ANNUAL SURVIVAL OF SNAIL KITES IN FLORIDA: RADIO TELEMETRY VERSUS CAPTURE-RESIGHTING DATA

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ABSTRACT.—We estimated annual survival of Snail Kites (*Rostrhamus sociabilis*) in Florida using the Kaplan-Meier estimator with data from 271 radio-tagged birds over a three-year period and capture-recapture (resighting) models with data from 1,319 banded birds over a six-year period. We tested the hypothesis that survival differed among three age classes using both data sources. We tested additional hypotheses about spatial and temporal variation using a combination of data from radio telemetry and single- and multistrata capture-recapture models. Results from these data sets were similar in their indications of the sources of variation in survival, but they differed in some parameter estimates. Both data sources indicated that survival was higher for adults than for juveniles, but they did not support delineation of a subadult age class. Our data also indicated that survival differed among years and regions for juveniles but not for adults. Estimates of juvenile survival using radio telemetry data were higher than estimates using capture-recapture models for two of three years (1992 and 1993). Ancillary evidence based on censored birds indicated that some mortality of radio-tagged juveniles went undetected during those years, resulting in biased estimates. Thus, we have greater confidence in our estimates of juvenile survival using capture-recapture models. Precision of estimates reflected the number of parameters estimated and was surprisingly similar between radio telemetry and single-stratum capture-recapture models, given the substantial differences in sample sizes. Not having to estimate resighting probability likely offsets, to some degree, the smaller sample sizes from our radio telemetry data. Precision of capture-recapture models was lower using multistrata models where region-specific parameters were estimated than using single-stratum models, where spatial variation in parameters was not taken into account. *Received 19 December 1997, accepted 21 September 1998.*

FOR MANY LONG-LIVED avian species, population persistence is more sensitive to annual survival than to fecundity (Mertz 1971, Nichols et al. 1980, Beisssinger 1995). Despite this, reliable estimates of survival are unavailable for many species, although extensive effort often is expended in estimating reproductive parameters. Investigators also must choose among available techniques for estimating demographic parameters. This selection often is based on logistic constraints, or unfamiliarity with potential estimators, rather than how procedure selection might influence resulting parameter estimates. Given current threats to

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many populations, reliable demographic data are essential for effective conservation arguments in the context of alternative management scenarios.

The Snail Kite (*Rostrhamus sociabilis*) is an endangered raptor whose range in the United States is limited to central and southern Florida (Sykes et al. 1995). Florida's wetlands have been severely altered during the past century by drainage, impoundment, changes in water flow regimes, increased nutrient loading, and invasion by exotic plants and animals (Walters et al. 1992, Davis and Ogden 1994). These disturbances have resulted in one of the largest ecosystem restoration projects ever undertaken (Davis and Ogden 1994). The Snail Kite, like many other species, is potentially influenced by these and other changes (Bennetts et al. 1994).

Consequently, reliable estimates of demographic parameters are essential to understanding population responses to environmental change (Nichols et al. 1980).

Although several previous reports exist on annual survival of Snail Kites in Florida, they were not based on reliable statistical estimators. Snyder et al. (1989) estimated minimum annual survival of Snail Kites by using the number of birds banded from 1968 to 1978 and observed alive in 1979. They did not use available capture-recapture estimators for these data because of limited efforts to resight banded birds (Snyder et al. 1989). Hence, their approach provides a crude indication of minimum annual survival but does not provide adequate estimates for demographic assessments. Several other authors have reported estimates of Snail Kite survival based on differences between annual surveys conducted in consecutive years (e.g. Sykes 1979; Beissinger 1988, 1995). This approach fails to account for the high potential of confounding changes in detection probability with changes in population size (Bennetts and Kitchens 1997a, Bennetts et al. 1999). Problems arising from using count data without accounting for detectability have been well recognized (Burnham 1981, Nichols 1992, Johnson 1995, Link and Sauer 1997). Bennetts et al. (1999) found that the number of Snail Kites counted during annual surveys was strongly influenced by differences in observers, effort, sites, and water levels, each of which likely influences detection probability. None of these influences has been taken into account for any survival estimates using these data. Thus, we believe that using the annual survey to estimate survival, without accounting for detection probability, fails to provide reliable estimates.

Here, we estimate survival using reliable statistical estimators based on data obtained from both radio telemetry and capture-recapture (resighting). The use of two field techniques facilitated the multiple objectives of a larger study focused on survival and movements (Bennetts and Kitchens 1997a) and also provided the opportunity to compare survival estimates derived from these independent data sources. We also were able to test hypotheses about factors likely to influence survival. Survival of young birds tends to be lower than that of adults in many species (e.g. Ricklefs 1973,

Loery et al. 1987). However, Ricklefs (1973) pointed out that "Just how much experience the young need to attain adult behavior and physiological capabilities (and thus adult survival rates) is open to question." Beissinger (1995) suggested that Snail Kites have three age classes with respect to survival (juveniles [0 to 1 year], subadults [1 to 2], and adults [>2]); nevertheless, the survival estimates that he used for his demographic models were the same for subadults and adults. We predicted that survival would be lower for juvenile Snail Kites than for adults or subadults. We further hypothesized that if survival of subadults differed from that of adults and juveniles, it would be intermediate between the two.

In addition to age effects, substantial variability exists in habitat quality over space and time, which could result in differences in survival (Bennetts and Kitchens 1997a, b). However, because Snail Kites are highly mobile, they have the potential to escape to other areas when local conditions are poor. Adults, having had more experience at alternative sites and the corresponding selective pressures of environmental variability, may be less susceptible to temporal variation than are younger birds. Consequently, we hypothesized that if temporal variation in survival exists, it would be higher for younger birds than for adults. Similar to our reasoning concerning temporal variation, we predicted that if regional variation in survival exists, it would be higher for younger birds than for adults.

METHODS

Study area.—Within the United States, Snail Kites occur only in Florida (Sykes 1984). They comprise a single population that shifts in distribution throughout the state, rather than separate subpopulations within the state (Bennetts and Kitchens 1997a, b). Data from studies of movements (Bennetts and Kitchens 1997a, unpubl. data) and genetics (Rodgers and Stangel 1996) show considerable interchange of kites among wetlands in Florida. Consequently, the spatial extent of this study included the entire range of Snail Kites within the United States, which consists of a network of wetlands throughout central and southern Florida (Bennetts and Kitchens 1997a, b).

Estimation of survival: Radio telemetry.—Adults were captured with a net gun (Mechlin and Shaiffer 1979), which uses a blank rifle cartridge to propel a 3-m triangular nylon net. Juveniles were captured

just prior to fledging, at approximately 30 to 35 days old, without a net gun. Radio transmitters (15 g) were attached to birds with backpack harnesses. Four separate harness straps were attached with a cotton "weak link" intended to allow the harness to fall off after transmitter batteries had failed (Bennetts and Kitchens 1997a). Our goal was to capture and radio tag 100 Snail Kites annually, of which 60% were adults and 40% juveniles, for three consecutive years from April 1992 through April 1995. Our targeted ratio of adults to juveniles was intended to emphasize adult survival because demography of Snail Kites probably is more sensitive to adult rather than juvenile survival (Nichols et al. 1980, Beissinger 1995). To maintain independence of our sample, only one juvenile per nest was equipped with a radio transmitter. We targeted a 50:50 sex ratio of adults to keep our sample balanced. The proportion of samples from each area was based on the annual survey to approximate the statewide distribution (Bennetts and Kitchens 1997a). Our targeted annual sample size of 100 was based on having sufficient statistical power (e.g. >0.8) to distinguish differences (e.g. $\Delta\phi$ ca. 0.1 to 0.2) among groups (e.g. age or sex) or time periods from a hypothesized survival estimate ($\hat{\phi}_H$) of 0.90 (Bennetts and Kitchens 1997a). Radio-tagged birds were located at approximately 14-day intervals from aircraft or ground searches to determine their locations and whether they were alive. All radios were equipped with mortality sensors that changed pulse rates if the transmitter had not moved for 6 to 8 h. Birds with a transmitter emitting a mortality signal were then located on the ground to verify their fate.

We estimated survival (ϕ) of radio-tagged kites using a staggered entry design (Pollock et al. 1989) with the Kaplan-Meier product-limit estimator (Kaplan and Meier 1958). We used an arbitrary starting date of 15 April 1992 for annual survival estimates. By this time during our first year, we had a sample ($n = 16$) sufficient to allow reasonable estimates of survival. Subsequent evaluation of annual survival was based on study years (SY) from 15 April to 14 April of consecutive years (Bennetts and Kitchens 1997a). The Kaplan-Meier estimator generates survivorship curves over the entire period of study. However, for the purposes of comparison among data sources, we have considered survival only in an annual context. Detailed information regarding seasonal patterns of survival are reported elsewhere (Bennetts and Kitchens 1999).

Estimation of survival: Banding data.—Our sample of banded birds for survival analyses was obtained through a cooperative banding effort with the Florida Game and Fresh Water Fish Commission. Our sample also was supplemented by resightings of birds banded during two previous studies by REB (unpubl. data) and J. A. Rodgers (unpubl. data) that were observed during this study. A previously band-

ed bird observed alive during our study at time *t* was treated as a newly marked individual.

We estimated annual survival from banding data using the capture-recapture (resighting) models originally developed by Cormack (1964), Jolly (1965), and Seber (1965). The basic Cormack-Jolly-Seber (CJS) approach has undergone extensive advancement in recent years to become a flexible and unified framework capable of handling simple to complex models of survival (Lebreton et al. 1992, Nichols 1992). Recent approaches enable evaluation of effects attributable to individual characteristics (e.g. age and sex) and environmental variables (e.g. weather). Additional models have the capability to incorporate transition probabilities and multiple strata (e.g. exchanges of individuals among geographically stratified populations; Brownie et al. 1993, Nichols et al. 1993). All analyses of capture-recapture data were conducted with program SURVIV (White 1983, White and Garrott 1990) or MSSURVIV (Hines 1994). Model notation follows Lebreton et al. (1992) wherein each parameter included in the model is listed with corresponding effects on that parameter indicated by subscripts. For example, model ($\phi_{t \cdot a}$, p_t) represents a model where survival (ϕ) is affected by both time (t) and age (a), and resighting probability (p) is affected only by time.

We conducted capture-resighting during six sampling occasions from 1992 to 1997. Our capture and resighting occasions corresponded with the peak fledging time of Snail Kites, March to June (Bennetts and Kitchens 1997a). Thus, survival estimates can be roughly interpreted as survival from one breeding season to the next, regardless of whether a given animal was breeding. Snail Kites have a relatively long breeding season and are not synchronous in their breeding attempts (Snyder et al. 1989, Bennetts and Kitchens 1997a). Consequently, the time span over which fledging, and therefore banding, occurred was relatively long. We tried to minimize the time span of our sampling by limiting our capture and resighting period to the peak four months of fledging.

Influences on survival.—We initially considered kites as adults after their first year postfledging. Snail Kites are capable of breeding at nine months of age (Snyder et al. 1989). For our capture-recapture models, resighting probability at the first resighting period after initial capture (time 2) were considered to be equal for juveniles and adults. Bennetts and Kitchens (1997a) tested this assumption by comparing models in which juveniles and adults had different resighting periods at time 2 with models in which resighting was equal for the two ages. They concluded that separate estimates for resighting probability were not warranted. We then tested the hypothesis that adult and subadult survival does not differ by reparameterizing a CJS model such that birds banded as juveniles were considered to have three age classes with respect to survival rates (i.e.
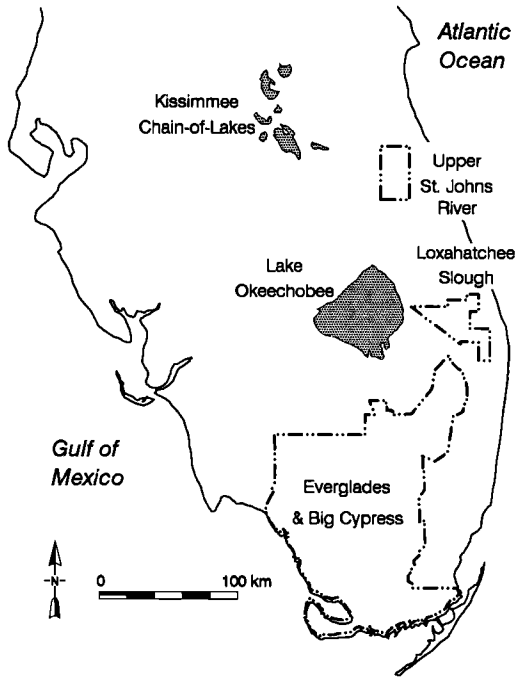
FIG. 1. Central and southern Florida showing major wetland regions used by Snail Kites. Scattered wetlands not within these regions were lumped into one peripheral region.

juvenile survival during their first year, subadult survival their second year, and adult survival after year two).

We tested temporal effects using a sequence of models analogous to models A, B, C, and D described by Jolly (1982) and Pollock et al. (1990). Model (ϕ_t, p_t), which is Jolly's model A, treats both survival (ϕ) and resighting probabilities (p) as variable over time (i.e. separate estimates of each parameter were derived for each year). Model (ϕ, p_t), or Jolly's model B, treats p, but not ϕ, as variable over time. Model (ϕ_t, p), Jolly's model C, treats ϕ, but not p, as variable over time. Model (ϕ, p), Jolly's model D, treats both ϕ and p as constant over time. We then incorporated age effects into this sequence of models (Pollock et al. 1990).

Based primarily on watersheds, climatic factors, physiography, and management regimes, we assigned each location to one of six regions to assess regional differences in survival (Fig. 1). We tested for regional differences in survival using radio telemetry data two ways. First, we tested the hypothesis that differences in juvenile survival were attributable to natal origin. For this analysis, a bird was assigned to its natal region, regardless of whether it moved after its initial capture. In most cases, we did not know the natal origin of adults or their history of locations

prior to capture. Consequently, we limited this approach to juveniles.

The second approach we used for testing regional differences in survival using radio telemetry data was based on time at risk in each region, rather than focusing only on natal region. Thus, we tested the hypothesis that survival was affected by current location (e.g. by local factors such as predation risk). For this analysis, a bird that moved from a given region to another was removed (i.e. censored) from the number of animals at risk for the region from which it moved and added to the number of animals at risk in the region to which it moved. All movements and corresponding changes in the number of animals at risk were assigned at the midpoint of the time interval between locations. All deaths were assigned to the region where the dead bird was found.

To test for regional effects of survival and resighting probabilities from capture-recapture data, we generated a suite of multistrata models analogous to the models described above, except that they enabled stratum-specific parameter estimation (Brownie et al. 1993, Nichols et al. 1993). No captures occurred in the peripheral region, and we had too few observations in the Loxahatchee Slough to include it in the analysis. Consequently, this analysis was limited to four of six regions. As above, we generated models with and without age dependency, enabling us to test hypotheses that ϕ and/or p were affected by age, time, and region. Regional effects on ϕ were tested only in relation to the region of last capture or resighting because capture-recapture data do not reveal where a bird has been during the interval between sighting periods. Estimates for the transition probabilities among strata (ψ; i.e. the probability that an animal in stratum r at time t was alive in stratum s at time $t +1$, given that it was alive at $t + 1$) were also generated from these models; however, our primary interest was a site-specific estimate of ϕ and p. Radio telemetry provides a more comprehensive assessment of movement probabilities, and these data are presented elsewhere (Bennetts and Kitchens 1997a).

Hypothesis testing and model selection.—All comparisons among survivorship curves generated by the Kaplan-Meier estimator for radio telemetry data were made using log-rank tests (Savage 1956, Cox and Oakes 1984). All comparisons were made using SAS (SAS 1988, White and Garrott 1990). For banding data we used a combination of likelihood-ratio tests (LRTs), Akaike's Information Criterion (AIC; Akaike 1973, Shibata 1989), and goodness-of-fit tests to determine the most parsimonious model based on all combinations of effects. Our testing procedures and philosophy have been described in detail elsewhere (e.g. Burnham and Anderson 1992, Lebreton et al. 1992, Brownie et al. 1993, Nichols et al. 1993). In contrast to LRTs, which were used for pairwise comparisons of nested models to test for specific ef-

TABLE 1. Capture-resighting summary of adult and juvenile Snail Kites in Florida from 1992 to 1997.

| | Year of next resighting | | | | | | | | | | | | |
| | Birds banded as adults | | | | | | Birds banded as juveniles[a] | | | | | | |
Year of last capture or resighting	92	93	94	95	96	97	Never re-sight-ed	92	93	94	95	96	97	Never re-sight-ed
1992	—	4	10	5	1	6	23	—	11	14	8	5	7	104
1993	—	—	14	4	2	10	26	—	—	10	9	17	14	206
1994	—	—	—	13	11	8	45	—	—	—	21	12	21	88
1995	—	—	—	—	5	5	14	—	—	—	—	36	59	148
1996	—	—	—	—	—	6	13	—	—	—	—	—	46	158
Total no.	0	4	24	22	19	27	—	0	11	24	38	70	147	—
Total new	49	52	53	2	0	8	—	149	245	118	205	134	304	—
Total no.[b]	49	56	77	24	19	35	—	149	256	142	243	204	451	—

[a] Considered to be adults at time 2 of each cohort.

[b] Includes total resighted and new captures; however analysis is parameterized such that juveniles resighted as adults also contribute to estimation of adult survival.

fects, AIC was used more as an optimization tool for any number of models, nested or not (Lebreton et al. 1992, Spendelow et al. 1995). Models with AIC scores differing by <1 to 2 were not considered statistically different (Sakamoto et al. 1986). All test statistics were generated using program SURVIV (White 1983, White and Garrott 1990) or MSSURVIV (Hines 1994).

RESULTS

We attached 282 radio transmitters on 271 Snail Kites; 11 birds were recaptured in a subsequent year and their radios replaced. We attached 82 radios during SY 1992 and 100 each

TABLE 2. Description of single-stratum Cormack-Jolly-Seber (CJS) models and their corresponding Akaike's Information Criterion (AIC) scores. Parameter structure indicates whether survival (ϕ) and/or resighting probability (p) was dependent on time (t) and/or age (a).

Model	No. of parameters	AIC
ϕ_t, p_t	9[a]	240.0
ϕ, p_t	6	256.4
ϕ_t, p	6	278.3
ϕ, p	2	331.7
ϕ_{t*a}, p_t	14[a]	176.6
ϕ_{t*a}, p	11	224.4
ϕ_a, p_t	7	196.2
ϕ_a, p	3	265.2
$\phi_{t(juv)*a}, p^b$	7	224.4
$\phi_{t(juv)*a}, p_t^b$	11	173.2

[a] Because ϕ and p were both variable over time, we were only able to estimate a product of the two for the last time period (Lebreton et al. 1992).

[b] Survival was time dependent for juveniles, but not adults.

during SYs 1993 and 1994. Of the 282 radios, 165 (59%) were placed on adults (82 males and 83 females) and 117 (41%) on juveniles. The total number of banded birds used in CJS models was 1,319; 164 were initially banded as adults and 1,155 as juveniles. An additional 290 resightings of birds initially banded as juveniles supplemented our sample of adults (Table 1).

Age effects.—Our results both from radio telemetry and capture-recapture data indicated that survival differed between adult and juveniles. Based on log-rank statistics using radio telemetry, survival differed between these age classes for SYs 1992 ($\chi^2 = 4.61$, df = 1, $P = 0.032$) and 1994 ($\chi^2 = 29.52$, df = 1, $P < 0.001$) but not 1993 ($\chi^2 = 0.027$, df = 1, $P = 0.869$). In both years where the estimates differed, adult survival was higher than juvenile survival. All capture-recapture models that included age effects on survival had lower AIC scores than corresponding models without age effects (Table 2), and LRTs between models with and without age effects on survival strongly rejected the more reduced models, further supporting the effect of age (Table 3).

We used two variations of our most parsimonious model ($\phi_{t(juv)*a}, p_t$) to test the hypothesis that survival of subadult (1 to 2 years) Snail Kites differed from that of adults. Both of these models had separate parameter estimates for subadult survival; however, in one model subadult survival was held constant among years, and in the other it was allowed to vary among years. LRTs between model ($\phi_{t(juv)*a}, p_t$) and each

TABLE 3. Likelihood-ratio tests between Cormack-Jolly-Seber (CJS) models used to test whether survival (ϕ) or resighting (p) probabilities differed among age classes or years (time).

General model	Reduced model	Parameter tested	Effect tested	χ^2	df	P
ϕ_a, p	ϕ, p	ϕ	Age	68.496	1	<0.001
ϕ_a, p_t	ϕ, p_t	ϕ	Age	62.197	1	<0.001
$\phi_{t \cdot a}, p$	ϕ_t, p	ϕ	Age	63.940	5	<0.001
ϕ_t, p_t	ϕ, p_t	ϕ	Time	21.393	3	<0.001
ϕ_t, p	ϕ, p	ϕ	Time	61.335	4	<0.001
$\phi_{t \cdot a}, p$	ϕ_a, p	ϕ	Time	56.779	8	<0.001
ϕ, p_t	ϕ, p	p	Time	83.300	4	<0.001
ϕ_t, p_t	ϕ_t, p	p	Time	43.358	3	<0.001
ϕ_a, p_t	ϕ_a, p	p	Time	77.001	4	<0.001
$\phi_{t(juv) \cdot a}, p_t$	$\phi_{t(juv) \cdot a}, p$	p	Time	59.180	4	<0.001
$\phi_{t \cdot a}, p$	$\phi_{t(juv) \cdot a}, p$	ϕ	Time[a]	7.997	4	0.092
$\phi_{t \cdot a}, p_t$	$\phi_{t(juv) \cdot a}, p_t$	ϕ	Time[a]	2.621	3	0.454
$\phi_{t(juv) \cdot a}, p$	ϕ_a, p	ϕ	Time[b]	48.782	4	<0.001
$\phi_{t(juv) \cdot a}, p_t$	ϕ_a, p_t	ϕ	Time[b]	30.961	4	<0.001

[a] Tests for time variation of survival of adults only.

[b] Tests for time variation of survival of juveniles only.

of these more general models failed to reject the more reduced model ($\chi^2 = 2.37$, df $= 1$, $P = 0.124$ and $\chi^2 = 2.38$, df $= 3$, $P = 0.498$ for each LRT, respectively), indicating that separate parameter estimates for subadult survival were not warranted for these data.

Time effects.—Both data sources indicated that survival differed among years for juveniles but not for adults. Estimates of survivorship functions for adults using radio telemetry data did not differ between SYs 1992 and 1993 ($\chi^2 = 2.84$, df $= 1$, $P = 0.092$), 1992 and 1994 ($\chi^2 = 1.76$, df $= 1$, $P = 0.184$), or 1993 and 1994 ($\chi^2 = 0.48$, df $= 1$, $P = 0.486$). In contrast, our estimates of juvenile survivorship differed between SYs 1992 and 1994 ($\chi^2 = 6.16$, df $= 1$, $P = 0.013$) and 1993 and 1994 ($\chi^2 = 12.41$, df $= 1$, $P < 0.001$), but not between 1992 and 1993 ($\chi^2 = 1.43$, df $= 1$, $P = 0.231$). We also found strong evidence, based on capture-recapture data, for the inclusion of time (year) effects for juvenile survival but not for adult survival. The AIC scores of models with time effects were lower than corresponding models without time effects. LRTs between models with and without time effects also supported this conclusion, except when time effects were limited to adult survival. Based on our results from radio telemetry data, we generated two models in which ϕ differed between adults and juveniles and was variable among years for juveniles, but not adults. For model ($\phi_{t(juv) \cdot a}, p$), p was constant among years, and for model ($\phi_{t(juv) \cdot a}, p_t$), p differed among years. Model ($\phi_{t(juv) \cdot a}, p_t$) had the lowest AIC score of any model, goodness-of-fit was reasonable ($G = 30.41$, df $= 19$, $P = 0.05$), and the LRT between models ($\phi_{t(juv) \cdot a}, p_t$) and ($\phi_{t \cdot a}, p_t$) failed to reject the more reduced model ($\phi_{t(juv) \cdot a}, p_t$). These results indicated that survival differed among years for juveniles but not adults, and that resighting probabilities also differed among years.

Regional effects.—We found little indication of regional differences in adult survival using data from radio telemetry or capture-recapture. Of 15 pairwise comparisons (using radio telemetry data) of adult survival between regions during each year (for which we had sufficient data), only one differed at $\alpha = 0.05$. Adult survival differed between the Everglades and Okeechobee regions during SY 1994 ($\chi^2 = 4.06$, df $= 1$, $P = 0.044$). If the α level was adjusted for inflation due to simultaneous comparisons (e.g. using a Bonferonni correction), none of the 15 comparisons was significant at $\alpha = 0.05$. For juveniles, none of eight survivorship functions (for which we had sufficient data), based on actual time in each region, was significant at $\alpha = 0.05$. For survivorship functions based on natal region, 1 of 10 comparisons was significant. The Okeechobee and Everglades regions differed during SY 1992 ($\chi^2 = 4.58$, df $= 1$, $P = 0.032$); however, this result also would not be significant at $\alpha = 0.05$ if adjusted for simultaneous comparisons.

We had some data limitations using multi-

TABLE 4. Description of multi-strata models and their corresponding Akaike's Information Criterion (AIC) scores. Parameter structure indicates whether survival (ϕ), resighting probability (p), and/or transition (movement) probability (ψ) was dependent on age (a), time (t), and/or region (r).

Model	No. of parameters	AIC
ϕ_{a*t*r} p_{t*r} ψ_{a*t*r}	176	989.2
ϕ_{t*r} p_{t*r} ψ_{t*r}	96	982.1
ϕ_r p_{t*r} ψ_r	36	940.5
ψ_{a*r} p_{t*r} ψ_{a*r}	52	900.5
ϕ_r p_r ψ_r	20	1,032.1
ψ_{a*r} p_r ψ_{a*r}	36	982.6
ϕ_{a*t*r} p_{t*r} ψ_{a*r}	80	881.3
ϕ_{a*r} p_t ψ_{a*r}	36	934.7
ϕ_{a*r} p_{t*r} ψ_{a*r}	46	896.9
$\phi_{a*t(juv)}$ p_{t*r} ψ_{a*r}	50	881.4
$\phi_{a*t(juv)*r}$ p_t ψ_{a*r}	52	894.6
$\phi_{a*t(juv)*r}$ p_{t*r} ψ_r	68	867.3
$\phi_{a*t(juv)*r(juv)}$ p_{t*r} ψ_{a*r}	65	862.7

TABLE 5. Annual estimates and standard errors for adult and juvenile survival ($\hat{\phi}$) of Snail Kites for study years (SYs) 1992, 1993, and 1994 using data from radio telemetry.

	Adults		Juveniles	
Year	$\hat{\phi}$	$\hat{SE}$ ($\hat{\phi}$)	$\hat{\phi}$	$\hat{SE}$ ($\hat{\phi}$)
1992	0.962	0.038	0.825	0.080
1993	0.858	0.063	0.867	0.088
1994	0.883	0.042	0.439	0.090
Overall[a]	0.894	0.029	0.671	0.059

[a] Estimated using a pooled sample of all years. The arithmetic mean gives equal weight to each annual estimate, whereas the pooled sample essentially weights by sample size.

strata capture-recapture models; two regions (Loxahatchee Slough and the peripheral region) had insufficient data for estimation. However, data from the remaining four regions supported the conclusion that survival did not differ among regions for adults, but did differ among regions for juveniles. A model ($\phi_{a*t(juv)*r(juv)}$ p_{t*r} ψ_{a*r}) in which survival (1) differed among age classes; (2) differed among years for juveniles, but not adults; and (3) differed among regions for juveniles, but not adults, had the lowest AIC score (Table 4). An LRT between this model and an analogous model (ϕ_{a*t*r} p_{t*r} ψ_{a*r}) in which survival differed among years and regions for both age classes was not significant ($\chi^2 = 11.42$, df = 15, $P = 0.722$), further supporting that these effects were warranted for juveniles but not adults. Similar to the single-stratum models, model ($\phi_{a*t(juv)*r(juv)}$ p_{t*r} ψ_{a*r}) indicated that resighting probabilities differed among years, but also indicated differences among regions.

Parameter estimates.—Overall estimates of adult survival were similar using the Kaplan-Meier estimator with radio telemetry data (Table 5) and the CJS models with capture-recapture data (Table 6). In contrast, estimates of juvenile survival tended to differ both in the overall estimates and even in the rank order of estimates among years. Overall estimates using multistrata models tended to be lower for both age classes than estimates derived from either Kaplan-Meier or CJS estimators (Table 7).

Estimates of resighting probabilities also differed substantially between single-stratum and multistrata models.

The precision of individual parameter estimates ranged from 3 to 92% coefficient of variation (CV) depending on the number of parameters being estimated and the distribution of our sample for a given estimate. CVs for our estimates of adult survival were 3.2% using the Kaplan-Meier estimator, 3.9% from our final single-stratum model ($\phi_{t(juv)*a}$ p_t), and 4.1% using our final multistrata model ($\phi_{a*t(juv)*r(juv)}$ p_{t*r} ψ_{a*r}). Average CVs for juvenile survival were 13.4% using the Kaplan-Meier estimator, 16.3% from our final single-stratum model ($\phi_{t(juv)*a}$ p_t), and 36.7% using our final multistrata model ($\phi_{a*t(juv)*r(juv)}$ p_{t*r} ψ_{a*r}).

Censoring of radio-tagged birds.—Censoring is the removal of radio-tagged animals from a sample when the transmitter signal can no longer be detected (White and Garrott 1990). An assumption for an unbiased estimate using the Kaplan-Meier estimator is that censoring is random with respect to fate (Pollock et al. 1989); i.e. the probability that a bird is censored is not related to its fate. In the case of simple radio failure this assumption probably is valid; however, when a radio ceases to function after an animal dies, this assumption may not be valid (White 1983). Censoring due to radio failure would not be expected to differ among adults and juveniles. Our results indicated that the mean time to censoring differed strongly from this expectation ($t = 3.77$, df = 179, $P < 0.001$). Juveniles, but not adults, had a substantial surge in the number of censored animals within the first 60 days after radio attachment (Fig. 2). This result would have been expected if juveniles left the study area or experienced un-

TABLE 6. Parameter estimates for the Cormack-Jolly-Seber (CJS) model $\phi_{t(juv)^*a}$, p_t, in which survival (ϕ) differed between adults and juveniles. Under this model, survival was constant among years for adults, but differed among years for juveniles. Resighting probabilities (p) differed among years.

	Adults		Juveniles		Adults	
Year	$\hat{\phi}$	SÊ ($\hat{\phi}$)	$\hat{\phi}$	SÊ ($\hat{\phi}$)	$\hat{p}$	SÊ ($\hat{p}$)
1992	0.861	0.034	0.518	0.072	0.125	0.032
1993	0.861	0.034	0.309	0.043	0.215	0.030
1994	0.861	0.034	0.568	0.080	0.197	0.026
1995	0.861	0.034	0.613	0.078	0.228	0.029
1996	0.861	0.034	0.241	0.065	0.495	0.066
Overall	0.861[a]	0.034[a]	0.448[b]	0.034[b]	0.200[c]	0.019[c]

[a] Adult survival in model ($\phi_{t(juv)^*a}$, p_t) is constant over time.

[b] Estimated using model (ϕ_a, p_t), which is identical to our selected model ($\phi_{t(juv)^*a}$, p_t) except that $\hat{\phi}_{juv}$ is constant over time. This approach is equivalent to using a weighted mean estimate where weights are based on the variance-covariance matrix.

[c] Estimated using model ($\phi_{t(juv)^*a}$, p), which is identical to our selected model ($\phi_{t(juv)^*a}$, p_t) except that $\hat{p}$ is constant over time.

detected mortality. Dead Snail Kites were usually found in water where radio signal strength was strongly diminished. We suspected that some mortality went undetected as a result. Consequently, during SY 1994 we increased our search effort for missing birds. We then examined the proportions of censored and dead birds during the first 180 days after radio attachment (i.e. before radio batteries should

have died). The proportion of adults censored and confirmed dead remained relatively constant among years ($\chi^2 = 1.02$, df = 2, $P = 0.601$; Fig. 3). In contrast, the proportion of juveniles censored and confirmed dead was similar during SY 1992 and 1993, but differed during SY 1994, when search effort was increased ($\chi^2 = 30.25$, df = 2, $P < 0.001$). During SY 1994, the proportion of birds confirmed dead increased

TABLE 7. Parameter estimates for our most parsimonious multi-strata model ($\phi_{a^*t(juv)^*r(juv)}$, p_{t^*r}, ψ_{a^*r}), in which survival differs between adults and juveniles, survival is constant among years and regions for adults, and survival differs among years and regions for juveniles. Resighting probability in this model differs among years and regions.

		Adults		Juveniles		Adults	
Year	Region[a]	$\hat{\phi}$	SÊ ($\hat{\phi}$)	$\hat{\phi}$	SÊ ($\hat{\phi}$)	$\hat{p}$	SÊ ($\hat{p}$)
1992	EVER	0.822	0.034	0.487	0.214	0.000	0.000
1992	OKEE	0.822	0.034	0.740	0.142	0.053	0.031
1992	KISS	0.822	0.034	0.367	0.116	0.358	0.135
1992	USJ	0.822	0.034	0.447	0.128	0.280	0.113
1993	EVER	0.822	0.034	0.404	0.097	0.222	0.057
1993	OKEE	0.822	0.034	0.436	0.089	0.110	0.037
1993	KISS	0.822	0.034	0.102	0.049	0.527	0.132
1993	USJ	0.822	0.034	0.343	0.128	0.113	0.065
1994	EVER	0.822	0.034	0.720	0.107	0.245	0.043
1994	OKEE	0.822	0.034	0.301	0.276	0.081	0.035
1994	KISS	0.822	0.034	0.275	0.097	0.248	0.080
1994	USJ	0.822	0.034	<0.001	<0.001	0.304	0.114
1995	EVER	0.822	0.034	0.454	0.074	0.199	0.037
1995	OKEE	0.822	0.034	0.437	0.198	0.387	0.103
1995	KISS	0.822	0.034	0.921	0.188	0.194	0.068
1995	USJ	0.822	0.034	1.000	0.317	0.368	0.127
1996	EVER	0.822	0.034	0.234	0.074	0.568	0.095
1996	OKEE	0.822	0.034	<0.001	0.412	0.389	0.121
1996	KISS	0.822	0.034	0.613	0.298	0.749	0.204
1996	USJ	0.822	0.034	0.248	0.175	0.756	0.242
Overall		0.822	0.034	0.441[b]	0.036[b]	0.308	0.092

[a] Regions are Everglades (EVER), Okeechobee (OKEE), Kissimmee (KISS), and Upper St. Johns (USJ). There were insufficient sightings to include the Loxahatchee Slough Region.

[b] Based on model (ϕ_a, p_r, ψ_{a^*r}) for which survival is considered constant among years and regions.
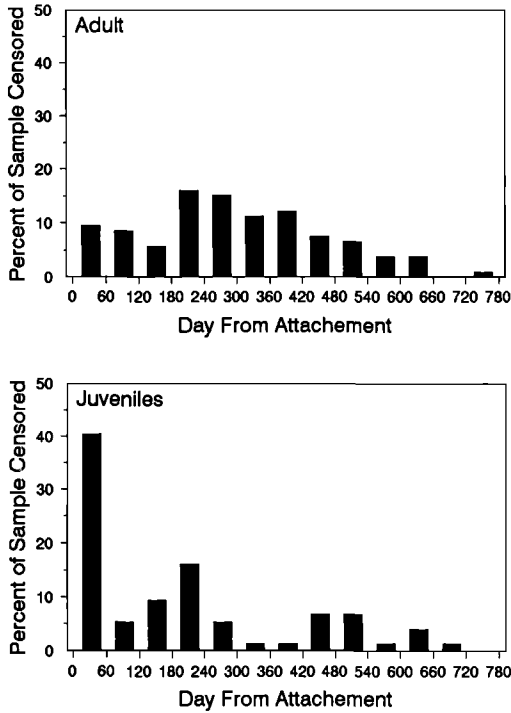
FIG. 2.   Percentage of radio-tagged adult and juvenile Snail Kites that were censored in each 60-day time interval from the time of attachment.
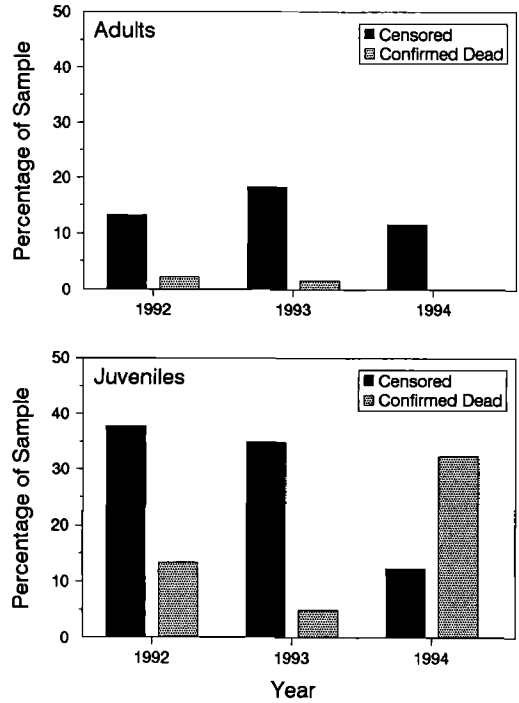

FIG. 3.   Percentage of adult and juvenile Snail Kites from each sampling cohort (i.e. year that they fledged or were captured) that died or were censored during the first 180 days after radio attachment each year.

substantially, and the proportion of censored birds decreased substantially. The proportion of censored juveniles during 1994 also closely matched the proportion of censored adults, which it had not during 1992 or 1993.

DISCUSSION

Comparison of estimates derived using radio telemetry and capture-resighting.—The results from radio telemetry and banding data generally were consistent in identifying sources of variation. Both data sets indicated that survival differed between age classes and among years for juveniles but not for adults. Single- and multistrata capture-recapture models also indicated similar sources of variation for survival and resighting probabilities, except that the multistrata models indicated additional regional effects. In contrast to sources of variation, some parameter estimates differed considerably among data sources. Although both sources of data indicated differences among years for juvenile survival, the parameter esti-

mates from these two data sets differed markedly and were not even consistent in their relative ranking among years. Estimates of juvenile survival during 1992 and 1993 were higher using radio telemetry data than for either capture-recapture model. We believe that this was due to a bias in our estimates using radio telemetry data during those years. Our results from censored radio-tagged birds indicated that we were finding dead juveniles during 1994 when search effort was increased, whereas a substantial number of dead birds may have gone undetected during 1992 and 1993. Thus, our survival estimates using radio telemetry probably were biased high for juveniles. In contrast, our estimates of adult survival were similar using radio telemetry data and CJS models, and each was within a 95% confidence interval of the other.

Another assumption in using radio telemetry to estimate survival is that the radio transmitter does not affect survival (White and Garrott 1990). Substantial recent evidence, however,

suggests that radio transmitters reduce survival for some species (e.g. Marks and Marks 1987, Burger et al. 1991, Paton et al. 1991). Bennetts and Kitchens (1997a) tested the hypothesis that radio transmitters negatively affect survival of Snail Kites using capture-recapture of birds with and without transmitters. They had reasonable power to detect any substantial differences, yet found no effect.

In contrast to radio telemetry, we had no reason to suspect that violations of our CJS model assumptions significantly biased our results. Probably the most substantial violation was for the assumption that capture and release of animals occurs over brief time intervals (Pollock et al. 1990). This assumption enables a clear definition of the interval over which survival is measured and helps to standardize intervals being compared. The life history of Snail Kites makes this assumption difficult to meet. However, we do not believe that violation of this assumption caused substantial bias to our estimates. For adults, the highest risk of mortality appeared to be during the fall and winter (Bennetts and Kitchens 1997a, Bennetts et al. 1999). Thus, all animals within a given study year experience the same period of high risk. For juveniles, the highest risk of mortality occurs during the first few months postfledging, and all juveniles within a given cohort also were exposed to that period of high risk.

Band loss probably was negligible on our study because 99% of the marked birds carried riveted aluminum bands that were extremely unlikely to have been lost. The bands on the remaining 1% of birds were made of PVC, and anecdotal evidence suggests that band loss from these bands also was negligible. We also believe that capture and release did not substantially influence the subsequent resighting of animals. Snail Kites are relatively tolerant of human presence and often allow humans to approach relatively close (Beissinger 1988). In addition, most birds were nesting at the time of resighting and tended to stay close enough to their nest to enable bands to be read with minimal difficulty.

Parameter estimates.—Because of the potential for biased estimates of juvenile survival using radio telemetry, we are more confident in our estimates using capture-recapture for this parameter. We also have greater confidence that our parameter estimates using single-stratum

models reflect actual survival. Our data indicated that, at least for juvenile survival, regional effects were warranted. However, capture-recapture models estimate apparent survival, such that permanent emigration (i.e. permanent for the study) is confounded with actual survival. Because our data were insufficient to partition among two age classes and all six regions using multistrata models, the potential exists for increased confounding of these two components of apparent survival. First, the four regions for which we had sufficient data were those with higher numbers of sightings. This could be due to greater use of these regions and/or a higher probability of observing birds that were present. This could account for the higher estimates of resighting probability observed from our multistrata models. Similarly, any permanent emigration to these regions would have been included in the resulting estimates as decreased apparent survival. Our single-stratum models included these regions because we were not attempting to derive separate parameter estimates. Thus, although we would expect our estimates of apparent survival using multistrata models to be less biased because we were accounting for regional heterogeneity, there also may have been more confounding of actual survival and permanent emigration in these estimates. This would explain the lower estimates of survival from our multistrata models compared with estimates from radio telemetry or single-stratum models.

Nichols et al. (1980) reported that survival of adult Snail Kites in Florida was 0.90. This was not based on a statistical estimator; rather, it was their "best guess" for demographic modeling. Similarly, Snyder et al. (1989) suggested that during non-drought years, annual survival of adult Snail Kites probably exceeds 0.90, although this value also was not derived using any specified estimator. Beissinger (1995) later reported adult survival during non-drought years as 0.95 based on Snyder et al.'s suggestion. Our estimates were similar (albeit slightly lower) to these previous estimates of adult survival ($\bar{x} = 0.89$ and 0.86 from Kaplan-Meier and CJS estimators, respectively), but they were based on reliable statistical estimators. In contrast to our estimates for adults, our estimates of juvenile survival were not consistent with some previous estimates. Beissinger (1995) reported juvenile survival during non-drought

years as 0.90. Nichols et al. (1980) reported a "best guess" of 0.58 for juvenile survival. Our data suggest that juvenile survival is substantially lower than Beissinger's estimate and more similar to the "best guess" reported by Nichols et al. (1980).

Effects of age, time, and region.—As predicted, we observed differences in survival between juvenile and adult Snail Kites, although separate estimates of subadult survival were not indicated by our data. The foraging skills of younger birds may be lower than those of adults, and younger birds also may be more vulnerable to predation. Our results also supported our hypothesis that younger birds are more sensitive to environmental variation than are adults. Survival of juveniles, but not adults, differed among years and regions. Environmental conditions, and consequently habitat quality for Snail Kites, may be quite variable in central and southern Florida (Beissinger 1986, Bennetts and Kitchens 1997a). Adult kites are well adapted to this variability and are quite capable of moving throughout their range in response to changing conditions (Bennetts and Kitchens 1997a, b). In contrast, juveniles that have not experienced alternative locations may be less efficient at locating new sites when local conditions are unfavorable. Consequently, juveniles may be more sensitive to both spatial and temporal variation in the environment.

Although our data indicate that juveniles, but not adults, are sensitive to environmental variability, it has been suggested that survival during drought years is substantially lower than during high-water years (Beissinger 1988, Takekawa and Beissinger 1989). Beissinger (1995) found survival during drought years to be one of the most sensitive parameters of his population viability model. Thus, adults may be susceptible to this more extreme case of environmental variability. Because we did not encounter drought conditions during the study, our results cannot reliably be extended to drought years. Thus, the need remains for reliable estimates of survival during drought years (see Beissinger 1995).

Implications of resighting probabilities.—The wide distribution of Snail Kites in Florida and their nomadic tendencies resulted in lower resighting probabilities than desired. Although the precision of survival estimates from our final single-stratum models was reasonable (CV = 0.04 and 0.08 for adults and juveniles, respectively), the precision of estimates from individual years and regions would have improved had we been able to obtain higher resighting probabilities. In addition to the effects of low resighting probabilities on precision, spatial and temporal differences in resighting probabilities may have important implications for monitoring Snail Kites. An annual survey of Snail Kites was conducted each year from 1969 to 1994. Reported uses of these data include estimating survival based on differences in counts between consecutive years (Beissinger 1988, 1995) and indexing population size for comparisons among areas or years (Rodgers et al. 1988). Using count data for these purposes requires an assumption that the survey represents a complete census, or that the proportion of birds detected is reasonably constant among the spatial and temporal units being compared (Lancia et al. 1994). Resighting probabilities that we estimated suggest that the annual survey fails to meet either of these assumptions. Our overall resighting probability using CJS models was 0.20, whereas a census is a complete count of animals (Lancia et al. 1994). Our results also indicated that resighting probability differed among years and regions, which is inconsistent with the assumption that the proportion of birds detected during the annual survey is constant. We note that our estimates were derived in spring, whereas the annual survey is conducted in autumn. However, our results raise concerns for the validity of using count data for indices of population change without accounting for spatial and temporal variation in detection probabilities. For a population that exhibits substantial shifts in spatial distribution among years, field techniques and model-based analyses that account for variability in detection are undoubtedly the most reliable means of estimating demographic parameters.

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Associate Editor: K. L. Bildstein