SOURCE–SINK DYNAMICS OF FLORIDA KEY DEER ON BIG PINE KEY, FLORIDA

PATRICIA M. HARVESON,[1] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA
ROEL R. LOPEZ, 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
PHILIP A. FRANK, U.S. Fish and Wildlife Service, National Key Deer Refuge, Big Pine Key, FL 33043, USA

Abstract: The endangered Florida Key deer (*Odocoileus virginianus clavium*) is endemic to the Florida Keys, Florida, USA, with Big Pine Key (BPK) supporting most (approx 60%) of the population. Habitat loss and fragmentation have altered the amount of available habitat, creating areas of varying suitability; north BPK (NBPK) is believed to contain more optimal habitat than south BPK (SBPK), which is more developed and fragmented. We evaluated the source–sink dynamics of Key deer using a sex- and stage-structured, stochastic matrix model. Model results indicated that the NBPK population of Key deer was increasing ($\lambda = 1.02$), whereas the SBPK population was decreasing ($\lambda = 0.87$). Without dispersal from the north, the SBPK population has a 97% probability of falling below 25 individuals (quasi-extinction threshold) in the next 20 years. The higher risk to Key deer in SBPK can be explained by relative habitat-quality differences between the 2 areas. House density, amount of roads, number of fences, and amount of development were all greater in SBPK. Collectively, study results indicate that SBPK can be described as an ecological sink with a nonviable population supplemented by deer dispersal from NBPK (source). Care should be taken to preserve the source population and its habitat. Thus, we propose limiting future development in NBPK (high-quality source habitat). The US 1 highway corridor project has the potential to decrease Key deer mortality due to vehicle collisions, and we recommend that future management goals continue to address mortality factors on SBPK (low-quality sink habitat).

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Key words: deer–vehicle collisions, Florida, Florida Key deer, *Odocoileus virginianus clavium*, source–sink, urban development.

Various theoretical models are used to aid conservationists in understanding population dynamics in heterogeneous and fragmented landscapes (Pulliam 1988, Akçakaya 2000, Morris 2003). Source–sink models can occur in systems where different demographic rates are attributed to different quality habitats (Holt 1985, Pulliam 1988, Dias 1996). Habitats of high quality (sources) yield a demographic surplus (births > deaths) whereas habitats of low quality (sinks) yield a demographic loss (deaths > births; Dias 1996). In a source–sink system, dispersal from a source population to a sink is necessary to prevent the sink population from going extinct. Although widely accepted, source–sink dynamics are difficult to quantify with most examples represented by plant, avian, or small mammal species (Watkinson and Sutherland 1995, Dias 1996, Diffendorfer 1998, Walters 2001). Some debate has occurred over the validity of source–sink claims in the literature in which methods have been questioned and other factors suggested such as pseudo-sinks, maladaptive responses, and various dispersal mechanisms (Watkinson and Sutherland 1995, Diffendorfer 1998, Remes 2000). Despite the problems in identifying source–sink dynamics, attempting to understand their function in fragmented landscapes is imperative to the overall recovery and management of endangered species.

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 17 islands in the lower Keys with most (approx 60%) residing on BPK (Fig. 1; Lopez 2001). 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). Urban development and its associated risks are considered the greatest threat to the Key deer population (Lopez et al. 2003). These risks include habitat loss and fragmentation, deer domestication, and deer–vehicle collisions (Hardin 1974, Folk 1991, Folk and Klimstra 1991*b*, Lopez et al. 2003). In a recent study, Lopez et al. (2003) reported that deer–vehicle collisions accounted for 50% of the total Key deer mortality on BPK. They reported that increases in urban development and habitat fragmentation contributed to higher, yet vari-

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

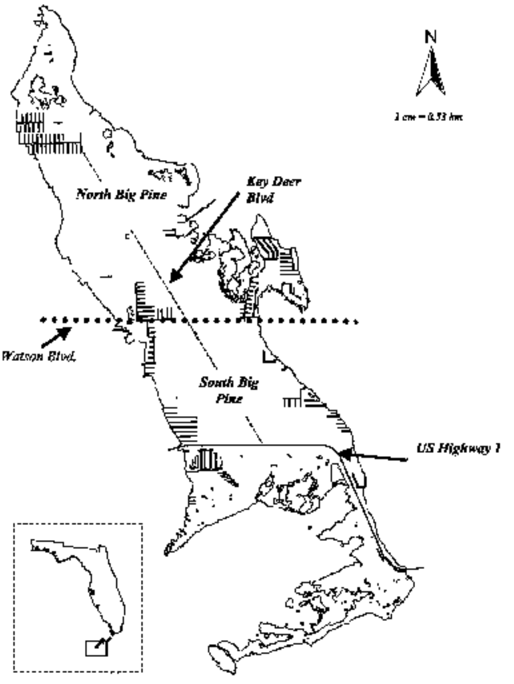

Fig. 1. Big Pine Key, Florida, USA, with Watson Boulevard dividing north Big Pine Key (NBPK) and south Big Pine Key (SBPK).

able, risks for Key deer with the greatest risk in SBPK—which has greater development—as compared to NBPK—which has more protected land (Fig. 1; Lopez et al. 2003). Furthermore, Lopez et al. (2003) also suggested that NBPK, with its high-quality habitat and high Key deer densities, was a potential source for SBPK, which was characterized as low-quality habitat with low Key deer densities.

We examined the effect of urbanization and fragmentation on the population dynamics of Key deer. While previous research has reported a difference in mortality rates by area (Lopez et al. 2003), we explore the impacts of these rates to the viability of the Key deer subpopulations (NBPK and SBPK) and the overall population on BPK. We also explored the differences between habitat on NBPK and SBPK to identify risk factors influencing Key deer mortality rates.

We tested our research hypothesis that NBPK was a source and SBPK was a sink by comparing (1) Key deer viability for both populations using a population model, (2) Key deer dispersal between NBPK and SBPK and its effects on population viability, and (3) habitat quality between NBPK and SBPK and its associated risks to Key deer (Boyce 1992, Burgman et al. 1993, Akçakaya 2000). We predicted that the greater developed and fragmented habitat on SBPK was a sink that would not be viable in the absence of dispersal from NBPK.

STUDY AREA

The Florida Keys are a chain of small islands located southwest of the southern tip of peninsular Florida in Monroe County, Florida, USA. Key deer range includes 17 islands in the lower Florida Keys comprising a total of 9,836 ha. Big Pine Key (Fig. 1) is the largest island within this range (2,531 ha). Watson Boulevard runs across the middle of BPK from east to west dividing the island in half (Fig. 1). The area north of Watson Boulevard is defined as NBPK (1,238 ha), and the area located to the south of Watson is defined as SBPK (1,293 ha). Island soil types vary from marl deposits to bare rock of the oolitic limestone formation (Dickson 1955). 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 1991).

METHODS

Model Overview

We modeled the NBPK and SBPK deer populations with a sex- and stage-structured, stochastic matrix model using RAMAS Metapop (Akçakaya and Root 2002). We classified Key deer into 3 age classes: fawn (<1 yr), yearling (1–2 yr), and adult (≥2 yr; Lopez et al. 2003). We were limited to 3 age classes due to the difficulty in aging deer beyond 3 years (Jacobson and Reiner 1989, Dimmick and Pelton 1994). We used density independence in the model to provide a conservative assessment in population growth when populations were below carrying capacity (Ginzburg et al. 1990). Model parameter estimates were taken from comprehensive Key deer studies from December 1968 to June 1972, and January 1998 to December 2000 on BPK (Hardin 1974, Silvy 1975, Lopez 2001). We used sensitivity and elasticity estimates to examine the effects of each parameter on model results (Caswell 2001).

Table 1. Annual model parameter estimates and standard errors for Florida Key deer by sex and age on north Big Pine Key (NBPK) and south Big Pine Key (SBPK), Florida, USA, 1968–1972 and 1998–2000.

			NBPK		SBPK	
Parameter	Sex	Age	Mean	SE	Mean	SE
Survival[a]	F	Fawn	0.470	0.061	0.470	0.061
		Yearling	0.848	0.033	0.710	0.082
		Adult	0.848	0.033	0.710	0.082
	M	Fawn	0.470	0.061	0.470	0.061
		Yearling	0.583	0.060	0.412	0.099
		Adult	0.583	0.060	0.412	0.099
Fecundity[b]	F_f	Yearling	0.365	0.087	0.306	0.096
		Adult	0.365	0.087	0.306	0.096
	F_m	Yearling	0.525	0.126	0.440	0.139
		Adult	0.525	0.126	0.440	0.139

[a] Survival estimates from Lopez (2001) and Lopez et al. (2003).

[b] Fecundity estimates represent recruitment by sex class (e.g., F_f = female recruitment in model, F_m = male recruitment in model; Hardin 1974, Lopez 2001).

Model Parameters

Survival.—Lopez et al. (2003) estimated Key deer survival and variance estimates from radiomarked animals by sex, age, and area using a known-fate model framework in program MARK (Table 1; White and Burnham 1999). For fawn survival, we used conservative estimates reported by Lopez (2001) adjusted to compensate for presumed overestimation reported by Lopez et al. (2003).

Fecundity.—We estimated fecundity based on Key deer necropsy data (Hardin 1974, Lopez 2001). Annual deer maternity was 1.05 fawns per breeding female (yearlings and adults; Hardin 1974). Key deer <1 year-of-age were not reproductively active (Hardin 1974, Folk and Klimstra 1991*a*). Furthermore, Hardin (1974) reported fetal sex ratios were male biased (59% males) in the Key deer population. From these data, fecundity estimates for yearlings ($F_y = RMS_y$) and adults ($F_a = RMS_a$) were determined as described by Akçakaya et al. (1999), where R is equal to the female fetal sex ratio, M is equal to maternity, and S_y and S_a are equal to yearling and adult survival, respectively (Table 1).

Initial Abundances.—We determined initial abundances used in model simulations from mark–resight estimates based on 247 road count surveys conducted from 1998 to 2001 on BPK (Lopez et al. 2004). A stable age distribution was assumed for both populations with 299 deer in NBPK (107 fawns, 49 yearlings, 143 adults) and 106 deer in SBPK (39 fawns, 20 yearlings, 47 adults; Akçakaya and Root 2002).

Dispersal.—We defined dispersal as the permanent movement of a deer from its birth place to the place where it reproduced (Caughley and Sinclair 1994). Key deer dispersal primarily occurs in the yearling age class (Silvy 1975, Lopez 2001). We assumed that dispersal for Key deer would occur following the transition of fawns into the next age class (as yearlings); therefore, using radiotelemetry data, we identified animals radiomarked as fawns or young yearlings with ≥20 locations from 1998 to 2000. We examined movement of yearlings from location as fawns to location as adults. Key deer dispersal was estimated from 36 radiomarked deer (19 M, 17 F) between NBPK and SBPK.

Environmental and Demographic Stochasticity

Environmental Stochasticity.—Environmental fluctuations in natural populations often result in unpredictable and variable vital rates (i.e., survival, fecundity; Akçakaya 2000). Environmental stochasticity can be incorporated into a model through matrix selection (randomly sampling from matrices based on vital rates in good and bad years) or by randomly sampling vital rates from normal distributions based on the mean and variance of each rate (Akçakaya 1991, 2000). We were unable to calculate vital rate matrices for good and bad years (due to lack of data), thus, survival and fecundity rates were varied based on a mean stage matrix and a standard deviation matrix for each area (Table 1).

Demographic Stochasticity.—Akçakaya (2000) recommended using demographic stochasticity in population models for rare species. We incorporated demographic stochasticity in model simulations by sampling the number of survivors and the number of individuals dispersing in a local population from a binomial distribution. Since the average number of offspring per female Key deer is >1 (1.05; Hardin 1974), we could not sample from a binomial distribution but instead assumed the data followed a Poisson distribution (Akçakaya 1991, 2000).

Model Use and Risk

The finite rate of increase (λ) is the proportional population growth under stable distribution, no density dependence, no stochasticity, and no dispersal (Akçakaya and Root 2002). A value >1 indicates that the population is growing, while a value <1 indicates that the population is declining. We used 3 measures to evaluate the viability

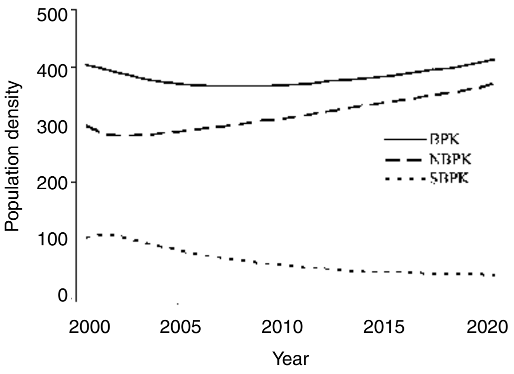

Fig. 2. Simulated population trajectory for Florida Key deer on Big Pine Key (BPK), north Big Pine Key (NBPK), and south Big Pine Key (SBPK), Florida, USA, 2000–2020.

of both Key deer populations: (1) the λ of each population, (2) the risk of each population going extinct in 20 years, and (3) the risk of each population falling below 25 individuals (quasi-extinction) in 20 years (Akçakaya 2000). We also examined the effects of dispersal on each population and its projected growth or decline. We simulated the population dynamics of Key deer for all of BPK, NBPK (without dispersal), and SBPK (without dispersal). For each local population, we ran 10,000 simulations over a 20-year period.

Habitat Quality

We evaluated 6 relative indicators of habitat quality for NBPK and SBPK: (1) number of houses, (2) amount of roads (km), (3) amount of fenced area (ha), (4) amount of developed land (ha), (5) amount of preferred habitat for Key deer (ha), and (6) amount of avoided habitat for Key deer (ha). Lopez (2001) reported that Key deer preferred upland areas (hammock, pineland, developed) and avoided lowlands (freshwater marsh, buttonwood, mangrove). Existing spatial data (MacAulay et al. 1994, Lopez 2001) were quantified in ArcView (Environmental Systems Research Institute 1999). We also summarized mortality data collected by National Key Deer Refuge (NKDR) biologists from direct sightings, citizen reports, or observation of turkey vultures (*Cathartes aura*) from 1990 to 2000 (Lopez et al. 2003).

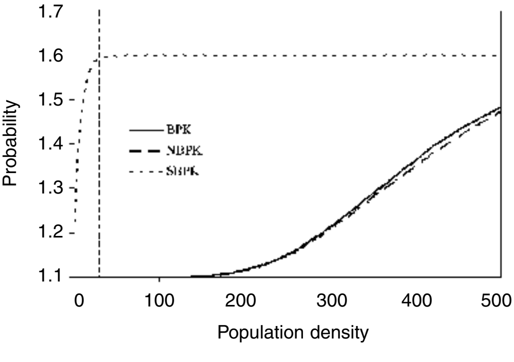

Fig. 3. Risk curve (probability of falling below 25 individuals in 20 yr, vertical dotted line) by population abundance for Key deer on Big Pine Key (BPK), north Big Pine Key (NBPK, no dispersal to south), and south Big Pine Key (SBPK, no dispersal to north), Florida, USA, 2000–2020.

RESULTS

As predicted, model results suggest that the Key deer population increased (λ = 1.02, variance = 0.015) on NBPK whereas the deer population on SBPK declined (λ = 0.87, variance = 0.017). Differences in λ are reflected in population trajectories for NBPK and SBPK (Fig. 2). The model predicted a low terminal extinction risk (<1%) for BPK and NBPK deer. However, when SBPK was modeled separately, terminal extinction risk increased to 24% (Fig. 3). We found similar trends in risk of quasi-extinction. Overall, our model predicted a low risk (<1%) of quasi-extinction for the BPK population.

Estimated Key deer dispersal differed between sex and area (NBPK: female = 0%, male = 33%; SBPK: female = 0%, male = 10%). In the absence of dispersal from NBPK to SBPK, risk of quasi-extinction for SBPK deer was 97% (Fig. 3). Model sensitivity and elasticity estimates indicated that adult female survival had the most influence on model matrices. Our results indicated that the models were least sensitive to male input parameters and were most sensitive to adult female survival. Sensitivity results for females were as follows: NBPK yearling fecundity = 0.07, adult fecundity = 0.33, fawn survival = 0.31, yearling survival = 0.14, adult survival = 0.72; SBPK yearling fecundity = 0.09, adult fecundity = 0.37, fawn survival = 0.29, yearling survival = 0.16, adult survival = 0.68.

The higher risk of extinction for SBPK deer in our model can be explained by relative habitat quality differences between the 2 areas. For most variables, SBPK contained poorer habitat quality and greater risk factors than NBPK (Table 2). Preferred and avoided habitats occurred in almost equal amounts on NBPK and SBPK. However, a greater proportion of preferred habitat on SBPK was developed (31%) as compared to NBPK (16%). Of 836 mortalities recorded on BPK between 1990 and 2000, more occurred on SBPK (576, 69%) than on NBPK (260, 31%).

DISCUSSION

Source–sink Dynamics

Three elements are necessary in identifying source–sink systems: (1) heterogeneous habitat and habitat-specific demographic rates; (2) active or passive dispersal; and (3) λ in source habitats should be >1, whereas λ in sink habitats should be <1 (Holt 1985, Pulliam 1988, Dias 1996, Diffendorfer 1998). Our model results support our hypothesis that the Key deer population on BPK is a source–sink system due to anthropogenic factors.

First, Key deer occupy a limited range within a highly fragmented landscape. Our analyses indicate that habitat on BPK is divided between areas of high quality (NBPK) and low quality (SBPK; Table 2). Urban development, including houses, fences, and roads (which present the greatest mortality risk to Key deer [Lopez et al. 2003]), was higher for SBPK. Furthermore, most (69%) Key deer mortalities occurred on SBPK despite higher deer densities reported by Lopez (2001) on NBPK. We attribute the greater risk on SBPK to low habitat quality, greater amount of urban development, and greater amount of roads, which pose an especially high mortality risk to Key deer because of the high traffic volume on US 1 highway (Lopez et al. 2003). As a result, we propose that the differing demographic rates (i.e., survival and fecundity) we observed in our study are attributed to differences in habitat quality between SBPK and NBPK.

Second, Key deer are active dispersers selecting habitat based on a variety of density-dependent factors such as availability, competition, and reproductive opportunities (Hardin 1974, Lopez 2001). Active dispersers select habitats based on differences in habitat quality, and individuals may choose to leave a source habitat whenever their expected reproductive success is higher in the sink (Pulliam 1988, Dias 1996, Diffendorfer 1998). Key deer on BPK dispersed from areas of high fitness and low reproductive opportunity (NBPK) to areas of low fitness and high reproductive opportunity (SBPK). We came to this conclusion because (1) dispersal was higher from NBPK than SBPK, and (2) only male deer dispersed. Female deer did not lack reproductive opportunities on NBPK and thus remained in the source where survival was greatest. High deer densities on NBPK reduced opportunities for yearling males to reproduce, and we hypothesize that they dispersed to SBPK for greater reproductive opportunities (Hardin 1974, Silvy 1975, Lopez 2001). While the conservative nature of our dispersal estimates were chosen to quantify overall immigration and emigration of subpopulations, we should note that the lack of female dispersers could be a result of the small sample sizes used in estimating dispersal. Therefore, dispersal may be underestimated, and other explanations such as maladaptive response or despotism might be the actual or contributing underlying factors to Key deer dispersal (Remes 2000, Conradt and Roper 2003).

Table 2. Anthropogenic factors, habitat availability, and associated risks to Florida Key deer on north Big Pine Key (NBPK) and south Big Pine Key (SBPK), Florida, USA, 2000.

	NBPK		SBPK		Area of
Risk	No.	%	No.	%	greater risk
Houses	1,082	40.4	1,597	59.6	SBPK
Roads (km)	51	40.2	75	59.8	SBPK
Fenced area (ha)	31	34.7	58	65.3	SBPK
Developed land (ha)	205	33.6	405	66.4	SBPK
Preferred habitat[a] (ha)	703	49.5	717	50.5	Same
Avoided habitat[b] (ha)	535	48.1	576	51.9	Same

[a] Preferred habitat includes pineland, hammock, and developed areas (Lopez 2001).

[b] Avoided habitat includes freshwater marsh, buttonwood, and mangrove areas (Lopez 2001).

Third, habitat-specific demographic rates and active dispersal from source to sink habitat collectively result in varying fitness between local populations (Holt 1985, Pulliam 1988, Dias 1996, Diffendorfer 1998). Assuming λ as a measure of local population fitness (Caughley 1977), model results indicated rate of increase for NBPK is >1 ($\lambda = 1.02$) and for SBPK is <1 ($\lambda = 0.87$). This supports our premise that NBPK is a source whereas SBPK is a sink. Sink habitats, however, can be categorized as absolute or pseudo-sinks (Watkinson and Sutherland 1995). In an absolute sink, the removal of immigration would result in extinction, and in a pseudo-sink, the removal of immigration would result only in population decrease and not extinction. Our Key deer model for SBPK indicates that without dispersal from NBPK, the population has a 25% probability of extinction in 20 years (Fig. 3). These results suggest that the SBPK population is an absolute sink supplemented by dispersal from NBPK. In contrast, NBPK is characterized by high-quality habitat and higher survival and fecundity rates. Our model indicates that the Key deer population on NBPK is increasing despite emigration and can be considered a source.

MANAGEMENT IMPLICATIONS

Collectively, our study results indicate that SBPK can be described as an ecological sink supplemented by deer dispersal from NBPK. Dias

(1996) noted that in a source–sink system, preserving only sink habitats likely will lead to population extinction. Care should be taken, especially when dealing with endangered species such as the Key deer, to preserve the source population and its habitat. Thus, we propose limiting future development in NBPK (high-quality source habitat). Future management goals should continue to address mortality factors on SBPK while still recognizing and preserving the important source population in NBPK. The US 1 highway corridor project, which includes the construction of fences and underpasses, has the potential to reduce Key deer mortality in SBPK due to vehicle collisions by 10% annually. This increase in survival could possibly stabilize ($\lambda = 1.0$) the SBPK deer population so that it would no longer be a sink.

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