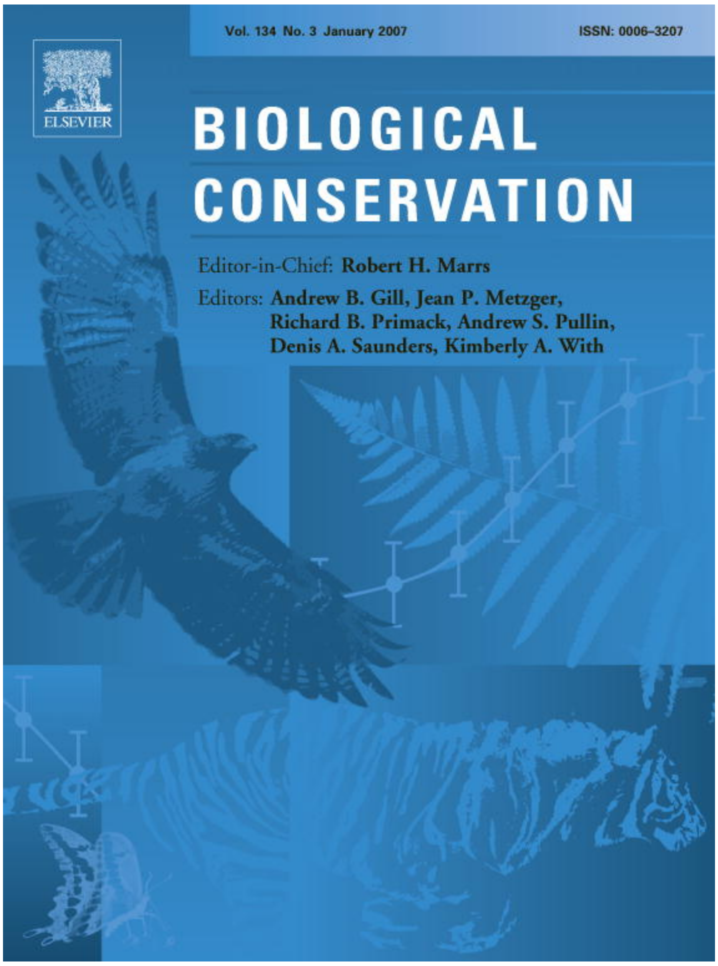
Vol. 134 No. 3 January 2007
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Robert H. Marrs
Editors: Andrew B. Gill, Jean P. Metzger,
Richard B. Primack, Andrew S. Pullin,
Denis A. Saunders, Kimberly A. With

BIOLOGICAL CONSERVATION 134 (2007) 321–331

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

Impacts of urbanization on Florida Key deer behavior and population dynamics

*Patricia M. Harveson**, *Roel R. Lopez*, *Bret A. Collier*, *Nova J. Silvy*

Department of Wildlife and Fisheries Sciences, 2258 MS, Texas A&M University, College Station, TX 77843-2258, USA

ARTICLE INFO

Article history:
Received 9 November 2005
Received in revised form
20 June 2006
Accepted 19 July 2006
Available online 24 October 2006

Keywords:
Body mass
Domestication
Habitat selection
Odocoileus virginianus clavium
Urban

ABSTRACT

Rapid human population growth and urbanization have had a negative impact on species biodiversity. As competition for resources between man and wildlife continues, it is important to understand the effects of urbanization on species. Endangered Key deer (*Odocoileus virginianus clavium*) are endemic to the Florida Keys which have undergone rapid human population growth and development over the past 30 years. Our study objectives were to evaluate the impacts of urban development on Key deer habitat use, population dynamics, behavior, and body mass. We used data from two comprehensive studies on Key deer spanning 30 years to evaluate these changes. Our results suggest that Key deer have become more urbanized, using urban areas more today than they did 30 years ago. Contrary to our predictions, survival was higher for more urban deer than for less urban deer. Problems still exist with mortality factors heavily impacting some portions of the deer population including lower survival associated with less urban male deer. Analysis of Key deer body mass also was converse to our predictions as deer weights appear to have increased over time. Collectively, our results suggest that over the past 30 years Key deer have become more urbanized and that deer plasticity has allowed them to adapt and persist in an urbanizing environment. However, the future ability of Key deer to persist in an environment with continued urban development is unknown. At some threshold, urban development would become unsustainable and unlike other forms of habitat change or environmental disturbances, urban development is in most cases irreversible requiring careful planning in habitat conservation strategies.

1. Introduction

Conservation of native wildlife is becoming increasingly difficult due to continued human population growth and expansion. As the human population continues to increase, so does the rate of consumption of our natural resources. In fact, human population growth is cited as the greatest threat to species biodiversity (Meffe and Carroll, 1997) with the proliferation of housing being the primary mechanism of this impact, and an accelerating threat to biodiversity (Liu et al., 2003). Expansion of road networks and higher traffic levels on current roads are direct impacts of household proliferation. In the contiguous United States, roads and roadsides cover approximately 1% of the surface area, and impact 22% of it ecologically (Forman, 2000). The expansion of households and roadways degrades wildlife habitat via fragmentation, outright destruction, facilitation of invasive exotic invasion, and wildlife-vehicle collisions (Gelbard and Harrison, 2003; Lopez et al., 2003). As competition for resources between man and wildlife continues, it is

---

* *Corresponding author*: Present address: Department of Natural Resource Management, Sul Ross State University, P.O. Box C-16, Alpine, TX 79832, USA. Tel.: +1 432 837 8826; fax: +1 432 837 8822.
E-mail address: harveson@gmail.com (P.M. Harveson).

0006-3207/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2006.07.022

important to understand the effects of urbanization on species.

The endangered Florida Key deer is the smallest subspecies of white-tailed deer in the United States. Key deer are endemic to the Florida Keys archipelago stretching southwest off the southern tip of peninsular Florida (Hardin et al., 1984). Key deer range is restricted to the Lower Florida Keys with approximately 60% residing on Big Pine Key (BPK) and 15% residing on No Name Key (NNK; Folk, 1992; Lopez, 2001). During the early 1900s, Key deer numbers declined due to unregulated hunting and in 1940, the total Key deer population was estimated at <50 animals (Hardin et al., 1984). In an effort to conserve and protect the deer, the National Key Deer Refuge was established in 1957 and incorporated 3457 ha of the historic Key deer range. The establishment of the refuge and increased law enforcement have resulted in the subsequent growth of the Key deer population, which grew to an estimated 300–400 animals by 1974 (Klimstra et al., 1974). Further, Key deer populations on BPK and NNK were estimated to have grown by 240% between 1971 (~200 deer) and 2001 (~453–517 deer; Lopez et al., 2004a). Paradoxically, during this time period the Florida Keys experienced rapid human population growth and urban development. The human population on Big Pine and No Name keys (the core of Key deer habitat) increased from 500 residents in 1970 to the current estimated 5000 on these two islands (Fig. 1; Lopez et al., 2004a,b). For nearly 50 years, urban development has been viewed as the primary threat to Key deer (Klimstra et al., 1974; Folk, 1992; Lopez et al., 2003) despite observed deer population increases.

1.1. *Has urban development been beneficial or detrimental to Key deer?*

We examine whether the past 30 years of urban development on BPK has been beneficial or detrimental to Key deer. Previous studies on Key deer have suggested conflicting answers. For example, urbanization has resulted in the modification of habitat and the creation of more upland habitat preferred by deer (Lopez et al., 2004b). Over the last 30 years, BPK has experienced a 10-fold increase in human population growth and urban development (Monroe County Growth Management Division, 1992) yet during this time, the Key deer population has grown by 240% (Lopez et al., 2004a). If we evaluate the impacts of urbanization with deer population growth alone, it would appear that urbanization has not harmed and may have possibly benefited the deer (Peterson et al., 2004; Lopez et al., 2004b).

Conversely, urban development and its associated risks have also been reported as the greatest threat to the Key deer population (Lopez et al., 2003). Prior to the 1940s, humans were directly responsible for the early exploitation and near extinction of Key deer. While deer mortality due to illegal hunting is now minimal, other anthropogenic impacts including habitat loss and fragmentation, deer domestication, and deer-vehicle collisions have been cited as risk factors for Key deer (Hardin, 1974; Folk and Klimstra, 1991; Folk, 1992; Lopez et al., 2003). In a recent study, deer-vehicle collisions were cited as the primary mortality factor for Key deer accounting for 50% of total Key deer mortality on BPK (Lopez et al., 2003). Anthropogenic factors also accounted for other means of mortality for Key deer including entanglement in fences, drowning in swimming pools, and attacks by dogs. Urbanization and particularly the high traffic volume on the US 1 highway have created areas of varying habitat quality and mortality risk on BPK. Harveson et al. (2004) reported that fragmentation and high deer mortality in south BPK has created a non-viable sink population that is supplemented by a source population in north BPK. Furthermore, Peterson et al. (2004) found that over the last 30 years both fawn mortality and range size decreased, and suggested that if ranges continued to shrink, then fawn mortality could increase due to lack of resources. Finally, Peterson et al. (2005) reported changes in deer sociobehavior due to illegal feeding, and sug-

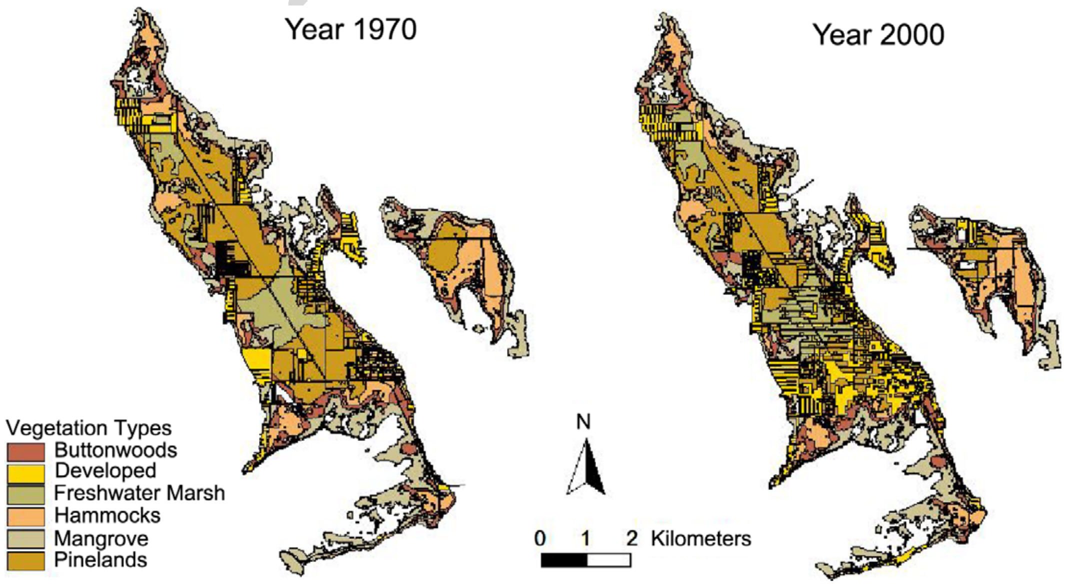

Fig. 1 – Big Pine Key and No Name Key habitat maps during the historic (1970) and current (2000) study periods.

gested that increased group sizes and densities around feeders were indicators of increased domestication of Key deer (Peterson et al., 2005).

1.2. Research objectives

Our goal was to evaluate the impacts of 30 years of increasing urban growth on the Key deer population by comparing two comprehensive studies on Key deer. The first study (Hardin, 1974; Silvy, 1975; hereafter referred to as historic) was conducted from December 1968 through June 1972 during a time of low human population density and urbanization (0.22 houses/ha) on BPK. The second study (Lopez, 2001; hereafter referred to as current) was conducted from January 1998 through December 2000 during a time of high human population density and urbanization (0.96 houses/ha) on BPK. We evaluated whether urbanization has negatively impacted Key deer by testing the following research hypotheses: (1) Key deer have become more urbanized due to increased human population growth and development, (2) increased urbanization and anthropogenic risk factors have negatively impacted Key deer population dynamics, (3) increased urbanization has resulted in changes in Key deer behavior and increased domestication, and (4) increased urbanization has resulted in long-term physiological effects on Key deer morphology.

2. Methods

2.1. Study area

The Florida Keys are a chain of small islands approximately 200-km long extending southwest from peninsular Florida in Monroe County, Florida. Soil types vary from marl deposits to bare rock of the oolitic limestone formation (Dickson, 1955). Island vegetation varies by elevation with red (*Rhizophora mangle*), black (*Avicennia germinans*), and white mangroves (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*) forests occurring near sea level (maritime zones). As elevation increases inland, maritime zones transition into hardwood (e.g., Gumbo limbo [*Bursera simaruba*], Jamaican dogwood [*Piscidia piscipula*]) and pineland (e.g., slash pine [*Pinus elliottii*], saw palmetto [*Serenoa repens*]) upland forests with vegetation intolerant of salt water (Dickson, 1955; Folk, 1992).

2.2. Data collection

Key deer were captured, marked, and/or radiocollared during two separate study periods from December 1968 through June 1972 (historic; Hardin, 1974; Silvy, 1975) and from January 1998 through December 2000 (current; Lopez, 2001) on BPK and NNK. Capture techniques included the use of portable drive-nets, drop-nets, and hand capture (Silvy, 1975; Silvy et al., 1975; Lopez, 2001). Captured deer were physically restrained for an average of 10–15 min, ear tattooed, and radiocollared with battery-powered mortality-sensitive radiotransmitters (AVM Electonics Corporation, Champaign, Illinois, USA, 1968–1972; Advanced Telemetry Systems, Isanti, Minnesota, USA, 1998–2000).

Deer were classified by sex and age when captured. Three age-classes were used: fawn (<1 year), yearling (1–2 years), and adult ($\geqslant$2 years; Lopez et al., 2003). Deer were monitored and telemetry locations were recorded 6–7 times per week at random intervals. With each day divided into 6–4-h segments, 1–4-h segment was randomly selected each day to locate all deer. If a mortality signal was detected, deer were immediately located and necropsied to determine cause of death (Nettles, 1981). Deer were censored from the data set after their last known encounter if their radios failed or disappeared (Pollock et al., 1989). Deer locations were recorded on maps and entered into a GIS database (ArcView GIS, ESRI, 1999).

2.3. Habitat use

We evaluated the hypothesis that Key deer have become more urbanized due to human population growth and development by examining changes in percent urban use and habitat selection by deer between the two studies. The terms urban and developed are used interchangeably and refer to native vegetation that has been altered for human use including cleared or disturbed areas, lowlands converted to uplands (dredged and filled), and residential dwellings and infrastructure (e.g., houses, yards, roads, businesses) (Lopez et al., 2004b).

2.3.1. Urban use

We tested the prediction that Key deer use of urban areas has increased between the historic and current study periods using radiotelemetry data. Deer locations were classified by habitat as urban and wild (non-urban). We estimated urban use by deer by calculating (1) the percent of urban radiotelemetry locations per deer and (2) the percent of urban area in each deer's range. We tested for differences in urban percent of locations and ranges between the current and historic study period using *t*-tests for unequal variances (Ott and Longnecker, 2001). We also evaluated the concept of an "urban deer." It has been suggested that urban use by deer was a continuum rather than dichotomously polarized as urban and wild deer (Peterson et al., 2005). Thus, we constructed histograms to evaluate the distribution of urban use by radiocollared deer.

2.3.2. Habitat selection

We tested the prediction that urbanization has altered Key deer selection of habitats by increasing the use of developed (urban) areas using radiotelemetry data collected in the historic and current study periods. Vegetation coverage maps from the Advanced Identification of Wetlands Project (MacAulay et al., 1994) were used to classify habitat into six vegetation types (hammock, pineland, freshwater marsh, buttonwood, mangrove, and developed; Lopez et al., 2004b). Historical vegetation coverages were created by reclassifying developed areas to original vegetation types as described by Lopez et al. (2004b). We evaluated first-, second-, and third-order habitat selection (Johnson, 1980; Lopez et al., 2004b) by Key deer. First-order selection was defined as habitat use by deer radiotelemetry locations compared to habitat availability in the study area. Second-order selection was defined as habitat use in a deer's range compared to habitat availability in the study area.

Third-order selection was defined as habitat use by deer point locations compared to habitat availability in a deer's range. We calculated a habitat selection ratio for each deer as $S = ([U + 0.001]/[A + 0.001])$, where U was equal to observed use and A to expected use (Manly et al., 2002). We calculated the mean ratio for current and historic deer to identify differences in habitat use between periods. We limited analysis to BPK because historic data did not include NNK.

2.4. *Population dynamics*

We tested the hypothesis that increased urbanization and anthropogenic risk factors have negatively impacted Key deer population dynamics by evaluating (1) the influence of deer urban use on survival and (2) changes in recruitment rate between study periods.

2.4.1. *Survival*

We predicted that percent urban use by deer would be negatively correlated with survival due to increased exposure to anthropogenic risk factors for deer. We used telemetry data collected from radiocollared deer during the historic and current study periods. Lopez et al. (2003) reported that fawn survival differed from yearling and adult survival for both sexes, thus, we only included yearling and adult radiocollared deer on BPK in analysis. Survival estimates were estimated using a known-fate model framework in Program MARK (White and Burnham, 1999). Encounter history files were created for individual deer including sex, area (north and south BPK), and study period for input into Program MARK. A covariate for urban use by each deer based on the percent of urban radiotelemetry locations was also included. Twelve models were constructed based on sex, area, study, and urban use and combinations of each were evaluated using Program MARK. Models were evaluated based on Akaike's Information Criterion (AIC_c) and the highest ranking model was selected to estimate survival (Burnham and Anderson, 1998).

2.4.2. *Recruitment*

We tested the prediction that recruitment has decreased between study periods using fawn and doe counts from deer census data. Road counts were conducted on various survey routes to estimate population density and structure from 1969 to 2001 on BPK and NNK. We limited data to the "Big Pine Key 44-mile" route (BPK44m; Lopez, 2001) because this survey was conducted in both the historic and current periods and covers the entire island. The BPK44m route is 71 km from the northern tip to the southern tip of the island. Weekly road counts were conducted $\frac{1}{2}$ h before sunrise (1969–1972) and $1\frac{1}{2}$ h before sunset (1998–2001). Road count data includes the location, sex, and age of deer seen. Fawn–doe ratios were calculated for each census observation group. Seasons were defined as winter (January–March), spring (April–June), summer (July–September), and fall (October–December). We used an ANOVA to test for differences in ratios by period and season. We used the Kolmogorov–Smirnov statistic with a Lilliefors significance level for testing normality and Levene's test for equality of error variances (SPSS 12.0.1; Ott and Longnecker, 2001). Fawn:doe ratios were not normally distributed and were square root transformed.

2.5. *Behavior*

We evaluated the hypothesis that increased urbanization has resulted in changes in Key deer behavior and increased domestication by examining the effect of urban use on Key deer flight distance and range size. We also examined differences in group size and density between urban and wild areas and study periods.

2.5.1. *Flight distance*

We tested the prediction that deer in urban areas are "tamer" and more approachable than deer in wild (non-urban) areas using flight distance data gathered from radiocollared deer during the current study period. We defined flight distance as the distance at which a person can approach a deer before it flees. Data were gathered during the regular monitoring of radiocollared deer during the current study. If deer were visually located, additional information was gathered including the distance at which the deer fled when approached by the observer (flight distance). We used this data to examine whether deer flight distance varied based on the type of habitat (urban vs. wild) the deer was located in. We used t-tests assuming unequal variances to compare mean flight distance between urban and non-urban areas. We used a nonparametric Kruskal–Wallis test to compare mean flight distance between habitat types because data did not exhibit normality even when transformed. Further, we explored the possible relationship between deer urban use and flight distance using regression analysis. We predicted that as urban use increased, flight distance would decrease. Thus, we tested whether urban use significantly influenced flight distance using linear regression and predicted a negative slope. Data were not normally distributed and were square root transformed.

2.5.2. *Range size*

We tested the prediction that Key deer range sizes are negatively correlated with urban use using range estimates calculated from radiotelemetry data during the historic and current study periods. Annual Key deer ranges were calculated using a 95% fixed-kernel home-range estimator (Worton, 1989; Seaman et al., 1998, 1999) with the animal movement extension in ArcView (Hooge and Eichenlaub, 1997). Calculation of the smoothing parameter (kernel width) was used in generating kernel range estimates (Silverman, 1986). Only deer with $\geqslant 175$ locations were used to calculate annual estimates, and only BPK deer ranges were included in analysis. For deer with >1 annual range estimate, only the most recent range was included. We used analysis of covariance to evaluate the relationship between annual range size and urban use by deer. We included sex as a factor because of known sex differences in range size (Lopez et al., 2005) and urban use as a covariate. Urban use was calculated as the number of telemetry locations in urban areas divided by the total number of telemetry locations for each deer. We used the Kolmogorov–Smirnov statistic with a Lilliefors significance level for testing normality and Breush–Pagan test for equality of error variances (SPSS 12.0.1; Ott and Longnecker, 2001). Annual range size data were not normally distributed and were natural log transformed.

2.5.3. *Group size*

We tested two predictions regarding Key deer grouping behavior: (1) that group sizes in urban areas are greater than in wild areas, and (2) that group sizes in the current period are higher than in the historic period. We used BPK44m survey data from 1971 (January–December) and 1999 (January–December) to estimate average group size and density in urban and wild areas on BPK. Survey data included the location, age, sex, and markings of observed deer. We classified observation area as urban if developed and all other areas as wild. Seasons were defined as winter (January–March), spring (April–June), summer (July–September), and fall (October–December). We calculated the seasonal mean group size for each survey observation during 1971 and 1999. Group size data were not normal and we used Mann–Whitney and Kruskal–Wallis nonparametric tests for differences between year, area, and season.

2.6. *Body mass*

We evaluated the hypothesis that urbanization has resulted in long-term physiological effects on Key deer morphology by comparing (1) Key deer body mass of captured deer during the historic and current study periods, and (2) carcass weights of adult Key deer mortalities from 1969 to 2003.

We tested the prediction that adult deer body mass (weight) has decreased between study periods using live deer capture data. Deer were captured during the historic and current study periods and body mass, age, and sex were recorded. We included only adult deer in analysis due to small sample sizes for fawns and yearlings. If a deer was captured and weighed more than once during a study, we used the mean weight for that deer in analysis. We compared the average body mass of adult deer by sex and study period. We tested for differences between mean weights by period using *t*-tests with equal variances not assumed for each sex.

We also tested the prediction that Key deer body mass has decreased using US Fish and Wildlife Service (USFWS) mortality data. Key deer mortality data has been actively collected and recorded by USFWS NKDR staff since 1968. Key deer mortalities were located by direct sightings, citizen reports, or observation of turkey vultures (*Cathartes aura*). Collected carcasses were necropsied immediately or held frozen prior to necropsy examination. Carcass quality or ability to determine cause of death ranged from good to marginal (Nettles, 1981; Nettles et al., 2002). Age, sex, body

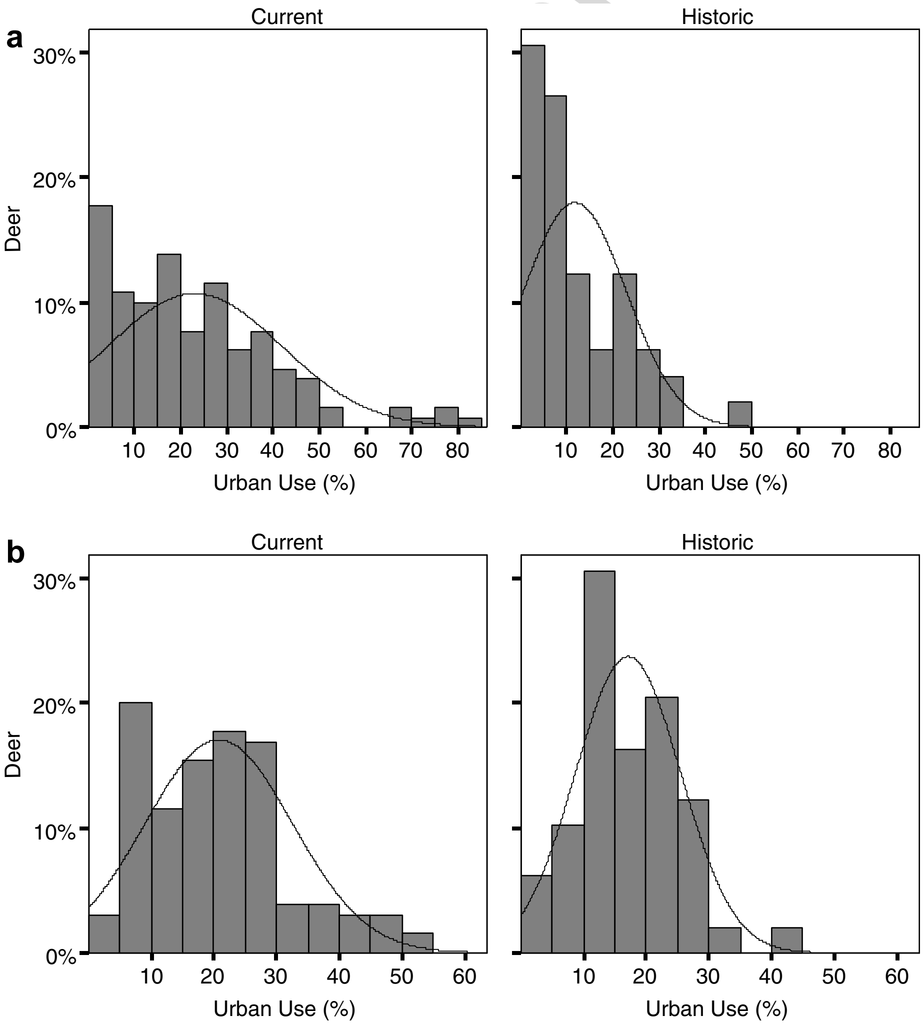

Fig. 2 – Histograms of (a) percent urban radiotelemetry locations and (b) percent urban area in ranges for Key deer by period (historic, 1968–1972; current, 1998–2000).

mass, and cause of death were recorded for each animal using procedures described by Nettles (1981), and all mortality locations were recorded. We used USFWS key deer mortality data from 1969 to 2003 to examine weight trends for adult deer. We grouped data into 5-year categories and graphed mean weights with 95% confidence intervals for male and female deer separately.

3. Results

3.1. Habitat use

3.1.1. Urban use

We analyzed the urban use (%) for 180 radiocollared deer (131 current, 49 historic). Our analysis indicated that mean percent urban use by Key deer differed significantly between periods for point location ($t = 4.946$, $P < 0.001$) and range ($t = 2.319$, $P = 0.022$) estimates. Urban use by deer was greater in the current period than in the historic period for both point locations (23% and 12%, respectively) and ranges (21% and 17%, respectively). In our analysis of the distribution of urban use by deer, histograms indicated that urban use differed by period but was relatively continuous rather than dichotomous during both periods (Fig. 2).

3.1.2. Habitat selection

One hundred and forty-three deer were used (94 current, 49 historic) for analysis of first-, second-, and third-order habitat selection. Habitat selection ratios were interpreted as follows: >1, habitat selected in greater proportion than available (preferred); <1, habitat selected in lesser proportion than available (avoided), and =1, habitat selected in proportion to availability (used proportionately). In the current study, deer preferred developed areas under all three orders of selection (Fig. 3). However, deer in the historic study preferred developed areas only under second-order analysis, and avoided urban areas under first- and third-order analyses.

3.2. Population dynamics

3.2.1. Survival

Key deer survival was estimated using 107 radiocollared yearling and adult deer on BPK. The highest ranking model included sex, study period, and urban use (Table 1). Thus, this model was used to estimate Key deer survival and evaluate the influence of each factor on Key deer survival. Overall, Key deer survival was higher in the historic study than in the current study, and survival was higher for female than for male deer (Table 2). Within each of these categories (study period * sex) survival was positively correlated with urban use by deer (Fig. 4).

3.2.2. Recruitment

Total fawn:doe ratios used in analysis was 95 (25 historic, 70 current). Results indicate that mean fawn–doe ratios differed by period ($F = 14.963$, $P < 0.001$) and season ($F = 61.100$, $P < 0.001$) with no period*season interaction ($F = 1.293$, $P = 0.282$) and an adjusted $R^2 = 0.729$. Current fawn:doe ratios were significantly lower than historic ratios for fall and winter seasons (Fig. 5).

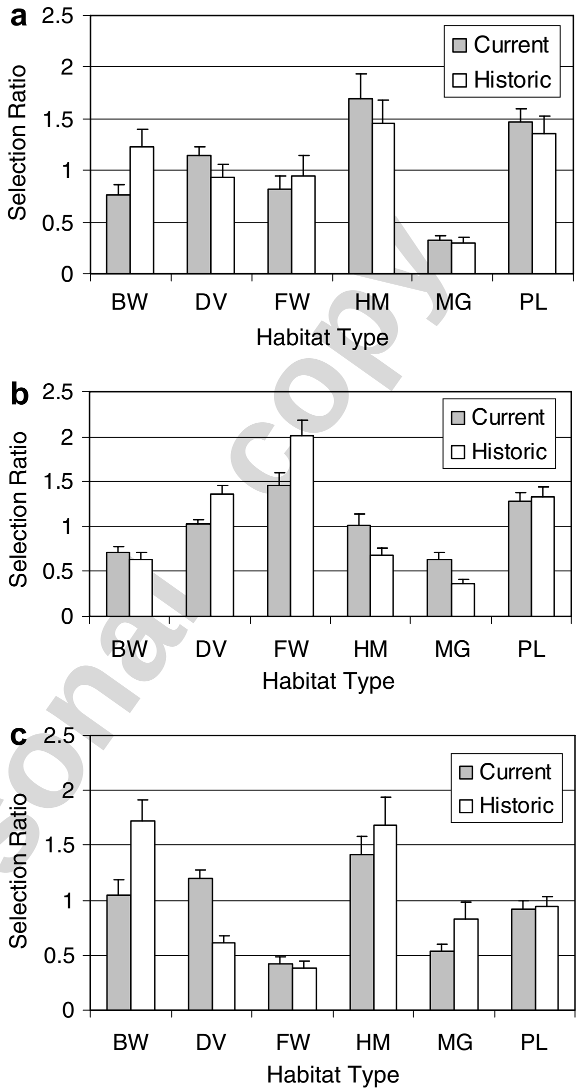

Fig. 3 – Key deer habitat (a) first-order (point-study area), (b) second-order (range-study area), (c) third-order (point-range) selection ratios (Johnson, 1980; mean, 1 SE), by period and habitat type (BW, buttonwood; DV, developed; FW, freshwater marsh; HM, hammock; MG, mangrove; PL, pineland) during the historic (1968–1972) and current (1998–2000) study periods on Big Pine Key, Florida.

3.3. Behavior

3.3.1. Flight distance

We examined possible differences in Key deer flight distance based on habitat type using 746 observations from 117 deer on BPK and NNK from 1998 to 2000. We found no significant difference ($t = -1.244$, $P = 0.217$) between mean flight distance in urban (mean = 2.2 m, SE = 0.24) and non-urban (mean = 3.0, SE = 0.62) areas. We also tested for differences between mean flight distances in five different habitat types. Freshwater marsh was excluded from analysis because of small sample size ($n = 1$). Mean flight distance was greatest for buttonwood (mean = 4.6 m, SE = 1.4 m) and lowest for pineland (mean = 1.9 m, SE = 0.4), however, differences between types were not significant ($X^2 = 6.732$, df = 4, $P = 0.151$).

Table 1 – Candidate models and selection results for estimated survival for yearling and adult Key deer ($n = 107$) on Big Pine Key, Florida

Candidate model	No. of parameters	Δ_i[a]	Akaike weight (w_i)	Evidence ratio (w_1/w_i)
$S_{\text{sex, study, urban use}}$	4	0.000	0.28	1.00
$S_{\text{sex, study}}$	3	0.455	0.22	1.27
$S_{\text{sex, study, area, urban use}}$	5	1.357	0.14	2.00
$S_{\text{sex, study, area}}$	4	1.404	0.13	2.15
$S_{\text{sex, area}}$	3	1.725	0.11	2.55
S_{sex}	2	3.401	0.05	5.66
$S_{\text{sex, urban use}}$	3	4.665	0.03	9.33
S_{area}	2	5.685	0.02	14.00
S_{study}	2	6.614	0.01	28.00
$S_{\text{urban use}}$	2	10.503	0.00	53.84
$S_{\text{seasonal urban use}}$	12	13.372	0.00	>100
$S_{\text{urban use/changes w/each interval}}$	5	31.091	0.00	>100

[a] Minimum $AIC_c = 146.607$.

Table 2 – Annual survival estimates and variances for yearling and adult Key deer on Big Pine Key by period (historic, 1968–1972; current, 1998–2000) and sex

Sex	Study period	Range value	Urban use covariate (Prop.)	Annual survival estimate	Annual survival SE
Male	Historic	Minimum	0.03	0.903	0.358
		Median	0.13	0.922	0.367
		Maximum	0.24	0.939	0.367
	Current	Minimum	0.03	0.473	0.000
		Median	0.27	0.638	0.005
		Maximum	0.92	0.899	0.379
Female	Historic	Minimum	0.00	0.976	0.251
		Median	0.06	0.979	0.226
		Maximum	0.34	0.991	0.149
	Current	Minimum	0.00	0.825	0.105
		Median	0.22	0.889	0.200
		Maximum	0.71	0.962	0.273

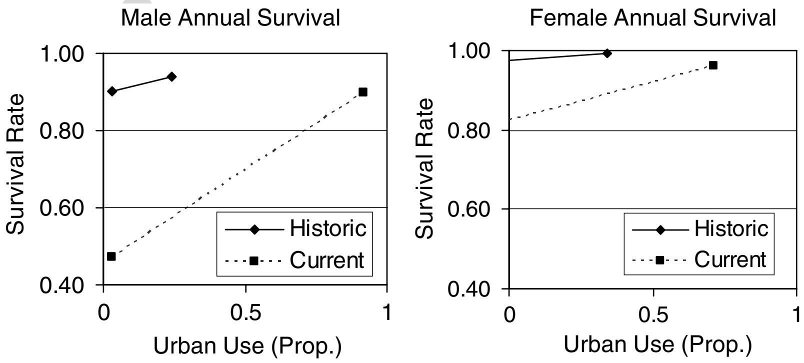

Fig. 4 – Annual survival for yearling and adult Key deer on Big Pine Key, Florida by period (historic, 1968–1972; current, 1998–2000), sex, and urban use (minimum and maximum values).

We tested the relationship between urban use and flight distance using data collected from 117 deer on BPK and NNK. Linear regression analysis suggests that urban use by deer is a significant predictor of flight distance ($F = 6.514$, $P = 0.012$) with an adjusted $R^2 = 0.045$. As urban use increased, flight distance decreased (slope = -1.959). However, the low adjusted R^2 value suggests that urban use explained only a small portion of the variability in flight distance.

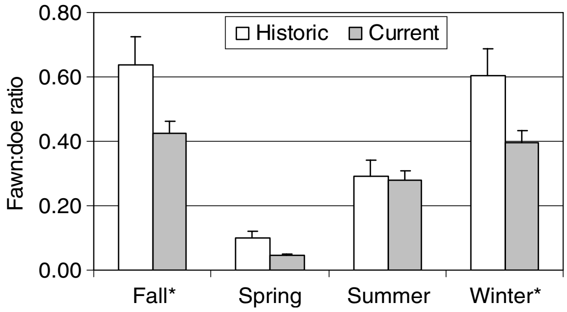

Fig. 5 – Key deer fawn:doe ratios (mean, 1 SE) by season and period (historic, 1968–1972; current, 1998–2000). Asterisk (*) indicates significant difference at $\alpha = 0.05$.

3.3.2. *Range size*

We removed four ranges with standardized residuals ±3.0. Total annual ranges used in analysis was 45 (12 male, 33 female). Transformed data were normal but did not have equal variances. Analysis of covariance suggests that mean range size differed by sex ($F = 18.718$, $P < 0.001$) and was influenced by urban use of deer ($F = 10.957$, $P = 0.002$) with adjusted $R^2 = 0.413$. As percent urban use by deer increased, range size decreased (Fig. 6).

3.3.3. *Group size*

We calculated average group size and deer density in urban and wild areas using 26 and 48 surveys conducted from January–December 1971 and January–December 1999, respectively. No differences were found between deer mean group size by area (urban or wild; $P = 0.591$) or season ($P = 0.294$) in 1971 (historic study, Fig. 7a). However, differences were found between deer mean group size by area ($P = 0.021$) and season ($P < 0.001$) in 1999 (current study, Fig. 7b) with winter in urban areas having the largest group sizes. Also, average yearly group size in 1999 was greater than in 1971 for both urban ($P < 0.001$; 2.23 and 1.31, respectively) and wild ($P < 0.001$; 1.92 and 1.29, respectively) areas.

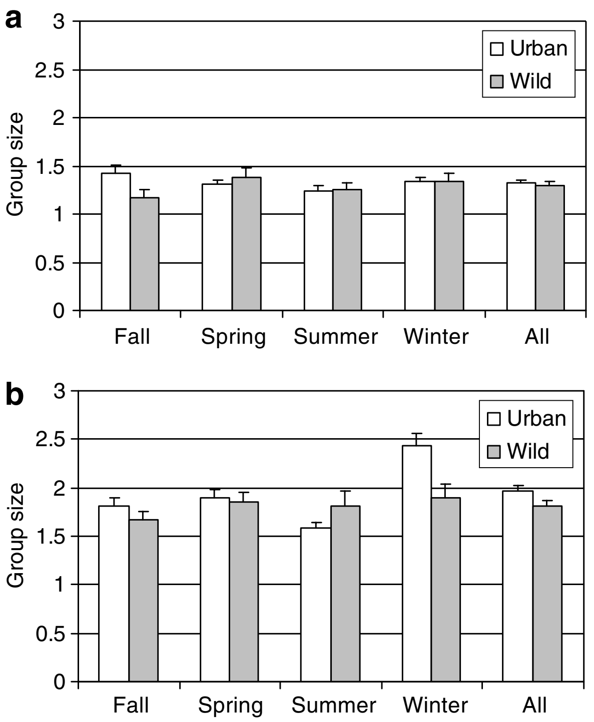

Fig. 7 – Key deer group size (mean, 1 SE) by season in urban and wild areas during Big Pine Key 44-mile deer surveys during (a) 1971 (historic study) and (b) 1999 (current study).

3.4. *Body mass*

We analyzed the weights of 252 adult deer captured during the historic (72 female, 38 male) and current (87 female, 55 male) study periods. Adult deer capture weights differed significantly between periods for both males ($t = 3.760$, $P < 0.001$) and females ($t = 5.249$, $P < 0.001$). Current adult female weights (mean = 32.0 kg, SE = 0.5 kg) were significantly greater than historic weights (mean = 28.8 kg, SE = 0.4 kg). Likewise, current adult male weights (mean = 42.7 kg, SE = 1.4 kg) were also sig-

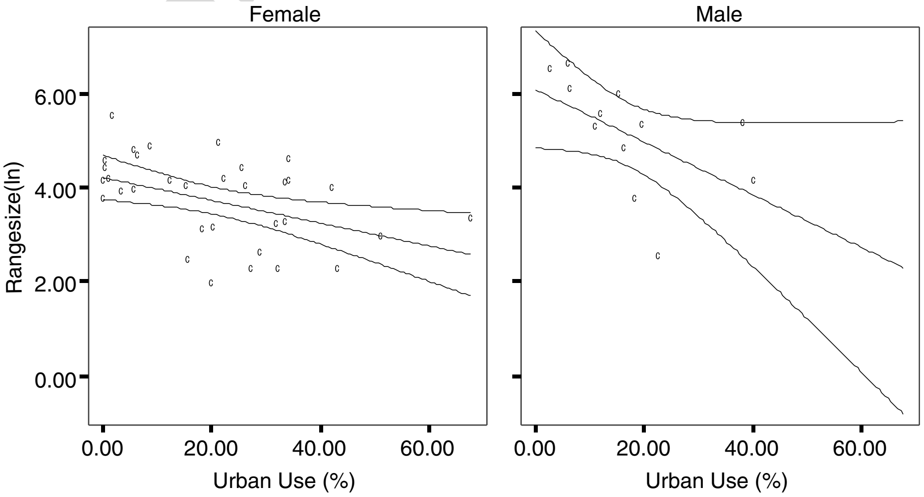

Fig. 6 – Trends of adult Key deer annual range size (ln transformation) by urban use for females and males on Big Pine Key, 1968–2000.

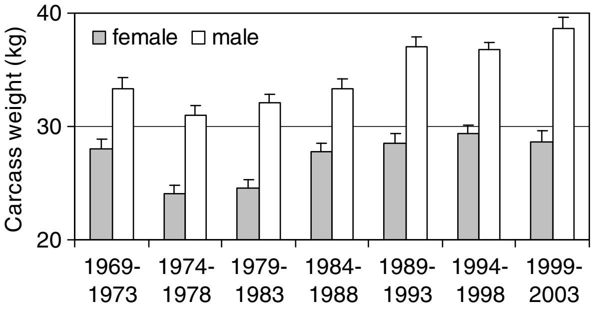

Fig. 8 – Key deer carcass weights (mean, 1 SE) from US Fish and Wildlife Service mortality data for adult female and male deer in 5-year increments, 1969–2003.

nificantly greater than historic weights (mean = 36.5 kg, SE = 1.0 kg). In our review of the USFWS mortality data, we removed data outliers (6 female, 3 male) and analyzed 605 male and 366 female mortality weights from 1969 to 2003. Mortality data indicated increasing trends in weight by time for both males and females similar to analysis results for capture data (Fig. 8).

4. Discussion

4.1. *Urbanization of Key deer*

Our results suggest that Key deer have become more urbanized, using urban areas more today than they did 30 years ago. The percent of deer telemetry locations in urban areas in the current study (23%) was nearly double the percent in the historic study (12%). Similarly, the percent of urban area in radiocollared deer ranges was significantly greater in the current study (21%) than in the historic study (17%). By calculating habitat selection, we found that the increased use of urban areas by Key deer is not a function of increased availability in urban area but rather a change in deer selection or preference. We also found that deer use of urban areas was fairly continuous and not polarized at either end of the scale (Fig. 2) suggesting that deer are not dichotomously “wild” or “urban” but are using different types of habitat to varying degrees. However, it appears from this analysis that deer in the historic study were at the lower end of the continuum of urban use when compared to the current study (Fig. 2).

4.2. *Population dynamics*

We found urban use to be an important factor in explaining deer survival (Table 1). We predicted that increased threats due to anthropogenic risk factors in urban areas would result in decreased survival for more urbanized deer. However, contrary to these predictions, our analysis indicated that as percent urban use by deer increases, survival also increases (Fig. 4). While there are many possible explanations for these results, we speculate that this positive relationship between deer urban use and survival is due to behavioral adaptations by Key deer. More urbanized Key deer may have learned to avoid or compensate for urban risk factors such as roads, dogs, fences, and swimming pools. This may explain why male deer with low urban use had the lowest survival rate. White-tailed deer are territorial and the current deer population density on BPK is high (Lopez et al., 2004a) which may require yearling males to disperse greater distances to find a home range. This dispersal through urban areas may lead to lower survival due to inexperience with anthropogenic risk factors.

Our analysis also suggests that fawn:doe ratios were lower during the current study in fall and winter (Fig. 5). Increased fawn mortality would be the most obvious explanation; however, Peterson et al. (2004) reported Key deer fawn mortality has decreased since the historic study. Another possible explanation is decreased fitness in deer due to lack of resources or higher stress. However, if body mass is an indication of fitness, then the increase in Key deer weight from the historic to current study periods suggests otherwise. It is possible that nutritional deficiencies due to non-natural foods (i.e., deer feeders) are negatively affecting reproduction (Maynard et al., 1979), but this has not been tested. Hence, we suspect that decreased recruitment is a density dependent response to the Key deer population nearing carrying capacity (*K*) (Halls, 1984) and predict that without increased dispersal to other islands, recruitment will continue to decrease in the future as deer densities exceed *K*.

4.3. *Behavior*

Domestication of Key deer has been speculated but few studies confirm these claims (Folk and Klimstra, 1991; Peterson et al., 2005). We found a significant but weak relationship between flight distance (a measure of domestication) and urban use on an individual deer basis. As flight distance decreased, urban use increased suggesting that the more urbanized a deer is, the more approachable or tamer it is. However, the small adjusted R^2 value for this model suggests that this relationship is weak and warrants further research.

Similarly, we found significant but relatively small differences in group size between study periods (historic and current) and area type (urban or wild). In the current study, Key deer group size was significantly greater than in the historic study for all seasons in both urban and wild areas. This increase in group size could be the result of increased deer densities or possibly a modification in deer behavior. Peterson et al. (2005) found similar results with larger group sizes associated with increased urban feeder use by Key deer.

Lopez et al. (2005) reported Key deer range sizes have decreased between the historic and current study periods and suggested this decrease was a result of (1) increased deer densities, (2) increased habitat quality due to development, and (3) Key deer domestication. Key deer densities have increased by 240% and other studies have reported similar reduced range sizes due to density increases (Bridges, 1968; Smith, 1970; Halls, 1984; Henderson et al., 2000; Lesage et al., 2000). In this study, we found that as urban use by deer increased, range size decreased (Fig. 6). Kilpatrick and Spohr (2000) reported similar smaller range sizes associated with white-tailed deer in urban areas compared to deer in forested and agricultural landscapes in Connecticut. Our results also support previously reported findings for Key deer (Lopez et al., 2005). First, differences in deer densities between urban and wild areas may be influencing range size. Deer densities are higher in urban areas and decreased range sizes for urbanized deer may be a density dependent response. Second, urban areas may provide more localized resources (food and water) than wild areas. Third, domestication of deer in urban areas is a possible explanation of decreased range size; however, our results on deer domestication were inconclusive.

4.4. *Body mass*

Changes in deer body mass have been reported in the literature as density dependent responses. Studies have shown that as deer densities increase and resources become limited, deer fitness and body mass decrease (Leberg and Smith, 1993; Pettorelli et al., 2002; Keyser et al., 2005). We analyzed changes in Key deer body mass (weight) between the historic and current study periods. During this time frame, the Key deer population on BPK increased from 247 to 406 animals. Nettles et al. (2002) reported increases in population-limiting diseases in Key deer which is characteristic of a population that is at or above *K*. Contrary to our predictions, the decrease in wild habitat due to urbanization combined with the increase in deer population size have resulted in an increase in deer body mass. So why then, has the Key deer population (which was well below *K* in the historic study) increased in body weight? We hypothesize that urbanization has increased the amount of resources available to deer through the conversion of lowlands to uplands and the associated availability of urban resources (i.e., deer feeders, nonnative vegetation, refuge, and freshwater; Lopez et al., 2004b; Peterson et al., 2005). However, we anticipate that this trend in increased body mass will not continue as the deer population reaches and exceeds *K* either through deer population growth and/or loss of usable space due to continued development.

5. Conclusion

Collectively, our results suggest that over the past 30 years Key deer have adapted to their urbanizing environment. Whether these behavioral adaptations (e.g., domestication) are desired is debatable, however, deer plasticity appears to have allowed Key deer to adapt and persist in a changing environment due to urbanization. The future impacts of additional urbanization on the deer population cannot be predicted. At some point, development will become unsustainable and it is impossible to predict where that point lies. Unfortunately, the negative impacts of urbanization on species often are not realized until after the damage has been done and these impacts are often irreversible. On a broader scale, more and more species will continue to be faced with the challenges of a changing environment as human population growth and urbanization continues to increase. The ability of species to adapt to these changes and our willingness to minimize our impacts will be determining factors in their future success as the competition for resources between man and wildlife continues.

Acknowledgements

We thank Texas A&M University graduate students and interns who assisted in the collection of field data. We also thank the staff of the US Fish and Wildlife Service National Key Deer Refuge. Funding was provided by the TAMU System, Hispanic Leadership Program in Agriculture and Natural Resources (US Department of Agriculture), Rob and Bessie Welder Wildlife Foundation, and US Fish and Wildlife Service. This manuscript is supported by the Welder Wildlife Foundation, Contribution No. 658.

REFERENCES

Bridges, R.J., 1968. Individual white-tailed deer movement and related behavior during winter and spring in northwestern Florida. Thesis, University of Georgia, Athens, USA.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, USA.

Dickson III, J.D., 1955. An ecological study of the Key deerFlorida Game and Fresh Water Fish Commission Technical Bulletin, vol. 3. Tallahassee, Florida, USA.

ESRI, 1999. Introduction to ArcView® GIS, Version 3.2. Environmental Systems Research Institute, Redlands, California, USA.

Folk, M.L., 1992. Habitat of the Key deer. Dissertation, Southern Illinois University, Carbondale, Illinois, USA.

Folk, M.L., Klimstra, W.D., 1991. Urbanization and domestication of the Key deer (*Odocoileus virginianus clavium*). Florida Field Naturalist 19, 1–9.

Forman, R.T., 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14, 31–35.

Gelbard, J.L., Harrison, S., 2003. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. Ecological Applications 13, 404–415.

Halls, L.K., 1984. White-Tailed Deer: Ecology and Management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Hardin, J.W., 1974. Behavior, socio-biology, and reproductive life history of the florida key deer, *Odocoileus virginianus clavium*. Dissertation, Southern Illinois University, Carbondale, Illinois, USA.

Hardin, J.W., Klimstra, W.D., Silvy, N.J., 1984. Florida Keys. In: Hall, L.K. (Ed.), White-Tailed Deer: Ecology and Management. Stackpole Books, Harrisburg, Pennsylvania, pp. 381–390.

Harveson, P.M., Lopez, R.R., Silvy, N.J., Frank, P.A., 2004. Source-sink dynamics of Florida Key deer on Big Pine Key, Florida. Journal of Wildlife Management 68, 909–915.

Henderson, D.W., Warren, R.J., Cromwell, J.A., Hamilton, R.J., 2000. Responses of urban deer to a 50% reduction in local herd density. Wildlife Society Bulletin 28, 902–910.

Hooge, B.N., Eichenlaub, B., 1997. Animal Movement Extension to ArcView, Version 1.1. Alaska Science Center, US Geological Survey, Anchorage, Alaska, USA.

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

Keyser, P.D., Guynn Jr., D.C., Hill Jr., H.S., 2005. Population density-physical condition relationships in white-tailed deer. Journal of Wildlife Management 69, 356–365.

Kilpatrick, H.J., Spohr, S.M., 2000. Spatial and temporal use of a suburban landscape by female white-tailed deer. Wildlife Society Bulletin 28, 1023–1029.

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. US Fish and Wildlife Service, Big Pine Key, Florida, USA.

Maynard, L.A., Loosli, J.K., Hintz, H.F., Warner, R.G., 1979. Animal Nutrition, seventh ed. McGraw-Hill, New York, USA.

Leberg, P.L., Smith, M.H., 1993. Influence of density on growth of white-tailed deer. Journal of Mammalogy 74, 723–731.

Lesage, L., Crete, M., Huot, J., Dumont, A., Ouellet, J.P., 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. Canadian Journal of Zoology 78, 1930–1940.

Liu, J.G., Daily, G.C., Ehrlich, P.R., Luck, G.W., 2003. Effects of household dynamics on resource consumption and biodiversity. Nature 421, 530–533.

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

Lopez, R.R., Harveson, P.M., Peterson, M.N., Silvy, N.J., Frank, P.A., 2005. From the field: changes in ranges of Florida Key deer – Does population density matter? Wildlife Society Bulletin 33, 343–348.

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, M.N., 2004b. Habitat use patterns of Florida Key deer: Implications of urban development. Journal of Wildlife Management 68, 900–908.

Lopez, R.R., Vieira, M.E.P., Silvy, N.J., Frank, P.A., Whisenant, S.W., Jones, D.A., 2003. Survival, mortality, and life expectancy of Florida Key deer. Journal of Wildlife Management 67, 34–45.

MacAulay, G.M., Leary, T.J., Sargent, F.J., Colby, M.M., Prouty, E.J., Friel, C.A., 1994. Advanced identification of wetlands in the Florida Keys, Final Report. Florida Department of Environmental Protection, Division of Marine Resources, Marathon, Florida, USA.

Manly, B.F., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies, second ed. Kluwer Academic Publishers, Norwell, Massachusetts, USA.

Meffe, G.K., Carroll, C.R., 1997. Principles of Conservation Biology, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, USA.

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

Nettles, V.F., 1981. Necropsy procedures. In: Davidson, W.R., Hayes, F.A., Nettles, V.F., Kellogg, F.E. (Eds.), Diseases and Parasites of White-Tailed Deer. Tall Timbers Research Station, Tallahassee, Florida, pp. 6–16.

Nettles, V.F., Quist, C.F., Lopez, R.R., Wilmers, T.J., Frank, P., Roberts, W., Chitwood, S., Davidson, W.R., 2002. Morbidity and mortality factors in Key deer, *Odocoileus virginianus clavium*. Journal of Wildlife Diseases 38, 685–692.

Ott, R.L., Longnecker, M., 2001. An Introduction to Statistical Methods and Data Analysis, fifth ed. Duxbury, Pacific Grove, California, USA.

Peterson, M.N., Lopez, R.R., Frank, P.A., Porter, B.A., Silvy, N.J., 2004. Key deer fawn response to urbanization: is sustainable development possible? Wildlife Society Bulletin 32, 493–499.

Peterson, M.N., Lopez, R.R., Laurent, E.J., Frank, P.A., Silvy, N.J., Liu, J.G., 2005. Wildlife loss through domestication: the case of endangered Key deer. Conservation Biology 19, 939–944.

Pettorelli, N., Gaillard, J.M., Van Laere, G., Duncan, P., Kjellander, P., Liberg, O., Delorme, D., Maillard, D., 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. Proceedings of the Royal Society of London Series B-Biological Sciences 269, 747–753.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53, 7–15.

Seaman, D.E., Griffith, B., Powell, R.A., 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26, 95–100.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R.A., 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63, 739–747.

Silverman, B.W., 1986. Density Estimation for Statistics and Data Analysis. Chapman and Hall, London, England.

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

Silvy, N.J., Hardin, J.W., Klimstra, W.D., 1975. Use of a portable net to capture free-ranging deer. Wildlife Society Bulletin 3, 27–29.

Smith Jr., F.H., 1970. Daily and seasonal variation in movements of white-tailed deer on Elgin Air Force Base, Florida. Thesis, University of Georgia, Athens, USA.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, S120–S139.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.