# SURVIVAL, MORTALITY, AND LIFE EXPECTANCY OF FLORIDA KEY DEER

ROEL R. LOPEZ,<sup>1</sup> Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA MARK E. P. VIEIRA, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA NOVA J. SILVY, 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 SHANE W. WHISENANT, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA DUSTIN A. JONES, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA

Abstract: Increases in motor vehicle traffic, habitat loss, and human-deer interactions due to urban development threaten the recovery and management of Florida Key deer (Odocoileus virginianus clavium). To evaluate these threats, we estimated current survival rates and compared them to historic estimates, evaluated the causes of mortality from 1966 to 2000, and determined life expectancy of deer from marked animals. We radiomarked Florida Key deer as part of 2 separate field studies (1968–1972, 1998–2000), in addition to collecting mortality data and survey estimates (1966-2000). We analyzed survival data from 314 (157 male, 157 female) radiomarked deer using a known-fate model framework in program MARK. We considered a suite of a priori models based on the biology and current knowledge of Florida Key deer, and ranked them using Akaike's Information Criterion (AIC.) model selection. Important factors explaining deer survival were sex and geographical location. Model-averaged annual male survival (0.412-0.842) was lower than female survival (0.695-0.888). Marked female deer (n = 35) lived an average of 6.5 years (maximum 19 years), while marked male deer (n = 43) lived an average of 2.9 years (maximum 12 years). Deer survival also increased as deer moved away from U.S. Highway 1 (US 1). Deer-motor vehicle collisions accounted for >50% of total deer mortality, half of which occurred on US 1. Annual deer mortality since 1972 has increased and is attributed to an increase in the deer population size (1972-2000, 240%). We recommend finding methods to reduce deer-motor vehicle collisions because of human safety concerns. As efforts to reduce deer-motor vehicle collisions continue, biologists need to address high deer densities in management of this locally abundant but endangered deer population.

## JOURNAL OF WILDLIFE MANAGEMENT 67(1):34-45

Key words: deer-motor vehicle collisions, Florida Key deer, life expectancy, mortality, Odocoileus virginianus clavium, sex-specific, source-sink, survival, urbanization.

The endangered Florida Key deer, the smallest subspecies of white-tailed deer in the United States, are endemic to the Florida Keys on the southern end of peninsular Florida (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 overall deer population on Big Pine Key (BPK) and No Name Key (NNK; Fig. 1; Lopez 2001). Threats to recovery and management of Florida Key deer include increases in motor vehicle traffic, habitat loss, and human-deer interactions due to urban development (Klimstra et al. 1974, Folk 1991). Deer-motor vehicle collisions are of particular concern and account for nearly half the total deer mortality (Lopez 2001). In the early 1990s, the U.S. Fish and Wildlife Service (USFWS), Florida Department of Transportation (FDOT), and local residents recognized the need to reduce deer killed by motor vehicles. Speed reduction, signage, no-passing zones, and increased law

enforcement surveillance have been implemented with mixed success (Calvo 1996). Most vehicle collisions with deer (approx. 50%; Lopez 2001) occur on US 1, which is the only highway linking the Keys to the mainland.

The Endangered Species Act of 1973 (ESA) was established to reduce species risk of extinction, to protect their habitat, and to prevent "take" of listed species. In 1982, the ESA was amended to authorize incidental taking of any endangered species by landowners and nonfederal entities, provided they develop a Habitat Conservation Plan (HCP; ESA, Section 10a, 16 U.S.C. §1539a). Because additional motor vehicle traffic and development on these 2 islands likely would result in take of Key deer, highway improvements could be permitted with the initiation and approval of an HCP. In 1998, a planning process began with FDOT, Monroe County, and Florida Department of Community Affairs (DCA) representatives to draft and submit a regional HCP to the USFWS for Key deer. Proposed development activities on BPK and NNK were to be evaluated in terms of risk to the deer population through a

<sup>&</sup>lt;sup>1</sup> E-mail: roel@tamu.edu

#### J. Wildl. Manage. 67(1):2003

population viability analysis (PVA; Boyce 1992, Burgman et al. 1993, Akcakaya 2000). Our intent was to develop survival and mortality estimates that could be used in a PVA.

Florida Key deer were radiomarked as part of 2 separate field studies: (1) 1968–1972, hereafter referred to as the historic study; and (2) 1998–2000, hereafter referred to as the present study. In addition, USFWS biologists have collected deer mortality and census data since 1966. Collectively, we used these data to compare estimated current survival rates to historic estimates, evaluate the causes of mortality from 1966 to 2000, and determine life expectancy of Florida Key deer.

#### STUDY AREA

The Florida Keys are a chain of small islands approximately 200 km long extending southwest from peninsular Florida. Big Pine Key (2,548 ha) and NNK (461 ha) are within the boundaries of the NKDR and Monroe County (Fig. 1) and support most (453-517, approx. 75%) Florida Key deer population (Lopez 2001). Soils vary from marl deposits to bare rock of the oolitic limestone formation (Dickson 1955). Typically, island areas near sea level (maritime zones) are comprised of red (Rhisophora mangle), black (Avicennia germinans), and white mangroves (Laguncularia racemosa), and buttonwood (Conocarpus erecta) forests. With increasing elevation, maritime zones transition into hardwood (Gumbo limbo [Bursera simaruba], Jamaican dogwood [Piscidia piscipu*laa*]) and pineland (slash pine [*Pinus elliottii*], saw palmetto [Serenoa repens]) upland forests with vegetation intolerant of salt water (Dickson 1955, Folk 1991). Almost 24% of native areas have been developed since 1955 (Lopez 2001).

#### METHODS

## Survival

*Deer Trapping.*—We radiomarked Florida Key deer as part of 2 separate research projects conducted December 1968–June 1972 and January 1998–December 2000 on BPK and NNK (Silvy 1975, Lopez 2001). We captured with portable drive nets (Silvy 1975), drop nets (Lopez et al. 1998), and hand capture (Silvy et al. 1975). We used physical restraint to hold animals after capture with an average holding time of 10–15 min (no drugs were used). Captures occurred in 3 distinct areas: north Big Pine Key (NBPK), south Big Pine Key (SBPK), and NNK (Fig. 1). We recorded sex, age, capture location, body mass, radio



Fig. 1. Study areas within the Florida Key deer range, Big Pine Key (north and south, separated by dotted line) and No Name Key, Monroe County, Florida, USA.

frequency, and body condition for deer prior to release.

We classified deer by sex, age (fawn, yearling, adult; Severinghaus 1949), study (historic, present), and area (NBPK, SBPK, NNK). Deer that moved from initial capture area were reclassified based on radiotelemetry locations. However, approximately 85% of radiomarked deer did not move from the area of their original capture site (Lopez 2001).

We marked captured deer in various ways depending on sex and age (Silvy 1975, Lopez 2001). We used a battery-powered mortality-sensitive radiotransmitter (148 MHZ, 425-450 g for plastic neck collars, 15-20 g for elastic collars, AVM Electronics Corporation, Champaign, Illinois, USA, 1968-1972; 150-152 MHz, 100-110 g for plastic neck collars, 10-20 g for antler transmitters and elastic collars, Advanced Telemetry Systems, Isanti, Minnesota, USA, 1998-2000) attached to plastic neck collars (8-cm-wide, primarily females of all age classes), leather antler collars (0.25-cm-wide, yearling and adult males only), or elastic expandable neck collars (3-cmwide, primarily male fawns/yearlings). Each captured animal received an ear tattoo as a permanent marker (Silvy 1975).

*Radiotelemetry.*—We monitored radiomarked deer for mortalities 6–7 times/week at random intervals. Each 24-hr period was divided into 6 equal 4-hr segments. We randomly selected a 4-hr segment each day during which all deer were located (Silvy 1975). If a mortality signal was detected, we immediately located and necropsied the animal to determine cause of death (Nettles 1981). We censored animals from the data set after their last known encounter if their radios failed or disappeared (Pollock et al. 1989).

Data Analysis.--Known fate models estimate survival probabilities, usually with high precision, even in cases of small sample size due to the precise evaluation of each animal's status at each sampling occasion (White and Burnham 1999). Every animal is classified as alive, dead, or censored. We converted field telemetry data into an encounter history file for input into program MARK using SAS (SAS Institute 1999). We created individual encounter histories for each deer, placing each animal into 1 of 36 classification groups based on 3 age classes, 2 sex classes, 3 area classes, and 2 study classes. Deer entered the next age class on 1 April (mean fawning date; Hardin 1974), spending a maximum of 1 year as fawns, 1 year as yearlings, and remaining in the adult age

class until death (Silvy 1975). We monitored radiomarked deer daily; then collapsed each 7 days of monitoring data into a weekly survival for each animal. Beginning with the week it was radiomarked, each deer had a weekly survival history during which it either lived, died, was censored, or the study ended (Pollock et al. 1989).

We evaluated 13 models a priori based on the biology and current knowledge of Florida Key deer (Table 1) using program MARK. This paradigm for model creation was assessed by Burnham and Anderson (1998) and shown to reduce the possibility of spurious results, as might occur with model overfitting when each potential model is inspected for fit before the next one is analyzed. Program MARK uses Akaike's Information Criterion (AIC<sub>e</sub>) model selection (Burnham and Anderson 1998) to rank each potential model.

We used a random effects model to obtain PVA survival estimates and variances (White 2000). Random effects modeling in program MARK assists in separating sampling variance from process variance. Only process variance should be included in PVA survival estimation because inclusion of sampling variability erroneously inflates the variance estimates and negatively biases viability (White 2000). Unfortunately,

Table 1. Akaike's Information Criterion (AIC<sub>c</sub>) ranking of 13 a priori models used to estimate model-averaged weekly survival rates for radiomarked Florida Key deer (n = 314) on north Big Pine Key (NBPK), south Big Pine Key (SBPK), and No Name Key (NNK), 1968–1972 and 1998–2000.

Model						
no.	Model description	Model structure	κ	AIC <sub>c</sub>	$\Delta {\rm AIC}_{\rm c}$	w <sub>m</sub>
7	Sex, area and sex*area effects for adults and yearlings on NBPK and SBPK, only age effect for NBPK and SBPK fawns, only area effect for all NNK deer	$S(\text{sex}^{\text{area}} + \text{all fawns having own } S + \text{all } NNK deer having own } S, including fawns)$	6	972.64	0.00	0.2578
8	Sex, area and sex*area effects for adults and yearlings on NBPK and SBPK, only age effect for all fawns, area effect for all NNK yearlings and adults	$S(\text{sex}^{*}\text{area} + \text{all fawns having own } S + \text{all}$ NNK deer having own $S$ , excluding fawns)	6	972.75	0.11	0.2435
9	Area and additive sex effect	S(sex + area)	4	973.06	0.42	0.2089
10	Sex, area, sex*area effects for adults and yearlings with age effect in fawns	$S(\text{sex}^*\text{area} + \text{all fawns having own } S)$	7	973.94	1.30	0.1344
11	Sex, area, sex*area effects for adults and yearlings, age and sex effect in fawns	S(sex*area + all fawns having own S, varying by sex)	8	975.46	2.82	0.0628
12	Sex, area, sex*area effects for NBPK and SBPK deer, with area effect for all NNK deer	$S(\text{sex}^{*}\text{area} + \text{all NNK deer having own } S)$	5	975.74	3.10	0.0547
13	Sex, area and sex*area effects	S(sex*area)	6	976.94	4.30	0.0301
1	Sex effect	S(sex)	2	980.69	8.05	0.0046
5	Age, sex and sex*age effects for yearlings and adults, only age effect for fawns	S(age*sex + no sex effects in fawns)	5	982.79	10.15	0.0016
6	Age, sex and age*sex interaction effects	S(age*sex)	6	984.31	11.67	0.0008
2	Area effect	S(area)	3	990.50	17.86	0.0000
4	Study effect	S(study)	2	998.93	26.30	0.0000
3	Age effect	S(age)	3	999.72	27.08	0.0000

weekly survival estimates approached a value of 1, and the temporal process variance was small. As a result, the contribution of sampling variance overwhelmed the process variance and could not be separated in our analysis. Therefore, estimates to be used in the PVA were slightly larger, which would negatively bias viability estimates (White 2000). Annual survival estimates were obtained from weekly estimates (n = 52) using

$$\bar{\hat{S}}_{yearly} = (\bar{\hat{S}}_{weekly})^n,$$

and annual survival SE estimates were calculated from model-averaged weekly SE estimates using

$$\hat{SE}(\hat{\bar{S}}_{weekly}) = \sqrt{V\hat{a}r(\bar{\bar{S}}_{weekly})}$$

and

$$\widehat{\operatorname{SE}}(\overline{\widehat{\operatorname{S}}}_{yearly}) = \sqrt{e^{2\ln(n) + 2(n-1)\ln(S_{weekly})} \operatorname{SE}(\overline{\widehat{\operatorname{S}}}_{weekly})^2}$$

We calculated model-averaged 95% confidence intervals for weekly survival rates with the logit transform (Burnham et al. 1987) using:

$$-95\% \text{CI}(\overline{\hat{p}_i}) = \frac{\overline{\hat{p}_i}}{\overline{\hat{p}_i} + (1 - \overline{\hat{p}_i})C} ,$$
$$+95\% \text{CI}(\overline{\hat{p}_i}) = \frac{\overline{\hat{p}_i}}{\overline{\hat{p}_i} + ((1 - \overline{\hat{p}_i})/C)} , \text{ where}$$
$$C = \exp\left(\frac{1.96 \text{ SE}(\overline{\hat{p}_i})}{\overline{\hat{p}_i}(1 - \overline{\hat{p}_i})}\right).$$

#### Mortality

*Necropsies.*—Beginning in 1966, NKDR staff recorded deer mortality by direct sightings, citizen reports, or observation of turkey vultures (*Cathartes aura*). Collected animals were held frozen prior to necropsy examination or necropsied immediately. Our ability to determine cause of death ranged from good to marginal (Nettles 1981, Nettles et al. in press**UPDATE?**). We recorded age, sex, body mass, and cause of death for each animal using procedures described by Nettles (1981), and entered all mortality locations into a GIS using ArcView (Version 3.2) and Microsoft Access (Version 97).

Population Trends.—U.S. Fish and Wildlife Service biologists conducted monthly spotlight

counts along a standard route for BPK (56-km) and NNK (3-km) beginning at 2000-2100 hr (Humphrey and Bell 1986, Lopez 2001). These surveys provided the refuge with an index to population size and also served as the official survey route for NKDR (Humphrey and Bell 1986, USFWS 1999). With the aid of spotlights, 2 observers in a vehicle (average travel speed, 16-24 km/hr) recorded the number of deer observed along the route in addition to sex and age estimates (Humphrey and Bell 1986). The starting and ending points for the survey route were identical each time. We compared the average number of deer seen annually to annual deer mortality from 1976 to 2000 to determine whether these variables were correlated.

Data Analysis.—We examined trends in deer mortality by sex, age, island, area, year/period, data source, and mortality agent. Spatial assignments by area were determined using ArcView. When appropriate, differences in deer mortality by category were tested using a Chi-square goodness-of-fit test (Ott 1993). The average number of deer seen annually was compared to annual deer mortality using a Spearman's rank correlation coefficient (Ott 1993).

### Life Expectancy

We defined life expectancy estimates as the mean age of death for members of a cohort and validated our estimate with mathematical models (e.g., Leslie matrix models; Caughley 1977, Caswell 2000). Following termination of the historic study in 1972, transmitters attached to neck collars and/or ear tattoos were not removed from animals, which offered a unique opportunity to calculate life expectancy for an unhunted, long-lived, wild deer population. Since the end of the historic study, NKDR refuge staff collected and recorded mortalities of marked deer. We used the NKDR database, in appropriate cases, to determine mean life expectancy estimates and maximum ages.

#### RESULTS

#### Survival

We captured and radiomarked 314 deer during both studies (historic: 21 fawn females, 8 yearling females, 39 adult females, 40 fawn males, 5 yearling males, 19 adult males; present: 10 fawn females, 22 yearling females, 57 adult females, 10 fawn males, 33 yearling males, 50 adult males). Ninety deer (52 historic, 38 present) died, 87

			Wee	kly		Annual					
				95%	95%			95%	95%		
Sex				LCI	UCI			LCI	UCI		
Age	Area <sup>a</sup>	ŝ	SE	(logit)	(logit)	ŝ	SE	(logit)	(logit)		
F											
Fawn	NNK	0.994	0.003	0.982	0.998	0.746	0.132	0.384	0.914		
Fawn	NBPK	0.994	0.003	0.985	0.998	0.726	0.109	0.449	0.880		
Fawn	SBPK	0.993	0.003	0.986	0.997	0.695	0.091	0.478	0.836		
Yearling	NNK	0.998	0.001	0.994	0.999	0.888	0.056	0.715	0.959		
Yearling	NBPK	0.997	0.001	0.995	0.998	0.848	0.033	0.770	0.902		
Yearling	SBPK	0.993	0.002	0.987	0.997	0.710	0.082	0.515	0.839		
Adult	NNK	0.998	0.001	0.994	0.999	0.888	0.056	0.715	0.959		
Adult	NBPK	0.997	0.001	0.995	0.998	0.848	0.033	0.770	0.901		
Adult	SBPK	0.993	0.002	0.987	0.997	0.710	0.082	0.515	0.839		
М											
Fawn	NNK	0.995	0.003	0.986	0.998	0.774	0.109	0.474	0.916		
Fawn	NBPK	0.992	0.003	0.985	0.996	0.668	0.091	0.458	0.812		
Fawn	SBPK	0.990	0.005	0.973	0.996	0.599	0.158	0.246	0.830		
Yearling	NNK	0.997	0.002	0.992	0.999	0.842	0.069	0.645	0.934		
Yearling	NBPK	0.990	0.002	0.985	0.993	0.583	0.060	0.457	0.690		
Yearling	SBPK	0.983	0.005	0.971	0.990	0.412	0.099	0.222	0.594		
Adult	NNK	0.997	0.002	0.992	0.999	0.842	0.069	0.645	0.934		
Adult	NBPK	0.990	0.002	0.985	0.993	0.583	0.060	0.458	0.690		
Adult	SBPK	0.983	0.005	0.971	0.990	0.412	0.099	0.222	0.594		

Table 2. Weekly and annual model-averaged survival<sup>a</sup>,  $(\overline{\hat{s}})$ , and variance estimates by sex, age, and area for radiomarked Florida Key deer (n = 314) on north Big Pine Key (NBPK), south Big Pine Key (SBPK), and No Name Key (NNK), 1968–1972 and 1998–2000.

<sup>a</sup> The study variable had no contribution to final model-averaged estimates (Table 1) and data were pooled between areas. Conversely, the age variable also was not significant (particularly between yearlings and adults); however, for modeling purposes in the population viability analysis (PVA), estimates were separated between age classes.

deer survived (45 historic, 42 present), and 137 deer (35 historic, 102 present) were censored. No deer died during capture, but 1 deer died due to radiocollar complications several months later.

All of the models evaluated had classification groups with sample sizes greater than 21. Results from the model selection procedure indicate that sex and area were important factors explaining deer survival (Table 1). In general, annual survival for males was lower than annual female survival. Model-averaged annual survival estimates ranged from 0.695 ( $\pm$  0.033 SE) to 0.888 ( $\pm$  0.132 SE) for females and 0.412 ( $\pm$  0.060 SE) to 0.842 ( $\pm$  0.158 SE) for males (Table 2). Annual survival for both sexes was highest for deer from NNK and lowest for deer from SBPK deer (Table 2; Figs. 2, 3).





Fig. 2. Annual female Florida Key deer survival and 95% error bars by age class and area (No Name Key [NNK], North Big Pine Key [NBPK], and South Big Pine Key [SBPK]), 1968–1972 and 1998–2000.

Fig. 3. Annual male Florida Key deer survival and 95% error bars by age class and area (No Name Key [NNK], North Big Pine Key [NBPK], and South Big Pine Key [SBPK]), 1968–1972 and 1998–2000.

TADIE 5. MULTAIILY AUEHL DY SEX AND UATA SUULCE IOFFIUNUA NEV UEEL UN DIU FINE NEV AND IND MAINE NEV. 1900–200	Table 3.	Mortality	agent by sex	and data sourc	e for Florida	Kev deer on	Bia Pine K	ev and No	Name Kev.	1966-200
--	----------	-----------	--------------	----------------	---------------	-------------	------------	-----------	-----------	----------

	No. (USFWS <sup>a</sup> )						No. (Historic)				No. (Present)				
Cause	F	М	Unknown	Total	%	F	Μ	Unknown	Total	%	F	М	Unknown	Tota	%
Entanglement	11	13	0	24	1.12	0	0	_	0	0.00	1	2	_	3	7.89
Dog	19	23	1	43	2.00	0	1	_	1	1.92	1	0	_	1	2.63
Disease	11	36	0	47	2.19	0	0	_	0	0.00	1	1	_	2	5.26
Drowning	14	38	8	60	2.79	2	3	_	5	9.62	0	1	_	1	2.63
Unknown	22	46	6	74	3.44	4	9	_	13	25.00	3	5	_	8	21.05
Other	117	162	28	307	14.27	2	5	_	7	13.46	3	1	_	4	10.53
Auto collision	594	988	14	1,596	74.20	8	18	_	26	50.00	8	11	_	19	50.00
Total	788	1,306	57 2	2,151	100.00	16	36	_	52	100.00	17	21	—	38	100.00

<sup>a</sup> 1966–2000.

## Mortality

Necropsy and telemetry data both indicated that deer–motor vehicle collisions accounted for most (>50%) deer mortality ( $X_6^2$  = 6,489.74; *P* < 0.001; Tables 3, 4; Figs. 4, 5). Other Key deer mortality agents included fence entanglement, dogs, disease, and drowning.

Sex Effect.—From 1966 until present, annual deer mortality was higher for males than females. Overall, recorded male mortality was over 1.5 times that of female mortality ( $X_1^2 = 97.62$ ; P < 0.001; Table 3; Fig. 4). Differential survival estimates observed between sexes from telemetry data supports differences in mortality between

Table 4. Deer-motor vehicle collision mortality by sex, age, and area for Florida Key deer (n = 1,596) on Big Pine Key and No Name Key, 1966–2000.

			Big Pine			
			Key Deer			
Sex	Age	US 1	Blvd	Other	No Name	Total
F	Fawn	25	31	47	11	114
	Yearling	59	29	25	5	118
	Adult	143	70	91	19	323
	Unknown	16	8	9	6	39
	Total	243	138	172	41	594
	% by Area	40.9	23.2	29.0	6.9	100.0
Μ	Fawn	85	46	51	12	194
	Yearling	157	35	44	18	254
	Adult	311	67	87	35	500
	Unknown	22	5	11	2	40
	Total	575	153	193	67	988
	% by Area	58.2	15.5	19.5	6.8	100.0
Unkn	own Fawn	2	2	4	1	9
	Yearling	0	0	0	0	0
	Adult	2	0	0	0	2
	Unknown	2	1	0	0	3
	Total	6	3	4	1	14
	% by Area	42.9	21.4	28.6	7.1	100.0
Total		824	294	369	109	1,596
% by	Area	51.6	18.4	23.1	6.8	100.0

sexes from necropsy data. Furthermore, data indicate seasonal differences in deer mortality with male mortality increasing during the breeding season (Fig. 6).

*Area Effect.*—Florida Key deer had a greater susceptibility to mortality, particularly from motor vehicle collisions, as deer moved closer to the US 1 corridor (SBPK). Highest deer mortality observed for both sexes was in SBPK, followed by NBPK and NNK (Fig. 7). Of the 1,596 deer–motor vehicle collisions, approximately 52% occurred on US 1 (Table 4).

Population Trends.—In general, we detected no difference in survival (Table 1) or mortality causes (Table 3) between studies. Despite similar results in survival and mortality estimates between studies, annual deer deaths increased since 1972. Annual deer mortality is a function of deer density or population size. We found a correlation ( $r_s = 0.743$ ; Fig. 8) between annual deer mortality and monthly road count data (1976–2000, n = 266 road counts).

The population sex ratio and distribution of Florida Key deer males and females on BPK were



Fig. 4. Annual Florida Key deer mortality (n = 2,151) by sex on Big Pine Key and No Name Key, 1966–2000.



Fig. 5. Annual Florida Key deer mortality (n = 2,151) by mortality agent on Big Pine Key and No Name Key, 1966–2000.

skewed. For example, of 6,575 deer observed in recent road counts (1998–2000, n = 379 road counts; Lopez 2001) for BPK, approximately 69% were females and 31% were males. The proportion of deer observed in NBPK was 75% females and 25% males, whereas the proportion of deer observed in SBPK was 56% females and 44% males. These data indicate a greater proportion of male deer reside in SBPK, where Key deer face the greatest threats (greater motor vehicle traffic lev-

els and greater number of fences; Lopez 2001).

*Biases.*—Deer mortality from vehicle collisions, based on radiotelemetry data, accounted for approximately 50% of the total deer mortality. However, mortality data collected by USFWS biologists indicate a slightly higher estimate of 74% (Table 3). The higher USFWS estimates probably are due to a greater probability of observers detecting mortality from vehicle collisions compared to other forms of deer mortality.

#### Life Expectancy

Life expectancy for known-fate marked female deer (n = 35) averaged 6.5 years (maximum 19 years). The mean lifespan for males (n = 43) was about 2.9 years (maximum 12 years). The combined average (n = 78) was approximately 4.5 years.

## DISCUSSION

Urban development and other anthropogenic factors threaten the viability of the Florida Key deer population (Folk 1991). The effect of deer-motor vehicle collisions on the Florida Key deer population, however, is relatively recent since a limited number of roads and motor vehicle traffic existed prior to 1960 (Folk 1991). Illegal hunting or poaching reduced deer numbers to an estimated 50 animals in the 1940s (Dickson



Fig. 6. Florida Key deer mortality (n = 2,151) by sex, month, and reproductive season on Big Pine Key and No Name Key, 1966–2000.



Fig. 7. Florida Key deer mortality by sex and area in 5-year increments on Big Pine Key, 1966-2000.

1955, Folk 1991), but protection of deer through law enforcement efforts resulted in a population increase to the current size of 453–517 deer (Lopez 2001). Despite increases in deer–motor vehicle collisions and urban development, the deer population has increased nearly 240% since 1972 (Lopez 2001). This study elucidated several survival and mortality patterns that are important in understanding the population dynamics of Key deer.

## Sex Effect

Male deer face a greater risk of mortality than females. Other studies (Nelson and Mech 1986; Nixon et al. 1991, 2001; Demarais et al. 2000) documented differential survival between sexes of white-tailed deer. Loison et al. (1999) and Demarais et al. (2000) hypothesized differences in social behavior for males and females, particularly reproductive behavior (e.g., greater male seasonal movements, male–male aggression), which resulted in differential survival between sexes.

Previous studies have reported that Florida Key deer males average daily movements are nearly double those of female deer, especially during the reproductive season (Silvy 1975, Lopez 2001). We propose that greater male movements likely would result in an increased mortality risk due to deer-motor vehicle collisions. However, the lower male survival we observed does not appear to have impacted population growth. Survey data (1968-2000) indicate that the deer population on BPK and NNK has grown 1-10% annually (Lopez 2001). Similar results (1-5% annual population rates) were observed from Leslie matrix analyses (Caswell 2000) that incorporated survival and fecundity estimates from study results presented in this paper (Lopez 2001).

Past studies have reported that fetal sex ratios for Florida Key deer were male-biased (57–74% males; Hardin 1974, Klimstra et al. 1974, Folk and Klimstra 1991*a*). Despite the observed malebiased fetal sex ratio, the overall population sex ratio for BPK was female-biased (69% females,



Fig. 8. Average Florida Key deer seen (line, males and females) on U.S. Fish and Wildlife Service (USFWS) monthly road counts and annual deer mortality (bars, males, females) on Big Pine Key and No Name Key, 1976–2000.

31% males; Lopez 2001). The female-bias sex ratio observed in BPK might be explained by (1) differential survival between sexes and/or (2) differential survival between areas. First, higher female survival eventually would favor a femalebiased population sex ratio. Second, a greater number of females were observed from road count data in NBPK as compared to SBPK (Lopez 2001). The distribution of males was exactly the opposite with more males observed in SBPK. As a result, we hypothesize that the overall male mortality risk is higher due to the greater proportion of males versus females in SBPK. For these reasons, we suggest that differential survival and distribution between sexes on the island resulted in a female-bias population sex ratio.

## Age Effect

Model selection results indicate that survival did not differ among the 3 age classes (Tables 1, 2). However, 3 of the top 4 models had some form of separate fawn survival, indicating that age might be a significant factor for survival in the fawn age class with adult and yearling survival

being similar. We attribute a lack of stronger detectability among age class survival to small sample sizes in highly parameterized models, particularly for the fawn classes. For example, other studies (Hardin 1974, Loison et al. 1999) report lower fawn survival compared to other age classes (vearlings, adults). Fawn survival in this study likely is overestimated due to the difficulty in capturing fawns <4 months of age (approx. 15% of total radiomarked fawns were <4 months of age). Furthermore, previous studies (Hardin 1974, Loison et al. 1999, Demarais et al. 2000) documented that most fawn mortality occurs in the first 6 months. Corrective measures include future research on fawn survival (particularly for fawns <4 months) using radiotelemetry to improve survival estimates. Research efforts should focus on the capture and radiomarking of deer fawns, which were not the primary study objective of previous studies (Hardin 1974, Silvy 1975, Lopez 2001).

#### Area Effect

Florida Key deer survival varied depending on the area occupied by radiomarked animals (Tables 2, 3). In general, deer survival increased as deer moved away from US 1 (lowest survival in SBPK, highest survival in NNK; Fig. 1). Higher speeds and greater traffic levels on US 1, which bisects SBPK, collectively increase deer susceptibility to deer-motor vehicle collisions. This relationship appears to impact both sexes similarly (Fig. 7).

Dias (1996) and Wilson (2001) suggested that areas occupied by a species could be divided into sources and sinks, depending on whether local reproduction is sufficient to balance mortality. Source populations are those where reproduction exceeds mortality with surplus individuals dispersing to sink populations where mortality exceeds local reproduction. Sink populations would not be viable in the absence of immigration (Dias 1996). In applying this concept to the deer population, NBPK can be described as a source (high-quality habitat and high deer densities) with SBPK being a sink (low-quality habitat and low deer densities; Lopez 2001, R. Lopez, Texas A&M University [TAMU], unpublished data). Future development on Big Pine Key should be directed into areas of high risk of vehicle mortality (sinks) rather than areas where vehicle mortality presently is low (sources).

#### **Population Trends**

Based on telemetry data, the proportion of deer dying from vehicle collisions did not change between the present and historic studies. However, other mortality agents have increased, such as deer entanglement in fences (>8%) and disease incidence (>5%) since 1972. Schulte et al. (1976) noted relatively low incidence or absence of diseases in Key deer. Since 1986, monitoring by the Southeastern Cooperative Wildlife Disease Study has documented population limiting disease increases in Florida Key deer, including intestinal parasites (e.g., large stomach worm [*Haemonchus contortus*]; Nettles et al. 2002). Increases in the incidence of diseases result from deer populations at or above carrying capacity (Nettles et al. 2002).

Incidences of deer drowning decreased (-7%) from the historic to the present study. The influence of mosquito ditches may explain this decrease. Mosquito ditches (approx. 30 cm wide, 1–2 m deep, lengths vary) were originally trenched in the 1950s to connect freshwater holes to saltwater channels (Folk 1991). This practice was used to prevent mosquito breeding by the introduction of saltwater into freshwater holes that served as breeding sites (Hardin et al. 1984, Folk 1991). Hardin (1974) reported the sus-

ceptibility of young fawns to drowning in these ditches when attempting to cross. The silting and filling of many mosquito ditches since the 1970s might explain the observed decrease in the incidence of drowning.

#### Data Biases

Previous studies report that deer-motor vehicle collisions account for 60-75% of total deer mortality (Hardin 1974, Hardin et al. 1984, Klimstra et al. 1974, Folk and Klimstra 1991b). Although we found similar results, it is important to note that the contribution of deer-motor vehicle collisions to overall deer mortality likely is overestimated due to high visibility of carcasses along roadways. In contrast, deer that die of natural causes have a lower probability of being located. Telemetry data from both the historic and present studies determined that mortality from auto collisions was lower than total deer mortality from USFWS trend data, illustrating how the mortality database likely overestimated mortality from auto collisions due to differences in detectability.

#### Life Expectancy

Ozoga (1969) reported that wild known-aged females in Michigan lived a maximum of 14 years. We observed high deer life expectancy despite mortality from deer-motor vehicle collisions. A matrix model, incorporating current survival and fecundity estimates, predicted the average life span to be 6.3 years for females and 2.5 years males (Lopez 2001).

## MANAGEMENT IMPLICATIONS

The Florida Key deers' restricted range and desire by humans to develop its habitat results in interesting and challenging management problems. With deer-motor vehicle collisions accounting for nearly half of the total deer deaths, the role of vehicle mortality in affecting the population size and structure of this federally protected species is significant. In January 2002, FDOT began efforts to reduce deer-motor vehicle collisions along a 2-km undeveloped section of US 1 on the east side of BPK. About 25% of annual deer-motor vehicle collisions occur on this section of US1 (Lopez 2001). The project (hereafter known as the US 1 Project) is scheduled to be completed by January 2003 and includes the use of fencing, underpasses, and deer guards (similar to cattle guards) to prevent deer access to the highway (C. Owens, FDOT, Environmental Manager, personal communication).

The deer population on BPK and NNK is approaching or near carrying capacity based on observed abomasal parasite counts (Nettles et al. 2002) and current population estimates (Lopez 2001). Maintaining high deer densities is not recommended because of potential damage to habitat, increased likelihood of disease transmission, and increased human-deer conflicts (McShea et al. 1997, Nettles et al. 2002). However, population-control measures are prohibited under the ESA. With completion of the US 1 Project and the reduction of deer-motor vehicle collisions, problems associated with high deer densities are expected to be compounded. In the past, mortality from deer-motor vehicle collisions reduced the overall potential growth of the deer population. Despite the biological benefits of controlling herd overabundance, we encourage minimizing deer-motor vehicle collisions because of human safety concerns.

As efforts to reduce deer-motor vehicle collisions continue, biologists will need to address management of high population densities in this endangered deer population in other ways. A radically different management paradigm for USFWS biologists is required. For example, stakeholders must accept the idea that controlling deer numbers when deer densities are high may be necessary in some situations. The first step in this process would include modifying the Recovery Plan to allow refuge managers to implement acceptable population-control practices (e.g., use of contraception) in the management of Florida Key deer. Future research should continue to monitor changes in survival, mortality, and population growth as deer densities continue to change and/or if managers attempt population control.

## ACKNOWLEDGMENTS

We thank TAMU student interns who assisted in the collection of field data, and J. W. Hardin, P. R. Krausman, C. A. Faulhaber, R. N. Wilkins, W. E. Grant, T. R. Peterson, G. C. White, P. Lukacs, and 1 anonymous reviewer for constructive criticism in the preparation of this manuscript. Special thanks to the staff of the National Key Deer Refuge, Monroe County, Florida. Funding was provided by the TAMU System, Rob and Bessie Welder Wildlife Foundation, Florida Fish and Wildlife Conservation Commission, and U.S. Fish and Wildlife Service (Special Use Permit No. 97-14). This manuscript is supported by the Welder Wildlife Foundation, Contribution No. 581.

## LITERATURE CITED

- AKCAKAYA, H. R. 2000. Population viability analyses with demographically and spatially structured models. Ecological Bulletins 48:23–38.
- BOYCE, M. S. 1992. Population viability analysis. Annual Reviews Ecology and Systematics. 23:481–506.
- BURGMAN, M. A., S. FERSON, AND H. R. AKCAKAYA. 1993. Risk assessment in conservation biology. Chapman & Hall, London, United Kingdom.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.
- , \_\_\_\_, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph Number 5.
- CALVO, R. 1996. US-1/SR-5 Key deer/motorist concept report. Florida Department of Transportation Technical Report, Miami, USA.
- CASWELL, H. 2000. Matrix population models: construction, analysis, and interpretation. Sinauer Press, Sunderland, Massachusetts, USA.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, USA.
- DEMARAIS, S., K. V. MILLER, AND H. A. JACOBSON. 2000. White-tailed deer. Pages 601–628 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Inc., Upper Saddle River, New Jersey, USA.
- DIAS, P. C. 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11:326–330.
- DICKSON, J. D., III. 1955. An ecological study of the Key deer. Florida Game and Fresh Water Fish Commission Technical Bulletin 3, Tallahassee, USA.
- FOLK, M. L. 1991. Habitat of the Key deer. Dissertation, Southern Illinois University, Carbondale, USA.
- ——, AND W. D. KLIMSTRA. 1991*a*. Reproductive performance of female Key deer. Journal of Wildlife Management 55:386–390.
- \_\_\_\_\_, AND \_\_\_\_\_. 1991b. Urbanization and domestication of the Key deer (*Odocoileus virginianus clavium*). Florida Field Naturalist 19:1–9.
- HARDIN, J. W. 1974. Behavior, socio-biology, and reproductive life history of the Florida Key deer, *Odocoileus virginianus clavium*. Dissertation, Southern Illinois University, Carbondale, USA.
- ——, W. D. KLIMSTRA, AND N. J. SILVY. 1984. Florida Keys. Pages 381–390 *in* L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.
- HUMPHREY, S. R., AND B. BELL. 1986. The Key deer population is declining. Wildlife Society Bulletin 14:261–265.
- KLIMSTRA, W. D., J. W. HARDIN, N. J. SILVY, B. N. JACOB-SON, AND V. A. TERPENING. 1974. Key deer investigations final report: Dec 1967–Jun 1973. U.S. Fish and Wildlife Service, Big Pine Key, Florida, USA.
- LEBERTON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118. COULD NOT FIND-DELETE?
- LOISON, A., M. FESTA-BIANCHET, J. M. GAILLARD, J. T. JOR-GENSON, AND J. M. JULLIEN. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539–2554.

J. Wildl. Manage. 67(1):2003

- LOPEZ, R. R. 2001. Population ecology of Florida Key deer. Dissertation, Texas A&M University, College Station, USA.
- ——, T. R. PETERSON, AND N. J. SILVY. 2001. Emphasizing numbers in the recovery of an endangered species: a lesson in underestimating public knowledge. Pages 255–258 *in* R. Fields, R. J. Warren, H. Okarma, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA. **COULD NOT FIND-DELETE?**
- —, N. J. SILVY, J. D. SEBESTA, S. D. HIGGS, AND M. SALAZAR. 1998. A portable drop net for capturing urban deer. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 52:206–209.
- MCSHEA, W. J., H. B. UNDERWOOD, AND J. H. RAPPOLE. 1997. Deer management and the concept of deer overabundance. Pages 1–11 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.
- NELSON, M. E., AND D. L. MECH. 1986. Mortality of whitetailed deer in northeastern Minnesota. Journal of Wildlife Management 50:691–698.
- NETTLES, V. F. 1981. Necropsy procedures. Pages 6–16 in W. R. Davidson, F. A. Hayes, V. F. Nettles, and F. E. Kellogg, editors. Diseases and parasites of white-tailed deer. Tall Timbers Research Station, Tallahassee, Florida, USA.
- —, C. F. QUIST, R. R. LOPEZ, T. J. WILMERS, P. FRANK, W. ROBERTS, S. CHITWOOD, AND W. R. DAVIDSON. 2002. Morbidity and mortality factors in Key deer, *Odocoileus virginianus clavium*. Journal of Wildlife Diseases. In press. UPDATE?
- NIXON, C. M., L. P. HANSEN, P. A. BREWER, AND J. E. CHELSVIG. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monographs 118:1–77.
- J. B. SULLIVAN, R. G. KOERKENMEIER, AND P. C. MANKIN. 2001. Survival of white-tailed deer in intensively farmed areas of Illinois. Canadian Journal of Zoology 79:581–588.

- OTT, R. L. 1993. An introduction to statistical methods and data analysis. Fourth edition. Duxbury Press, Belmont, California, USA.
- OZOGA, J. J. 1969. Some longevity records for female white-tailed deer in northern Michigan. Journal of Wildlife Management 33:1027–1028.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.
- SAS INSTITUTE. 1999. SAS/STAT user's guide, version 8, fourth edition. SAS Institute, Cary, North Carolina, USA.
- SCHULTE, J. W., W. D. KLIMSTRA, AND W. G. DYER. 1976. Protozoan and helminth parasites of Key deer. Journal of Wildlife Management 40:579–581.
- SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.
- SILVY, N. J. 1975. Population density, movements, and habitat utilization of Key deer, *Odocoileus virginianus clavium*. Dissertation, Southern Illinois University, Carbondale, USA.
- —, J. W. HARDIN, AND W. D. KLIMSTRA. 1975. Use of a portable net to capture free-ranging deer. Wildlife Society Bulletin 3:27–29.
- U.S. FISH AND WILDLIFE SERVICE. 1999. South Florida multi-species recovery plan: Key deer recovery plan. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.
- WHITE, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 in L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, USA.
- , AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:S120–S138.
- WILSON, H. B. 2001. The evolution of dispersal from source to sink populations. Evolutionary Ecology Research 3:27–35.

Received 31 December 2001. Accepted 10 September 2002. Associate Editor: Krausman.