HABITAT-USE PATTERNS OF FLORIDA KEY DEER: IMPLICATIONS OF URBAN DEVELOPMENT

ROEL R. LOPEZ,[1] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA
NOVA J. SILVY, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA
R. NEAL WILKINS, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA
PHILIP A. FRANK, U.S. Fish and Wildlife Service, National Key Deer Refuge, Big Pine Key, FL 33043, USA
MARKUS J. PETERSON, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA
M. NILS PETERSON, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA

Abstract: Urban development in the Florida Keys, USA, mandates an understanding of how habitat requirements for Florida Key deer (*Odocoileus virginianus clavium*) interact with vegetation changes caused by development. Our study objectives were to (1) determine Key deer habitat use at different spatial scales, (2) evaluate vegetation changes and identify vegetation types most threatened by development, and (3) provide guidelines to direct land acquisition programs in the future. We identified 6 vegetation types: pineland, hammock, developed, freshwater marsh, buttonwood, and mangrove. Key deer (n = 180; 84 F, 96 M) preferred upland vegetation types (>1 m above mean sea level; pineland, hammock, developed) and avoided tidal or lower-elevation areas (<1 m above mean sea level; freshwater marsh, buttonwood, mangrove). Analyses of Geographic Information System (GIS) coverages suggested that historical development impacted near-shore habitats while recent trends pose a greater risk to upland areas (pineland, hammock). Because uplands are preferred by Key deer, conservation measures that include land acquisition and habitat protection of these areas may be needed.

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Since the rise of landscape ecology and hierarchy theory (O'Neill et al. 1986, Urban et al. 1987), wildlife ecology has increasingly focused on patterns and dynamics of ecological processes at varying spatial and temporal scales. Urban development results in abrupt rescaling of temporal and spatial patterns (O'Neill et al. 1986). In addition to direct impacts on areas developed, urban development also can modify plant succession, hydrology, and microclimate on adjacent native habitats through actions such as fire suppression, introduction of non-native species, drainage control, and creation of abrupt habitat margins. A hierarchical perspective can simplify the complexity of processes operating at landscape scales. Moreover, the practical use of these concepts is increasingly important in managing wildlife populations with changing land-use patterns.

Habitat loss and fragmentation due to urban development are a concern in recovery and management of the endangered Key deer (Klimstra et al. 1974, Folk 1991, U.S. Fish and Wildlife Service 1999). Key deer, the smallest subspecies of white-tailed deer in the United States, are endemic to the Florida Keys (Hardin et al. 1984). Key deer occupy 20–25 islands within the boundaries of the National Key Deer Refuge (NKDR), with approximately 75% of the deer population on Big Pine Key (BPK) and No Name Key (NNK; Lopez 2001, Lopez et al. 2004). From 1970 to 2000, the human population on BPK and NNK increased nearly 10-fold, resulting in rapid urbanization and environmental conflict (Lopez 2001, Lopez et al. 2003*b*). With increasing urban development throughout the Florida Keys, we need to understand Key deer habitat requirements and how Key deer are likely to respond to different urbanization pressures. This knowledge can guide planning programs toward conservation and acquisition of habitat types identified as important to Key deer or threatened by development.

In 1998, the Florida Department of Transportation, Monroe County, and Florida Department of Community Affairs began a planning process for a regional Key deer Habitat Conservation Plan (HCP) in support of an Incidental Take Permit under Section 10(a) of the Endangered Species Act of 1973. The Key deer HCP will determine the amount of future development permissible on BPK and NNK (Lopez 2001). Risks to the deer population from proposed development activities were evaluated with population viability analysis (PVA; Boyce 1992, Burgman et al. 1993,

[1] E-mail: roel@tamu.edu

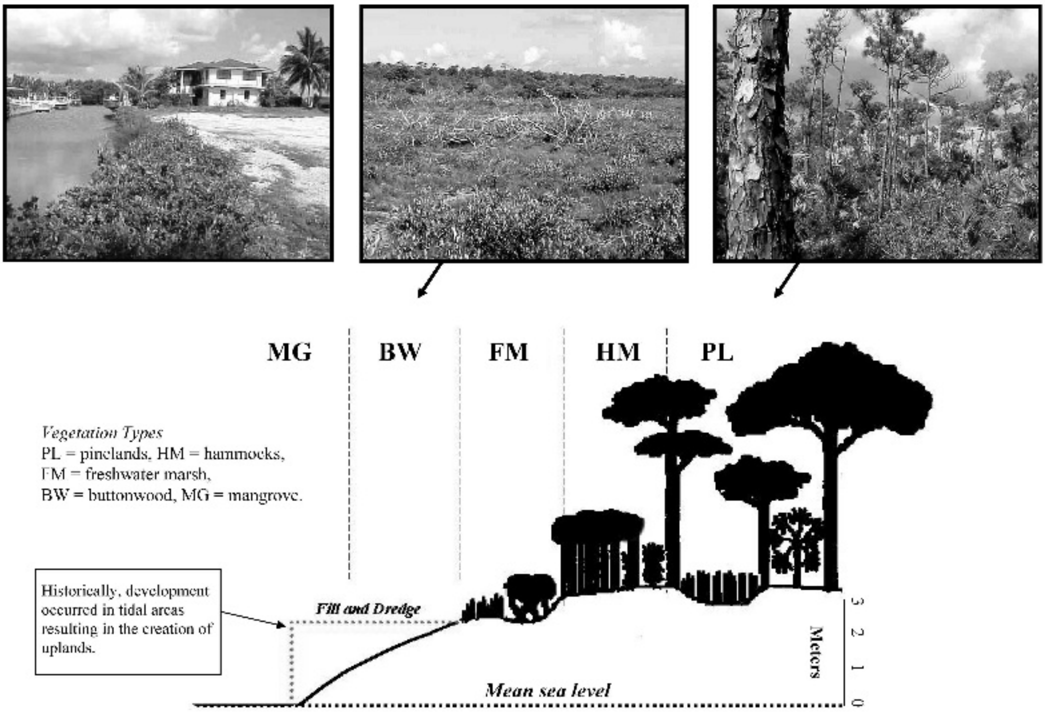

Fig. 1. Relationship of vegetation types to mean sea level (m) in the lower Florida Keys, Florida, USA. Photos illustrate development (left, note canal on left and increase in elevation due to fill), lowland (center, buttonwood/mangrove forest), and upland (right, pineland; Modified from Folk 1991).

Akçakaya 2000). A spatially explicit demographic model was developed for this purpose (Lopez 2001), but final model implementation also requires an analysis of Key deer habitat use. Our objectives were to (1) evaluate Key deer habitat use at 3 spatial scales, (2) determine changes in area and pattern of vegetation types, (3) identify temporal patterns in vegetation types most threatened by development, and (4) provide guidelines to direct future land acquisition programs based on our synthesis of Key deer habitat use and anthropogenic scaling of deer habitat.

STUDY AREA

The Florida Keys are a chain of small islands approximately 200 km long extending southwest from peninsular Florida, USA. Big Pine Key (2,548 ha) and NNK (461 ha) are within the boundaries of the NKDR and Monroe County and support approximately 75% of the deer population (Lopez 2001). Soils vary from marl deposits to bare rock of the oolitic limestone formation (Dickson 1955). Island elevation for BPK and NNK was 0–3 m above mean sea level (Florida Natural Areas Inventory 1990, Folk 1991).

Vegetation Types

Native flora of the Lower Keys was primarily West Indian in origin (Dickson 1955). We identified 6 vegetation types in our study: pinelands (632 ha), hammock (386 ha), developed (644 ha), freshwater marsh (234 ha), buttonwood (349 ha), and mangrove (764 ha). Vegetation types are described from low to high elevations because elevation influences these plant communities (Folk 1991; Fig. 1).

Mangrove.—Mangrove forests were dense, low forests occurring along flat, maritime zones with an average elevation 0–1 m above mean sea level (Folk 1991; Fig. 1). Dominant plants were red (*Rhizophora mangle*), black (*Avicennia germinans*), and white (*Lagyncularia racemosa*) mangroves. Other plants associated with mangrove forests included glasswort (*Salicornia* spp.), salt grass (*Distichlis spicata*), Key grass (*Monanthochoe littoralis*), and sea daisy (*Borrichia arborescens*; Florida Natural Areas Inventory 1990).

Buttonwood.—Transitional areas between mangrove and upland forests consisted of buttonwood prairie, salt marsh, and open scrub (Dickson 1955, Folk 1991; Fig. 1). Average elevation for buttonwood areas was 0.5–1 m above mean sea level (Folk 1991). Although these areas were not normally tidally influenced, most plant species were resistant to salt water (Folk 1991). Red, black, and white mangroves were present in the lower zones of buttonwood transitions. Buttonwood (*Conocarpus erectus*), joewood (*Jacquinnia keyensis*), wild dilly (*Manilkara bahamensis*), blacktorch (*Erithalis fruticosa*), and saffron plum (*Bumelia celastrina*) replaced mangroves with increasing elevation (Florida Natural Areas Inventory 1990).

Freshwater Marsh.—Freshwater marshes were lowland areas or basins either surrounded by upland forests or between upland areas and transition zones (Fig. 1). Average elevation of freshwater marshes was 1–2 m above mean sea level (Folk 1991). Plant species were similar to hammocks or pinelands, except that standing freshwater is maintained for extended periods during the year. As a result, many wetland plant species such as sawgrass (*Cladium jamaicense*), buttonwood, spike rush (*Eleocharis* spp.), saw sedge (*Cyperus ligularis*), white-top sedge (*Dichromen floridensis*), and broom sedge (*Andropogon glomeratus*) were found in these areas (Florida Natural Areas Inventory 1990).

Hammock.—Hammocks were upland forests characterized by broadleaf evergreen trees (Fig. 1). Plant diversity was high, with many plants of West Indian origin including gumbo limbo (*Bursera simaruba*), Jamaican dogwood (*Piscidia piscipula*), poisonwood (*Metopium toxiferum*), pigeon plum (*Coccoloba diversifolia*), blolly (*Pisonia discolor*), stoppers (*Eugenia* spp.), and sea grape (*Coccoloba uvifera*; Florida Natural Areas Inventory 1990). Average elevation was 2–3 m above mean sea level, so hammocks were rarely affected by tides except during extreme weather events such as hurricanes (Dickson 1955, Folk 1991).

Pineland.—Pinelands consisted of an open canopy of slash pines (*Pinus elliottii*) with a patchy understory/ground cover of tropical and temperate shrubs, palms, grasses, and herbs (Florida Natural Areas Inventory 1990). Historically, natural fires maintained these areas. Average elevation was 2–3 m above mean sea level with plant species intolerant of saltwater intrusion (Fig. 1). Plant diversity in pinelands was high, with plant species like blackbead (*Pithecellobium keyense*), saw palmetto (*Serenoa repens*), Keys thatch palm (*Thrinax morrisii*), silver palm (*Coccothrinax argentata*), and locustberry (*Bursonima lucida*). Natural waterholes in hammock, pineland, and freshwater marsh areas provided Key deer with water (Lopez et al. 2003*a*).

Developed.—Many native vegetation types were developed for human use in the last several decades (Folk 1991). Lowland areas were dredged and filled in the late 1940s through the 1970s (Fig. 1; Gallagher 1991). Invasive exotic plants, including Australian pine (*Casuarina equisetifolia*) and Brazilian pepper (*Schinus terebinthifolia*), were abundant on many scarified or disturbed sites created by development and threaten neighboring native areas (U.S. Fish and Wildlife Service 1999).

METHODS

Deer Trapping

We radiomarked Key deer as part of 2 separate research projects conducted December 1968 through June 1972 and January 1998 through December 2000 on BPK and NNK (Silvy 1975, Lopez 2001). We captured deer using portable drive-nets (Silvy 1975), drop-nets (Lopez et al. 1998) and by hand (Silvy et al. 1975) equally in urban and natural areas. Following capture, we used physical restraint to hold animals (average holding time 10–15 min, no drugs were used). Captured deer were radiomarked in a variety of ways depending on sex and age (Silvy 1975, Lopez et al. 2003*b*). We used a battery-powered mortality-sensitive radiotransmitter (AVM Electronics Corporation, Champaign, Illinois, USA, 1968–1972; Advanced Telemetry Systems, Isanti, Minnesota, USA, 1998–2000) attached to plastic neck collars (primarily females of all age classes), leather antler collars (yearling and adult males only), or elastic expandable neck collars (primarily male fawns/yearlings). Each captured animal was tattooed in an ear as a permanent marker (Silvy 1975).

Radiotelemetry

Radiomarked deer were monitored 6–7 times per week at random intervals. We divided each 24-hr period into 6 4-hr segments and randomly selected 1 4-hr segment during which all deer were located (Silvy 1975). Deer locations were determined via homing and marked on georeferenced maps (Silvy 1975, White and Garrott 1990). We entered radiotelemetry locations into ArcView GIS (Environmental Systems Research Institute 1998).

Vegetation Mapping

We generated vegetation cover maps in ArcView GIS for the following time periods: predevelopment, 1955, 1970, 1985, and 2000. Baseline vegetation data were obtained from the Advanced Identification of Wetlands Project

(MacAulay et al. 1994) and used to generate vegetation cover maps for each year. We generated historical vegetation coverages by reclassifying developed areas to original or expected vegetation types. For example, in the construction of the 1985 vegetation map, development occurring 1985–2000 was reclassified on the 2000 coverage to expected vegetation types (e.g., a developed area completely surrounded by hammock was reclassified to hammock). We used aerial photographs (1955–2000), vegetation maps from previous studies (Dickson 1955, Silvy 1975, Folk 1991), and land ownership data (tax roll records queried to identify homes built between certain years) for each period to verify reclassifications.

Data Analysis

Habitat Use.—Terms used to describe Key deer habitat use were: (1) preferred—used in greater proportion to availability, selected for; (2) avoided—not used in proportion to availability, selected against; and (3) habitat use/selection—the preferential use or avoidance of vegetation types by an animal, with use and selection being used interchangeably. We evaluated Key deer habitat use with a habitat-selection ratio (referred to by Manly et al. [2000] as a selection function) by sex and island. We did not compare selection ratios between age class and period due to small sample sizes (White and Garrott 1990). Furthermore, we did not compare deer use between "urban" and "wild" deer (Folk and Klimstra 1991) because of the difficulty in defining and categorizing deer in such a manner. We used habitat-selection ratios as opposed to other inferential statistical procedures for 2 reasons. First, Cherry (1998) and others (Johnson 1999, Anderson et al. 2000, Guthery et al. 2001) questioned the utility of testing point-null hypotheses known to be false a priori, such as whether deer use habitat at random. Second, wildlife managers require estimates of how human-induced habitat alterations within Key deer range influence the dynamics of Key deer populations. For example, habitat-selection ratios developed by our study will serve as parameters driving the spatially explicit PVA model being used to develop the HCP for Key deer.

We calculated habitat-selection ratios for each deer and vegetation type by dividing observed use by availability (Manly et al. 2000). Observed use by vegetation type was determined from radiotelemetry locations for each deer. We determined expected availability by multiplying radiotelemetry locations for each deer by the observed proportion of a given vegetation type in the study area or animal's home range (Aebischer et al. 1993). A selection ratio (S) then was calculated as $S = ([U + 0.001]/[A + 0.001])$, where U was equal to observed use and A to expected use (availability). To avoid a zero in the numerator or denominator, we added 0.001 to both use and availability (Aebischer et al. 1993, Bingham and Brennan 2004). Selection ratios >1 suggest animal use greater than expected, while $S < 1$ suggests avoidance (Manly et al. 2000). When comparing use in the form of an animal's home range (e.g., Johnson's [1980] second-order selection, range-study area), we multiplied total radio locations by the proportion of each vegetation type.

Habitat-selection ratios were evaluated for Key deer at 3 spatial scales. First, we compared the proportion of radio locations in each vegetation type (observed) to the proportion of vegetation types for the entire island or study area (expected, also called point-study area selection). This comparison is analogous to the first-order selection described by Johnson (1980). Second, we compared vegetation types in the 95% minimum convex polygon range of each deer to vegetation types for the entire island or study area (also called range-study area selection). This comparison is analogous to Johnson's (1980) second-order selection. Finally, we compared the proportion of telemetry locations in vegetation types (observed) to vegetation types available within the 95% minimum convex polygon range of each deer (Johnson's [1980] third-order selection, also called point-range selection). Key deer ranges were calculated using the animal movement extension (Hooge and Eichenlaub 1999) in ArcView GIS. Evaluating habitat use at different spatial scales reduced the potential bias associated with arbitrarily defining what was perceived to be available to an animal (Porter and Church 1987). Further, a multiscale approach provided additional insight into habitat use at different scales (Aebischer et al. 1993, Garshelis 2000).

Vegetation Changes.—We evaluated trends in vegetation changes between time periods using GIS data. Lopez (2001) hypothesized that Key deer density was a function of the area of uplands. We evaluated changes in the amount of upland area by year. Additionally, we calculated the amount of usable space (Guthery 1997), defined as total upland area minus development and road "footprints." The total development footprint was determined from the Monroe County tax roll (Monroe County Growth Management Division

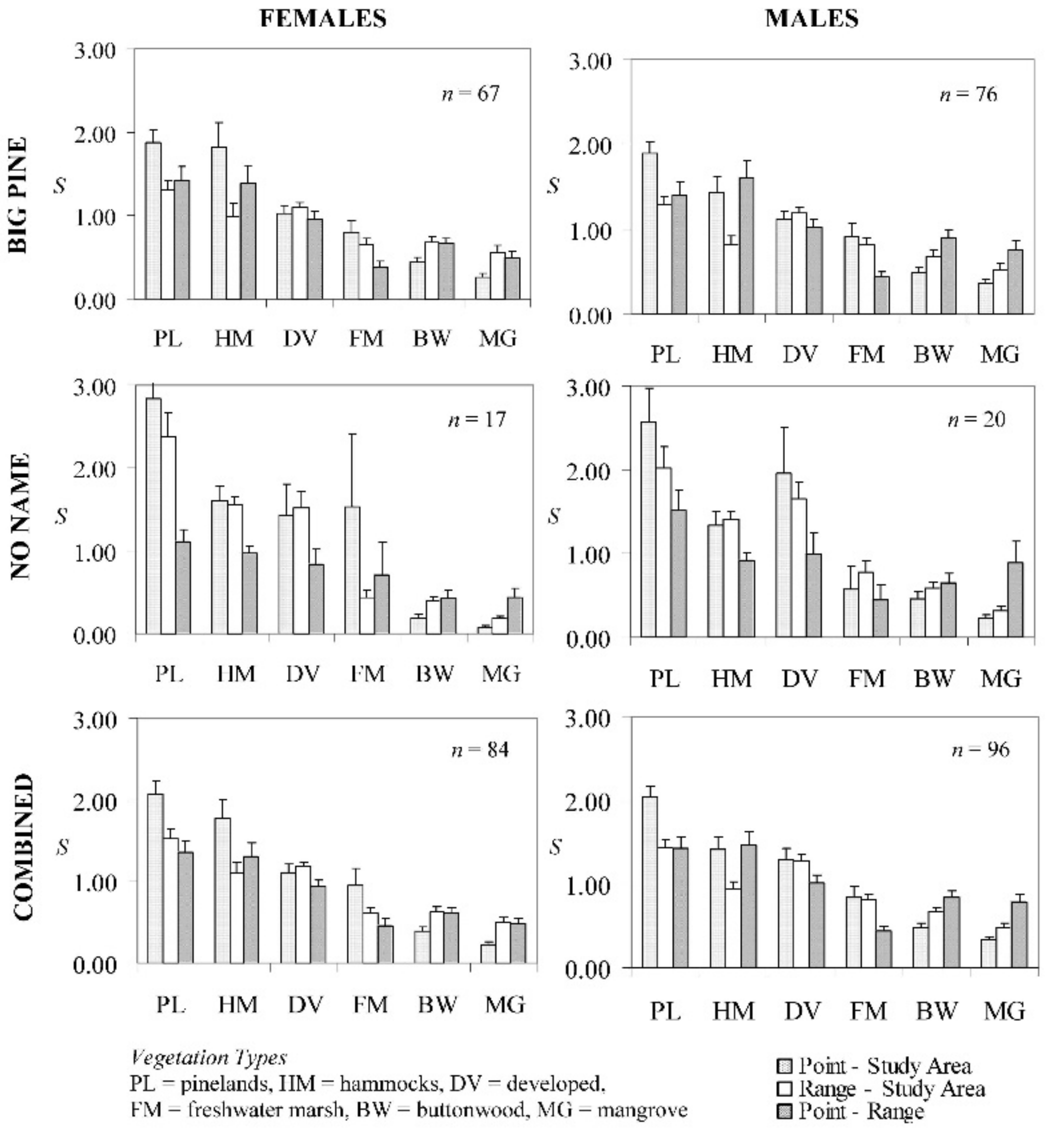

Fig. 2. Key deer habitat-selection ratios (*S*) and SE error bar by island, sex, and vegetation type in the Florida Keys, Florida, USA.

1992) and parcel data. Habitat loss due to roads was determined from road coverages from 1955–2000 (Lopez 2001).

RESULTS

Habitat Use

We radiomarked 180 deer (females: $n = 84$ [BPK= 67, NNK=17]; males: $n = 96$ [BPK= 76, NNK=20]) and used 40,248 radio locations with an average of 222 (SD = 176, range = 30–743) locations per animal. In our evaluation of habitat-selection ratios, we observed several selection patterns by Key deer. Though the degree of selection and/or order varied, Key deer generally preferred ($S = 0.82$–2.84) upland vegetation types and avoided ($S = 0.08$–1.54) lowlands at different scales and between sexes and islands (Fig. 2). When data were pooled, Key deer preferred upland vegetation types ($S = 0.98$–2.05) and avoided lowlands ($S = 0.28$–0.89; Fig. 3).

Urban Development

Since the arrival of settlers (approx 1900s), approximately 641 ha (21% of total area) were

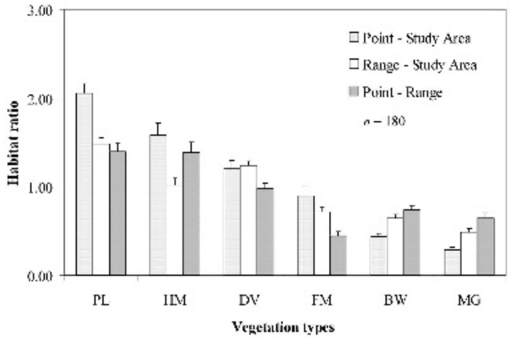

Fig. 3. Pooled Key deer habitat selection (*S*) and SE bar by vegetation types (PL = pineland, HM = hammock, DV = developed, FM = freshwater marsh, BW = buttonwood, and MG = mangrove) on Big Pine and No Name keys, Florida, USA, 1968–1992 and 1998–2000.

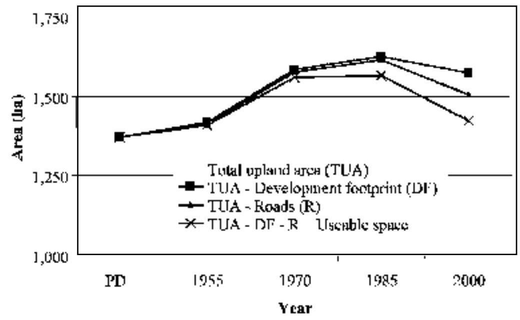

Fig. 5. Annual changes to the total upland area (pineland, hammock, development, ha) due to development "footprint" and road construction on Big Pine and No Name keys, Florida, USA, pre-development (PD)–2000. Usable space for Key deer is defined as the total upland area minus development footprint and road construction.

developed on BPK (610 ha, 24%) and NNK (31 ha, 7%). The largest land conversion (clearing for large subdivisions) occurred prior to 1985, while most home construction occurred later. During this period (prior to 1985), the amount of natural habitats did not change except where development occurred. Initially, habitat loss occurred primarily in mangrove and buttonwood areas, but since 1970, development moved to pineland and hammock areas (Fig. 4). Although development increased the total area of uplands, ongoing construction in existing subdivisions reduced the amount of usable space available to Key deer in these areas (Lopez 2001, Fig. 5). By 2000, the footprint of homes, businesses, and roads removed approximately 232 ha from usable Key deer habitat (Fig. 5). Key deer have increased from 50 in the 1930s (Frank et al. 2003) to approximately 400–500 in 2001 (Lopez et al. 2004). If deer densities are a function of usable space (Guthery 1997, Lopez 2001), we predict that the relationship between deer density and urban development observed on BPK and NNK would be hyperbolic (Figs. 5–6).

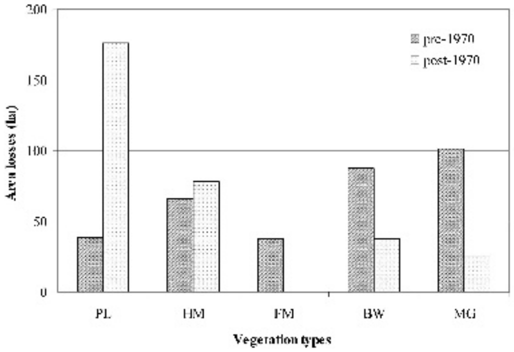

Fig. 4. Loss of native vegetation types (PL = pineland, HM = hammock, DV = developed, FM = freshwater marsh, BW = buttonwood, and MG = mangrove) pre- and post-1970 for Big Pine and No Name keys, Florida, USA.

DISCUSSION

Habitat Use

Selection ratios suggest that mangrove, buttonwood, and freshwater marshes seem to be relatively less useful to Key deer than uplands. Uplands, particularly pinelands and hammocks, are preferred sources of food, water, and cover for Key deer (Klimstra et al. 1974, Silvy 1975, Folk 1991). The importance of pinelands and hammocks in providing food sources to Key deer has been well documented (Klimstra and Dooley 1990, Folk 1991, Carlson et al. 1993) with 30–50% of important Key deer forage species found exclusively within these 2 habitat types (Folk 1991, Klimstra and Dooley 1990). Key deer pref-

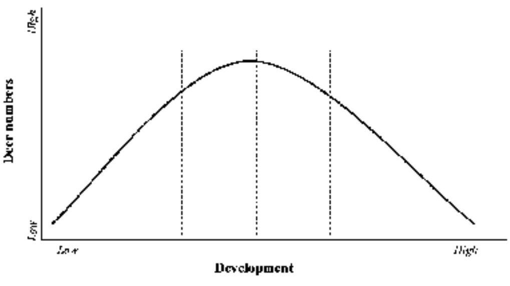

Fig. 6. A conceptual model illustrating the temporal change in the relationship between development and the Key deer population in the Florida Keys, Florida, USA.

erence of uplands is consistent with most studies of white-tailed deer where habitat use is characterized by vegetation diversity (Demarais et al. 2000) and is supported by our study.

While pineland and hammock habitats accounted for 34% of Key deer range, permanent freshwater sources in these habitat types accounted for approximately 58% of all freshwater sources (Lopez et al. 2003*a*). This suggests that freshwater availability also may influence habitat use, similar to the conclusions of Folk (1991). Freshwater marsh also was a source of freshwater for Key deer (Folk 1991) and accounted for approximately 28% of all freshwater sources (Lopez et al. 2003*a*). Possible reasons for apparent avoidance of freshwater marsh include (1) our analytic technique and (2) limited food resources in freshwater marsh. One assumption of habitat-selection ratios is that time spent in a given resource area is proportional to its importance to the animal in question (Manly et al. 2000). The infrequent use of freshwater marsh might simply reflect the time required to drink water rather than importance of the area as habitat type. Freshwater marsh is typically dominated by saw grass and saw palmetto (Folk 1991). Although these areas can provide excellent escape cover, they offer only limited food resources. For these reasons, the importance of freshwater marsh to Key deer should not be determined solely by selection ratios. Uplands also may be important sources of escape and fawning cover for Key deer. Hardin (1974) found that approximately 85% of Key deer fawning occurred in pinelands and hammocks with no observed fawning in developed areas. Other studies (Silvy 1975, Folk 1991) reported that hammocks and pinelands are important bedding and loafing areas. Collectively, the presence of food, freshwater, and cover support the importance of uplands for Key deer.

Urban Development

Lopez (2001) hypothesized that islands with high deer densities were those with a substantial upland component, while islands that were mostly tidal (e.g., Summerland, Ramrod) supported fewer deer than similar-sized islands with more upland area (e.g., NNK, Little Pine Key). If this is true, change in the amount of uplands might explain the increase in Key deer numbers in the last 30 years (Lopez et al. 2004). Historically, development of tidal areas were attributed to market demand to build home sites with water access. Since the enactment of federal and state laws such as the Florida Coastal Management Act (Title XXVII, Chapter 380, Part II, Florida Statute), development of these vegetation types has been restricted (Gallagher 1991), which led to increased development of uplands (Fig. 4). If current development trends continue, we predict that the amount of usable uplands for Key Deer will decrease (Fig. 5), thus decreasing Key deer numbers and increasing secondary impacts such as road mortality and fence entanglement (Lopez et al. 2003*b*). As a result of these dynamics, the conceptual relationship between Key deer density and urban development is hyperbolic (Fig. 6), as suggested by empirical evidence in our study (Fig. 5).

Our study illustrates the importance of landscape ecology and hierarchy theory (O'Neill et al. 1986) in wildlife management, particularly in how anthropogenic rescaling can permanently change ecological processes. Historically, urban development likely resulted in an increase in Key deer population numbers. However, assuming a continued positive relationship between urban development and Key deer population growth would be erroneous and should be viewed with caution as continued development may result in irreparable negative impacts to the deer population.

MANAGEMENT IMPLICATIONS

To ensure the long-term viability of Key deer, future land acquisitions should target upland habitats. We do not intend this recommendation to discourage purchase of tidal areas, but rather to prioritize land acquisition efforts at those habitats most critical to Key deer survival and those areas with less protection under current land-use law.

Temporal and spatial change in habitat should be considered in urban wildlife management where change often occurs quickly and mistakes are more costly because of both public exposure and the weakness of adaptive management in an environment where change implies time-consuming public policy. Wildlife managers should be aware of these potential impacts in planning management strategies for urban wildlife populations and their habitats.

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