 m tall (understory), Key deer herbivory should not influence the same plant species >1.2 m tall (above the browse tier). A 10 × 50 m quadrat, bisected by the 1 × 50 m quadrat, was used to estimate basal areas of large tree species with a dbh > 12.7 cm. Basal areas (m^2 ha^{-1}) were compared to examine any fundamental differences in successional stage for a given habitat, which could influence understory or sub-canopy structure and composition. Total basal areas (sum of basal areas for all species combined) were standardized by dividing by the number of plant species (>12.7 cm dbh) sampled per habitat per island. Canopy cover, a habitat variable that could affect understory plant composition, was measured with a concave densiometer set on a tripod (45 cm high) placed every 10 m along the 1 m × 50 m quadrat. Percent canopy cover (5 samples per quadrat) was averaged for each habitat per island. Methodology for densiometer measurements was according to Lemmon (1957).

3.4. Deer exclosures

In August 2001, three square 37 m^2 deer exclosures were constructed on No Name Key in hardwood hammock with corresponding control (open) plots. To facilitate labor and to decrease construction costs, exclosure plots were located near roads (within 15 m–50 m) using a stratified random scheme. To illustrate, using digital maps of No Name in ArcView 3.2, 35-m wide buffers starting 15 m from roads were established near hammock plant communities; then, a random point generator was used to select three points (exclosure locations) within the buffer. A handheld GPS was used to locate the three sites in the field where the exclosures were subsequently erected. We non-randomly selected control plots, each located within 10 m of exclosure plots, to attain a similar plant composition compared to exclosures. Galvanized chain-linked fencing 1.8 m high was erected to exclude Key deer, but raised 15 cm above ground level 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 by height class: <0.05 m, 0.05–0.6 m, 0.6–1.2 m, 1.2–1.8 m, and >1.8 m. To limit edge effects, data were not recorded in a buffer zone (0.3 m W × 2.1 m H) within the plot perimeters. Herbaceous cover was too sporadic in each plot for adequate comparisons, so results were not included.

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

4. Data analysis

4.1. Cafeteria feeding trials

For Key deer feeding trials, plant species data were summarized across sites and the difference in proportion of leaf weight consumed between plant species was tested for significance using a χ^2 procedure for multiple proportions (Zar, 1999). Analyses only included plant species consumed with a frequency >0 across sites. Because background vegetation differed between feeding trial sites, which could cause differential feeding behavior by deer, differences in proportion of leaf weight consumed per site was tested. Proportion of leaf weight consumed was summarized across plant species within sites and the same χ^2 procedure above tested for statistical differences among multiple proportions. A Tukey-type post hoc test with angular transformation was used to determine comparison-wise differences in proportions consumed among the sites (Zar, 1999). Potentially, different groups of deer were present for each trial causing intra-site replication per plant species to be suspect and precluded testing (statistically) site × species interactions.

4.2. Vegetation sampling

Densities of the 16 plant species utilized in feeding trials were compared among deer treatments to test for herbivore effects. The densities of 10 additional plant species, not tested in feeding trials, were also compared among deer treatments. Predominately, additional species were considered less preferred as they were not commonly browsed throughout a given year and ranked below the top 28 plant species (75% of the total volume) out of >164 species found in Key deer rumen samples (Klimstra and Dooley, 1990). However, Guapira discolor is considered a preferred species because it was previously noted as highly browsed by Key deer (Klimstra et al., 1974). Two other plant species, Thrinax morrissii and Manilkara bahamensis, had a high frequency and volume in rumen analysis (Klimstra and Dooley, 1990); however, this was mainly from seasonal fruit consumption by Key deer, which may or may not affect recruitment of plant species. Thus, an effect of deer density on these two species is uncertain, and they were excluded from the following analyses grouped by deer preference.

Plant species were grouped by deer-preference (preferred and less preferred) and by height class (<1.2 m and >1.2 m tall). The density of each preference group was tested separately by height class for differences among deer treatments using a split-plot ANOVA with deer treatment (low, medium, high) and habitat (hammock, buttonwood, mangrove) as factors with island nested within deer treatment. Mean percent canopy cover and mean total basal areas (all species combined) were each tested using a split-plot ANOVA with deer treatment and habitat type as fixed factors, with island nested within deer treatment. When necessary, data were transformed prior to analysis to improve normality or homogeneity of variance.

Plant species diversity was compared among islands using Fisher's α, which has high discriminant ability and is unaffected by sample size (Magurran, 1988). Plant densities were used for diversity calculations, and data were combined for

all height classes and sampled habitats on each island. Linear regression was used to analyze patterns of diversity among islands using each deer density and island size as separate factors. Both factors were log transformed to improve linearity.

4.3. Deer exclosures

For the exclosure study, plant abundance data (mean difference between first and last sampling dates) were tested using a 1-way ANOVA for preferred species and Mann–Whitney U for less preferred species with deer treatment (exclosure/open) as the main effect. Changes in plant heights were examined by finding the percent change of plant abundance within each height class by preference category (preferred, less preferred) using the following equation: % change within each height class = [(species Y abundance Jan04 – species Y abundance Aug01)/species Y total abundance] × 100, where Y is all species within a deer preference category and Y total abundance is Aug01 + Jan04. Differences between deer treatment for the change in abundance of each height class were tested using t-tests. Data were square root transformed when necessary to meet parametric assumptions. All analyses were tested for significance at the $\alpha = 0.05$ level.

5. Results

5.1. Cafeteria feeding trials

Key deer showed strong preferences for certain plant species as measured at the population level (χ^2 of species pooled across sites = 1896.9, df = 11, $P < 0.001$; Table 2). The overall consumption of plant species differed between sites (χ^2 of species pooled within site = 100.1, df = 3, $P < 0.001$) indicating a spatial difference in deer-plant selection. 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 consumption of *Morinda royoc* and especially *Byrsonima lucida* at site 4 (Table 2). The most preferred species, consistent among sites, were *Bursera simaruba*, *Erithalis fruticosa*, *Rhizophora mangle*, *Bumelia celastrina* and *Jacquinia keyensis*. Consumption was more variable for moderately preferred species such as *Morinda royoc*, *Pithecellobium keyense*, and *Randia aculeata*. *Piscidia piscipula*, *Laguncularia racemosa*, *Eugenia axillaris* and *Eugenia foetida* were never eaten, while the remaining plant species were scarcely consumed and were variably browsed among sites. Only two species, *Morinda royoc* and *Pithecellobium keyense*, were switched in preference ranking according to the methods used (RPV versus RPI; Table 2).

5.2. Vegetation sampling

No trend in total basal area (all species combined) was evident between deer treatments ($F_{2,9} = 0.197$, $P = 0.825$) or the treatment × habitat interaction ($F_{2,9} = 3.27$, $P = 0.086$) (Fig. 1). However, for *Bursera simaruba* in hammock, mean basal area (m^2ha^{-1}) (±SE) were as follows per deer treatment (low, medium, high): low = 1.50 (0.49), medium = 2.27 (1.35), and
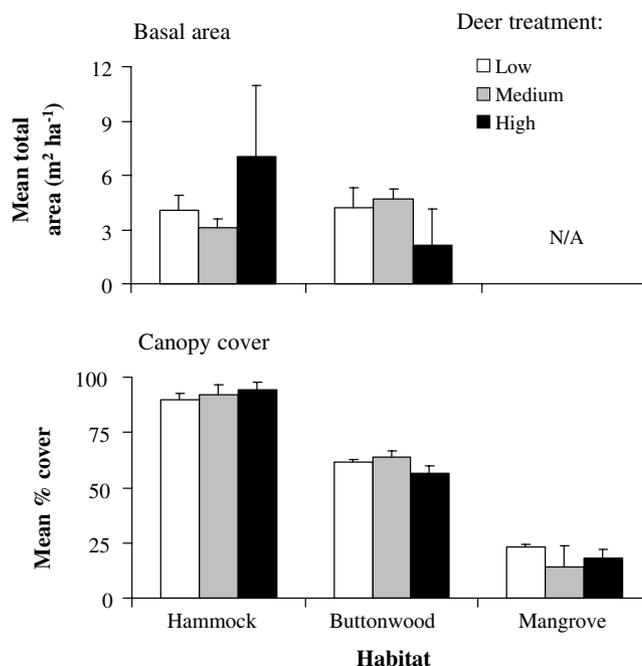

Fig. 1 – Habitat characteristics (mean ± SE) for deer treatments including total basal area (all tree species > 12.7 cm dbh) and percent canopy cover.

high = 19.22 (9.30). The high variance in basal area for high deer treatment was mainly due to larger *B. simaruba* trees on Big Munson. There were no significant differences in percent canopy cover between deer treatments ($F_{2,9} = 0.271$, $P = 0.768$), nor for treatment × habitat ($F_{4,18} = 1.37$, $P = 0.284$), but canopy cover varied between habitats ($F_{2,18} = 228.96$, $P < 0.001$) with hammock having the highest percent cover (Fig. 1). Therefore, each deer treatment had reasonably similar intrinsic properties (except for basal area of *B. simaruba*).

High deer treatment negatively influenced the overall densities of preferred plant species <1.2 m tall ($F_{2,9} = 7.17$, $P = 0.014$) (Fig. 2), though the interaction with habitat was not significant ($F_{4,18} = 0.76$, $P = 0.565$). Deer herbivory negatively affected each highly preferred species (Supplemental Data). The densities of preferred species >1.2 m tall did not differ between deer treatments ($F_{2,9} = 2.89$, $P = 0.107$) nor was the interaction significant ($F_{4,18} = 1.98$, $P = 0.141$), though densities were low in hammock on islands with high deer density (Fig. 2). For less preferred species <1.2 m and >1.2 m tall there was no relationship between plant density and deer treatment (each $P > 0.355$) nor habitat × deer treatment interaction (each $P > 0.199$). However, relative densities of less preferred species [(density of less preferred/(density of less preferred + preferred)) × 100] summarized over habitats and height classes was 84% and 66% for islands with high and low deer treatment, respectively, indicating higher proportions of less preferred species compared to preferred species on islands with many deer.

Plant species diversity (Fisher's α) for all habitats combined significantly varied with island size ($F_{1,10} = 14.35$, $P = 0.004$, $R^2 = 0.59$) but not with deer density ($F_{1,10} = 0.20$, $P = 0.668$, $R^2 = 0.02$) (Fig. 3).
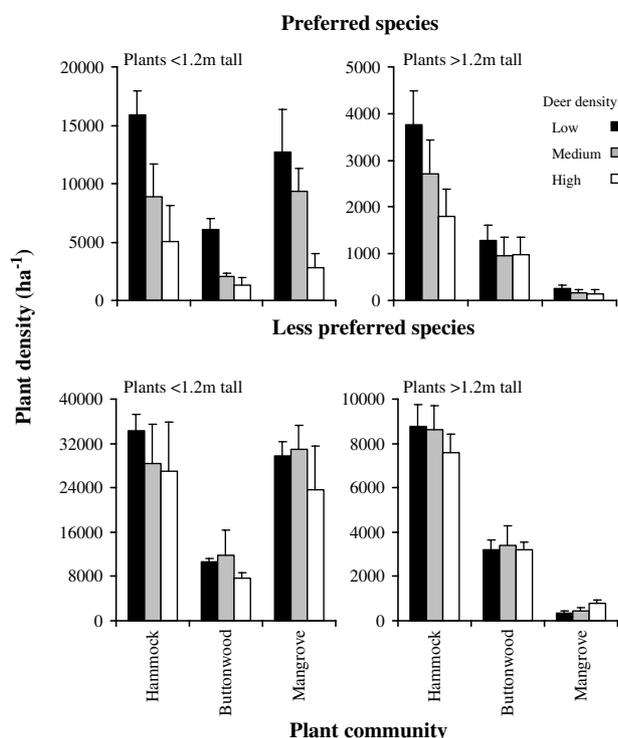
Fig. 2 – Mean (±SE) plant species densities among deer treatments in three plant communities. Plant species are categorized by height class (<1.2 m and >1.2 m tall) and by Key deer preference (preferred and less preferred).
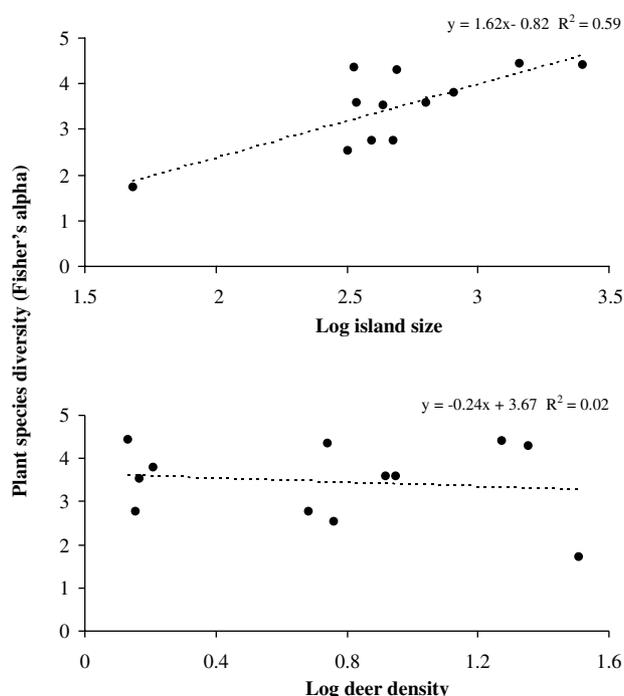

Fig. 3 – Plant species diversity (Fisher's a) in relation to log island size (km^2) and log deer density (deer km^{-2}). Diversity was measured from all plant height classes and plant communities combined per island. Also shown are the linear equations and R^2 values.

5.3. Deer exclosures

Differences in woody species abundance between exclosures and control plots on No Name illustrated the strong effect Key deer can have on plant communities (Fig. 4), though some species were affected more than others (Supplemental Data). Preferred plant species abundance significantly increased inside deer exclosures and decreased in open plots ($F_{1,4} = 8.28$, $P = 0.045$) (Fig. 4). Most preferred species also grew taller inside exclosures (Table 3), except Bursera simaruba that did not grow beyond the smallest height class (<0.05 m). Less preferred woody species significantly differed between treatments ($U = 0.00$, $P = 0.046$), increasing more in open plots than inside exclosures (Fig. 4). The heights of less preferred species tended to increase more in open plots (Table 3). Also two new species established, Bumelia salicifolia in exclosures and Ximennia americana in open plots, yet neither species were highly preferred by Key deer (Klimstra and Dooley, 1990).

6. Discussion

In the understory (plants <1.2 m tall), Key deer browsing is negatively affecting densities of highly preferred plant species and (indirectly) positively affecting densities of certain non-preferred plant species, suggesting that Key deer are strongly influencing plant community composition on islands with high deer densities. Preferred plant species were historically prevalent in the understory of Big Pine and No Name Keys when the Key deer population was smaller (Dickson, 1955;
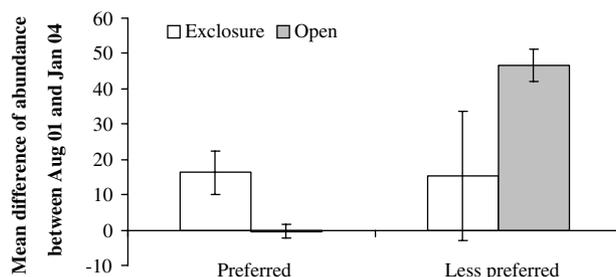

Fig. 4 – Mean (±SE) difference (between Aug 2001 and Jan 2004) of plant species abundance in exclosures (deer absent) and corresponding open plots (deer present). Plant species are categorized by deer preference (preferred and less preferred).

Folk, 1991), but have declined since the 1990 s (Barrett, 2004) as Key deer densities markedly increased. On islands with high deer densities, very low densities of deer-preferred plant species <1.2 m tall, such as Bursera simaruba, Erithalis fruticosa (state listed – threatened), Rhizophora mangle (species of special concern), Bumelia celastrina, Jacquinia keyense (state listed – threatened), and Guapira discolor threatens their regeneration by leaving few seedlings to replace senescing or wind-thrown trees. Also, preferred species are not growing sufficiently above the browse-tier, and height growth of highly palatable species (e.g., Bursera simaruba in this study) can remain impeded even following relief (exclosures) from deer herbivory (e.g., Kuiters and Slim, 2002). Furthermore,

Species type						
Height class (m)	Preferred			Less preferred		
	Ex	C	P	Ex	C	P
<0.05	5.5	−14.1	**0.023**	0.5	3.1	0.180
0.05–0.6	17.7	7.0	0.217	5.6	26.9	**0.040**
0.6–1.2	1.8	0.0	**0.067**	3.3	−2.2	**0.065**
1.2–1.8	1.8	0.0	**0.067**	−0.9	0.3	0.329
>1.8	2.4	0.0	**0.025**	0.2	0.1	0.797

Table 3 – Mean percent change (between Aug01 and Jan04) in plant species abundance, according to Key deer preference (species type), within height classes inside exclosure (Ex) and control (C) plots

Bold P values indicate statistically significant (some marginal) difference between Ex and C from t-tests.

continuous depletion of preferred plant species by Key deer might eventually cause plant species diversity to decline, as found in other studies (e.g., Rooney et al., 2004; Webster et al., 2005), eventually diluting the island size effect. Islands with medium deer density should also be closely monitored because some browse-intolerant plant species may considerably decline in abundance from even moderate browsing pressure (Nugent et al., 2001).

On islands with many Key deer, all plant communities sampled in this study experienced strong impacts from deer herbivory. However, state-imperiled hardwood hammock 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 thus substantial deer use (Lopez et al., 2004b). This could cause conflicts in managing both endangered Key deer and plant communities. Historically, substantial development in the Florida Keys prompted conservationists to: (1) protect endangered Key deer, and (2) preserve plant communities via land acquisition. As many plant communities are considered Key deer habitat in the NKDR, challenges arise in applying these two strategies. For example, safeguarding mangrove communities benefits both strategies by preserving wetland area and *Rhizophora mangle*, a principal food of Key deer (Klimstra and Dooley, 1990). Yet, heavy browsing by Key deer can deplete *R. mangle* densities, which can have considerable community-wide effects because *R. mangle* aids in stabilizing marginal and coastal areas (Davis, 1940) and may act as a pioneer species for upland plant communities in south Florida (Alexander, 1955). Although a healthy population size of Key deer should be maintained, keeping their local densities at non-destructive levels to protect plant communities will require adaptive and flexible conservation plans. Furthermore, because deer can affect rare or endangered plant species (Miller et al., 1992; Maschinski, 2001; Fletcher et al., 2001; Hampe and Arroyo, 2002; Mysterud and Ostbye, 2004; Gomez-Aparicio et al., 2005) as found in this study, species management can become increasingly complicated (i.e., plant versus animal conservation). These implications should be considered in recovery plans for other endangered [deer] species, though local issues will undoubtedly vary for each species.

The exclosure study on No Name suggests that less preferred plant species increase more in open plots as preferred species decline. Also, certain nonpreferred plant species, such as *Piscidia piscipula* and *Coccoloba diversifolia,* had much higher

densities on islands with many deer (Supplemental Data), 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 (Tilghman, 1989; Seagle and Liang, 1997; Augustine and McNaughton, 1998; Cornett et al., 2000; Horsley et al., 2003). If Key deer herbivory remains chronically high on certain islands, increased competition by unpalatable plant species may further hinder the regeneration of browse-sensitive plant species.

The present study suggests that conservation biologists should carefully monitor the success of endangered species in restoration programs, so that the protected species do not reach 'destructive' densities. Relatively high local densities, exceeding 17 deer km^{-2} of the endangered Key deer on No Name, Big Pine, and Big Munson Keys have several possible ramifications for natural communities. Browsing impacts could ultimately decrease the availability of nutritional forage leading deer to malnutrition and disease (Davidson and Doster, 1997), indirectly affect other species that share the same habitat (e.g., Pollard and Cooke, 1994; McShea and Rappole, 2000), and affect forest species regeneration, as found in many deer studies world-wide (e.g., Alverson et al., 1988; Tilghman, 1989; Veblen et al., 1989; McShea et al., 1997; Russell et al., 2001; Schabel, 2001; Vourc'h et al., 2001; Zamora et al., 2001). It appears, however, that amelioration of Key deer herbivory pressure (via deer exclosures) may allow browse-susceptible plant species to reestablish and grow above the browse-tier, albeit over a longer time frame for some species, e.g., *Bursera simaruba*. Furthermore, Key deer have only recently reached relatively high densities on certain islands (Lopez et al., 2004a) and browsing effects are likely incipient because most plant species have relatively high densities of individuals above the browse tier (>1.2 m tall) on each island, thus, allowing time for land managers to develop criteria to maintain sufficient numbers of Key deer above an endangered species status yet below levels that are destructive to local forest species.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2005.10.026.

REFERENCES

Alexander, T.R., 1955. Observations on the ecology of the low hammocks of southern Florida. Quarterly Journal of the Florida Academy of Sciences 18, 21–27.

Alverson, W.S., Waller, D.M., Soleim, S.L., 1988. Forests too deer: edge effects in northern Wisconsin. Conservation Biology 2, 348–358.

Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62, 1165–1183.

Ball, J.P., Danell, K., Sunesson, P., 2000. Response of an herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. Journal of Applied Ecology 37, 247–255.

Barrett, M.A., 2004. An analysis of Key deer herbivory on forest communities in the lower Florida Keys. Ph.D. Dissertation. University of South Florida, Tampa, Florida.

Coomes, D.A., Allen, R.B., Forsyth, D.M., Lee, W.G., 2003. Factors preventing the recovery of New Zealand forests following control of invasive deer. Conservation Biology 17, 450–459.

Cornett, M.W., Frelich, L.E., Puettmann, K.J., Reich, P.B., 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. Biological Conservation 93, 359–369.

Davidson, W.R., Doster, G.L., 1997. Health characteristics and white-tailed deer population density in the southeastern United States. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institution Press, Washington, DC, pp. 164–184.

Davis, J.H., 1940. The ecology and geologic role of mangroves in Florida, Carnegie Institution of Washington, 517, 303–412.

Diaz, A., 2000. Can plant palatability trials be used to predict the effects of rabbit grazing on the flora of ex-arable lands. Agriculture, Ecosystems, and Environment 78, 249–259.

Dickson, J.D. III, 1955. An Ecological Study of the Key Deer. Technical Bulletin 3. Florida Game and Freshwater Fish Commission, Tallahassee, Florida, 104p.

Fletcher, J.D., Shipley, L.A., McShea, W.J., Shumway, D.L., 2001. Wildlife herbivory and rare plants: the effects of white-tailed deer, rodents, and insects on growth and survival of Turk's cap lily. Biological Conservation 101, 229–238.

Florida Natural Areas Inventory, 1990. The natural communities of Florida. Florida Department of Natural Resources, Tallahassee, Florida.

Folk, M.L., 1991. Habitat of the Key deer. Ph.D. Dissertation, Southern Illinois University, Carbondale, Illinois.

Frank, D.A., Groffman, P.M., 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79, 2229–2241.

Gomez-Aparicio, L., Zamora, R., Gomez, J.M., 2005. The regeneration status of endangered *Acer opalus* subsp. *granatense* throughout its geographical distribution in the Iberian Peninsula. Biological Conservation 121, 195–206.

Hampe, A., Arroyo, J., 2002. Recruitment and regeneration of an endangered South Iberian Tertiary relict tree. Biological Conservation 107, 263–271.

Hobbs, N.T., 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60, 695–713.

Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13, 98–118.

Inouye, R.S., Allison, T.D., Johnson, N.C., 1994. Old field succession on a Minnesota sand plain: effects of deer and other factors on invasion by trees. Bulletin of the Torrey Botanical Club 121, 266–276.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Klimstra, W.D., Hardin, J.W., Silvy, N.J., Jacobson, B.N., Terpening, V.A., 1974. Key deer investigations final report: Dec 1967-Jun 1973. U.S. Fish and Wildlife Service, Big Pine Key, Florida.

Klimstra, W.D., Dooley, A.L., 1990. Foods of the Key deer. Florida Scientist 53, 264–273.

Krebs, C.J., 1989. Ecological Methodology. Harper and Row, New York, New York.

Kuiters, A.T., Slim, P.A., 2002. Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biological Conservation 105, 65–74.

Lemmon, P.E., 1957. A new instrument for measuring forest overstory density. Journal of Forestry 55, 667–668.

Liu, H., Platt, S.G., Borg, C.H., 2003. Seed dispersal by the Florida box turtle (*Terrapene carolina bauri*) in pine rockland forests of the lower Florida Keys, United States. Oecologia 138, 539–546.

Lopez, R.R., 2001. Population ecology of the Florida Key deer. Ph.D. Dissertation. Texas A&M University, College Station, Texas.

Lopez, R.R., Silvy, N.J., Pierce, B.L., Frank, P.A., Wilson, M.T., Burke, K.M., 2004a. Population density of the endangered Florida Key deer. Journal of Wildlife Management 68, 570–575.

Lopez, R.R., Silvy, N.J., Wilkins, R.N., Frank, P.A., Peterson, M.J., Peterson, N.M., 2004b. Habitat use patterns of Florida Key deer: Implications of urban development. Journal of Wildlife Management 68, 900–908.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, New Jersey.

Maschinski, J., 2001. Impacts of ungulate herbivores on a rare willow at the southern edge of its range. Biological Conservation 101, 119–130.

McLaren, B.E., 1996. Plant-specific response to herbivory simulated browsing of suppressed balsam fir on Isle Royale. Ecology 77, 228–235.

McNaughton, S.J., 1976. Serengeti migratory wildbeest: facilitation of energy flow by grazing. Science 191, 92–94.

McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), 1997. The Science of Overabundance. Deer Ecology and Population Management. The Smithsonian Institution Press, Washington, p. 402.

McShea, W.J., Rappole, J.H., 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology 14, 1161–1170.

Miller, S.G., Bratton, S.P., Hadidian, J., 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. Natural Areas Journal 12, 67–74.

Monroe County Growth Management Division, 1992. Monroe County year 2010 comprehensive plan. Monroe County Planning Department, Key West, Florida.

Mysterud, A., Ostbye, E., 2004. Roe deer (*Capreolus capreolus*) browsing pressure affects yew (*Taxus baccata*) recruitment within nature reserves in Norway. Biological Conservation 120, 545–548.

Nugent, G., Fraser, W., Sweetapple, P., 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. Biological Conservation 99, 65–79.

Pollard, E., Cooke, A.S., 1994. Impact of muntjac deer *Muntiacus reevesi* on egg-laying sites of the white admiral butterfly *Ladoga camilla* in a camridgeshire wood. Biological Conservation 70, 189–191.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181, 165–176.

Rooney, T.P., Weigman, S.M., Rogers, D.A., Waller, D.M., 2004. Biotic impoverishment in unfragmented forest understory communities. Conservation Biology 18, 787–798.

Ross, M.S., Coultas, C.L., Hsieh, Y.P., 2003. Soil-productivity relationships and organic matter turnover in dry tropical forests of the Florida Keys. Plant and Soil 253, 479–492.

Russell, F.L., Zippin, D.B., Fowler, N.L., 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: A review. The American Midland Naturalist 146, 1–26.

Schabel, H.G., 2001. Deer and daurwald in germany: Any progress. Wildlife Society Bulletin 29, 888–898.

Seagle, S.W., Liang, S.Y., 1997. Bottomland forest composition and seedling diversity: simulations succession and browsing by overabundant deer. In: McShea, W.J., Underwood, H.B.,

Rappole, J.H (Eds.), The Science of overabundance: Deer Ecology and Population Management. Smithsonian Institution Press, Washington, DC, pp. 346–365.

Seagle, S.W., McNaughton, S.J., Ruess, R.W., 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. Ecology 73, 1105–1123.

Silvy, N.J., 1975. Population density, movements, and habitat utilization of Key deer, *Odocoileus virginanus clavium*. PhD. Dissertation, Southern Illinois University, Carbondale, Illinois.

Tilghman, N., 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53, 524–532.

U.S. Fish and Wildlife Service, 1999. Key deer recovery plan: a revision. U.S. Fish and Wildlife Service, Atlanta, Georgia, pp. 3–12.

Veblen, T.T., Mermoz, M., Martin, C., Ramilo, E., 1989. Effects of exotic deer on forest regeneration and composition in northern Patagonia. Journal of Applied Ecology 26, 711–724.

Vourc'h, G., Martin, J., Duncan, P., Escarre, J., Clausen, T.P., 2001. Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. Oecologia 126, 84–93.

Webster, C.R., Jenkins, M.A., Rock, J.H., 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation 125, 297–307.

Zamora, R., Gomez, J.M., Hodar, J.A., Castro, J., Garcia, D., 2001. Effect of browsing by ungulates on sapling growth on Scots pine in a Mediterranean environment: Consequences for forest regeneration. Forest Ecology and Management 144, 33–42.

Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice Hall Inc., Upper Saddle River, New Jersey.