

WITHIN-YEAR SURVIVAL PATTERNS OF SNAIL KITES IN FLORIDA

ROBERT E. BENNETTS¹

*Department of Wildlife Ecology and Conservation, Florida Cooperative Fish and
Wildlife Research Unit,
P.O. Box 110450, University of Florida, Gainesville, Florida 32611 USA*

WILEY M. KITCHENS

*Florida Cooperative Fish and Wildlife Research Unit, P.O. Box 110450, University of Florida,
Gainesville, Florida 32611 USA*

Abstract.—We studied within-year survival of Snail Kites (*Rostrhamus sociabilis*) over a 3-yr period to determine the time required for survivorship of juvenile kites to become similar to adults. We also were interested in how the risk of mortality changes over time for each age class, which can further our understanding of what factors influence survival. Juvenile Snail Kites experienced a period of relatively high risk for their first four months after fledging, after which survivorship became similar to adults. This initial period of high risk corresponded to the time that fledglings were becoming independent of their parents, foraging on their own, and dispersing into unfamiliar areas. Adults experienced their highest risk, which was less than that of juveniles, during the winter and early spring. We offer several hypotheses about why this period of highest risk for adults might correspond to a time of lower food availability and/or increased risk of predation.

PATRON DE SUPERVIVENCIA, ENTRE AÑOS, DE *ROSTRHAMUS SOCIABILIS* EN LA FLORIDA

Sinopsis.—Estudiamos, entre años, la supervivencia de individuos de *Rostrhamus sociabilis* a través de un periodo de tres años para determinar el tiempo requerido por los juveniles para alcanzar la misma tasa de supervivencia de los adultos. Se quiso determinar además, de como el riesgo de mortalidad cambia a través del tiempo para los diferentes grupos de edades, para tratar de entender que factores afectan la supervivencia. Los juveniles pasan por un periodo de alto riesgo durante los primeros cuatro meses, luego de haber abandonado el nido. Luego de este periodo la supervivencia se torna similar a la de los adultos. Este periodo de alta mortalidad corresponde al tiempo en que los juveniles se independizan de sus padres, buscan alimento por su propia cuenta e invaden territorios con los cuales no estan familiarizados. Los adultos pasan por el periodo de mayor riesgo (que es menor que el de los juveniles) durante el invierno y la primavera temprana. Ofrecemos varias hipótesis para explicar la razón de mayor riesgo de este periodo, el cual corresponde a un lapso en donde hay menor disponibilidad de alimentos y/o incremento en el riesgo de ser depredados.

Juvenile survival of many avian species is often lower than that of adults (e.g., Loery et al. 1987, Nichols et al. 1992). This difference may be attributable to a lack of experience of younger birds for foraging, dispersal, and avoidance of predators. There is considerably less evidence for the time when the survival rate of younger birds approaches that of adults (Ricklefs 1973, Loery et al. 1987). Bennetts et al. (1999) recently examined annual survival of Snail Kites (*Rostrhamus sociabilis*) in Florida using a combination of radio telemetry and capture-recapture data. They found that annual survival of juveniles (birds of age <1 yr) was lower than that of adults (birds of age >1 yr), but that delineation of an intermediate

¹ *Current address: Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France.*

subadult age class (age 1–2 yr) was not supported by their data. This suggests that survival rates between age classes were similar after one year, but does not indicate when survival becomes similar. Neither capture-recapture nor telemetry data enables any evaluation of the patterns of survival within the sampling intervals. However, the intervals using radio telemetry are usually short compared to capture-recapture data, even though estimates are often reported on an annual basis. Thus, within-year data can provide considerable information regarding the time period when juvenile and adult survival rates converge. These patterns also may provide considerable insights about how the risk of mortality changes over time, which can further our understanding of what factors influence survival. Here we use survivorship functions derived from radio-telemetry data to refine our knowledge of the time when juvenile Snail Kite survival becomes similar to that of adults and to evaluate the seasonal patterns of risk for each age class.

STUDY AREA AND METHODS

Within the United States, Snail Kites occur only in Florida (Sykes 1984), and all evidence suggests that they constitute a single population that shifts in distribution throughout the state, rather than separate subpopulations within the state (Bennetts and Kitchens 1997a, 1997b). Consequently, the spatial extent of this study covered the entire range of Snail Kites in the United States, which is comprised of a network of wetlands throughout Central and South Florida (Bennetts and Kitchens 1997a, 1997b).

Our goal was to annually capture and radio tag 100 Snail Kites, with a ratio of 60% adults to 40% juveniles, for three consecutive years from April 1992–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. Snail Kites are sexually dichromatic and birds >2 yr old can readily be distinguished in the field. Birds <2 were assigned to a gender class based on our best estimate, but in rare cases ($N = 3$) the gender assignment had to be corrected after resighting birds in a subsequent year. The proportion of samples from each area was based on an annual survey to approximate the statewide distribution (Bennetts and Kitchens 1997a).

Adult kites were captured using a net gun (Mechlin and Shaiffer 1979), which uses 22-caliber blank cartridges to propel a 3-m triangular nylon net. Juveniles were captured on the nest just prior to fledging, at about 30–35 d old. Fifteen-gram radio transmitters were attached to birds with backpack harnesses. Radio-tagged birds were located at about 14-d intervals from aircraft or ground searches to determine their location and whether they were alive. All radios were equipped with mortality sensors that changed pulse rates if the transmitter had not moved for 6–8 h. Birds

with a transmitter emitting a mortality signal were located on the ground to verify the kite's fate.

The general effects of age and annual differences on survival of Snail Kites have been discussed in detail elsewhere (Bennetts and Kitchens 1997a, Bennetts et al. 1999). In this paper, we were interested in the timing of mortality rather than the magnitude of annual survival estimates. Bennetts and Kitchens (1997a) also evaluated seasonal and annual effects on survival using logistic regression. Of particular interest here was that an age \times season interaction was significant, which indicates that the seasonal patterns of survival were not similar between age classes. Also of interest was that neither a season \times year interaction nor a three-way interaction of age \times season \times year were significant. Based on these results and our interest in the timing of mortality rather than annual differences in magnitude, we pooled our samples among years for each age class. However, we did not pool age classes because of apparent differences in timing. However, pooling or not pooling our sample did not alter any of the conclusions reported here.

We generated survivorship functions 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 for survivorship functions. By this time during our first year we had a sufficient sample size ($N = 16$) of adults to allow reasonable estimates of survival. This time was also prior to peak fledging throughout most of the kite's range in Florida. Thus juveniles were added to our sample as they fledged, rather than some having fledged during the previous calendar year. Thus survivorship functions are based on a study year from 15 April of calendar year t to 14 April of calendar year $t + 1$. 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) with a modified version of the SAS code (SAS Institute Inc. 1988) reported by White and Garrott (1990).

Cox (1972) proposed a nonparametric model for the instantaneous probability of an animal's death, expressed as a hazard function. The hazard function is a measure of instantaneous risk of mortality as a function of age or time. We estimated the hazard function (\hat{h}_i) for discrete 1-mo intervals as the number of animals dying during the interval divided by the number of animals surviving over that interval (Lee 1992). In contrast to survivorship functions that assess if there are differences in survivorship, the hazard function better illustrates how the risk of mortality changes over time. Because risk of juvenile mortality may be more related to age than time, we estimated an additional hazard function for juveniles based on age. We did not do this for adults because we rarely knew their age, and age was less likely to have been a factor for adults.

RESULTS

We attached 282 radio transmitters on 271 individual Snail Kites. Eleven of the 271 birds were recaptured in a subsequent year and their trans-

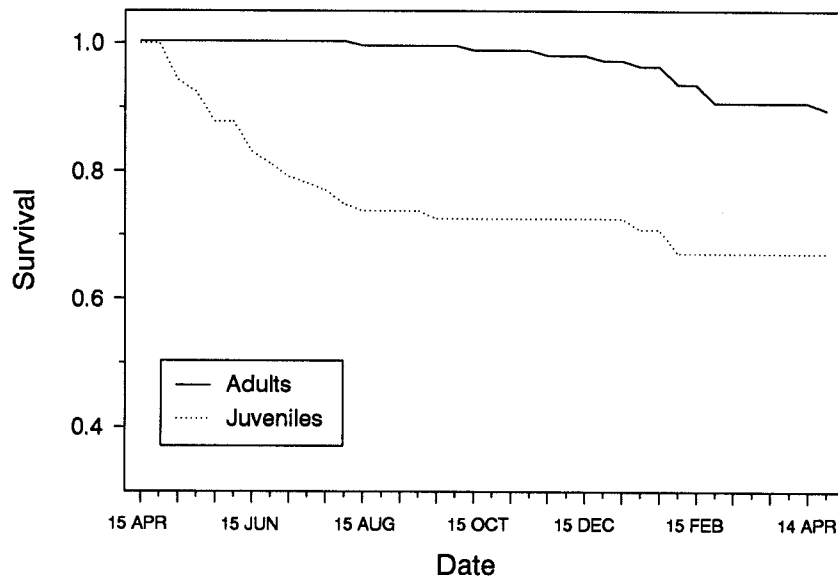


FIGURE 1. Survivorship functions of adult and juvenile Snail Kites from a pooled sample of 3 years.

mitters replaced. Of the 282 transmitters, 165 were placed on adults (45 during 1992 and 60 each during 1993 and 1994). We attached a total of 117 radios on juveniles (37 during 1992 and 40 each during 1993 and 1994). Of the adults, 82 (49.7%) were males and 83 (50.3%) were females.

A log-rank test supported the hypothesis that survivorship functions differed between adult and juvenile Snail Kites ($\chi^2 = 20.76$, $df = 1$, $P < 0.001$). These differences were significant ($\chi^2 = 33.69$, $df = 1$, $P < 0.001$) for the first four months of the study year (i.e., through 14 August), but not significant ($\chi^2 = 0.47$, $df = 1$, $P = 0.494$) for the remaining eight months. Juvenile survivorship decreased sharply for the first four months of the study year, after which it leveled off considerably to a much slower rate of decline until a relatively smaller decrease at about eight months (Fig. 1). In contrast, adult survivorship declined at a relatively slow rate for about the first eight months, after which there was a relatively moderate decrease in survival similar to that of juveniles. Thus, survivorship functions of the two age classes became quite similar after the first four months.

The risk of mortality (\hat{h}_t) was not constant over time for either age class (Fig. 2). Juveniles had the highest risk of mortality during the first four months; whereas this was a period of low risk for adults. Both age classes then experienced increased risk of mortality during January and February. The highest risk of juvenile mortality corresponded to 30–60 d post-fledging, with the second highest mortality during the first 30 d (Fig. 3).

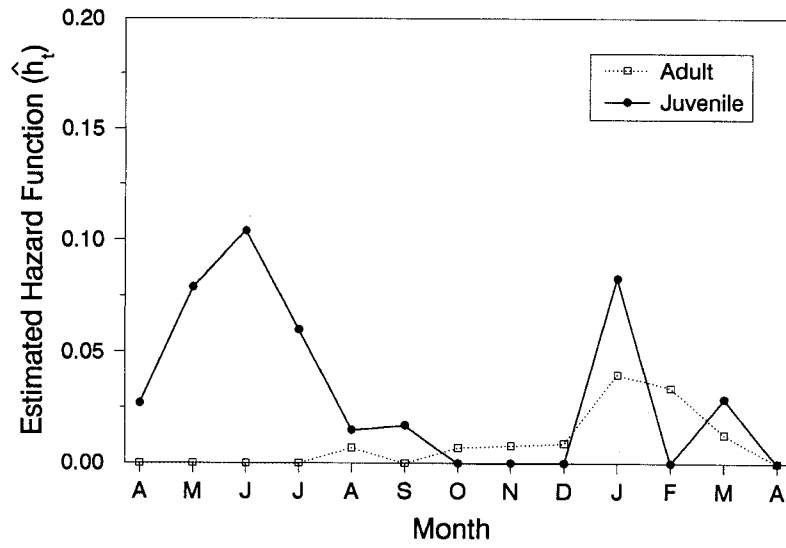


FIGURE 2. Estimated hazard functions (\hat{h}_t) constructed at monthly intervals for adult and juvenile Snail Kites.

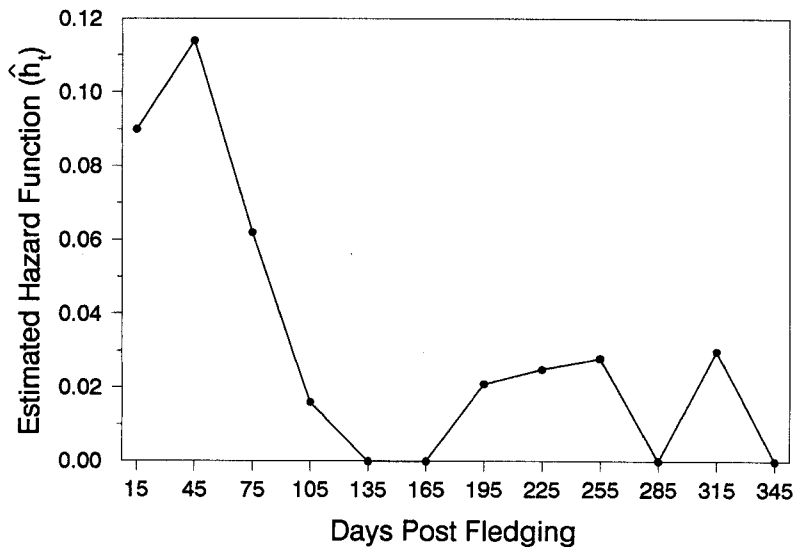


FIGURE 3. Estimated hazard function (\hat{h}_t) for juveniles based on age, rather than time. This function was constructed at monthly intervals starting at the time of fledging.

DISCUSSION

We found significant differences in seasonal patterns of survivorship between adult and juvenile Snail Kites. Juveniles experienced greatest risk of mortality during late spring and early summer; whereas adults were at greater risk during winter and early spring. The period of high risk for juvenile kites during late spring is not surprising. Our estimated hazard function based on age, rather than time, revealed that the period of greatest risk is 30–60 d after fledging. Although juveniles are least experienced during the first 30 d, they also are still attended by their parents. Snyder et al. (1989) suggested that the post-fledging dependency period lasts for about six weeks. Hence, 30–60 d after fledging, juveniles are becoming independent of their parents, foraging on their own, and dispersing into unfamiliar areas (Bennetts and Kitchens 1997a). Juveniles that survived the first few months post fledging also appeared to be vulnerable at the same time as peak mortality for adults.

In contrast to juveniles, it was less clear why adult kite mortality was highest in winter. However, during late winter and early spring there is a potential for increased risk of predation, which probably was the most frequent cause of adult mortality (Bennetts and Kitchens 1997a, Bennetts et al. 1998). Late winter and early spring corresponds to the time that adults begin courtship. Consequently, they are exhibiting more conspicuous behaviors (e.g., such as courtship flights and vocalizations) to potential predators. Adults also may be less wary of predators if their attention is on procurement of a mate. Evidence also suggests that Great Horned Owls (*Bubo virginianus*), which forage at night, were the most common predators. During the winter, leaves are absent from willows, that are the most commonly used species for communal roosting by Snail Kites (Sykes et al. 1995, Darby et al. 1996). Thus, concentrations of roosting kites may have been more visible to nocturnal predators during this period.

Apple snails (*Pomacea paludosa*) are the almost exclusive food of Snail Kites. These snails are aquatic, and are most vulnerable to kites while at the water surface. Apple snails have both gills and lungs and the frequency at which they come to the surface for air is inversely related to the amount of dissolved oxygen in the water (McClary 1964). Colder temperatures result in higher levels of dissolved oxygen and reduced activity and oxygen consumption by snails, both of which reduce the frequency of surfacing by snails (Freiburg and Hazelwood 1977, Hanning 1978). Consequently, cold temperatures during winter result in fewer foraging bouts and lower capture success by Snail Kites (Cary 1985, Sykes et al. 1995).

Estimated survivorship and hazard functions based on time, and hazard functions of juveniles based on age all indicated that the period of greatest risk for juvenile Snail Kites was during their first four months, after which survivorship became remarkably similar to that of adults. However, we emphasize that our study was conducted during a period of favorable

environmental conditions. During periods of food shortage (e.g., widespread droughts), there may be a greater disparity between age classes or an increased time for the risk of juvenile mortality to become similar to that of adults.

ACKNOWLEDGMENTS

Financial support was provided by the National Park Service, U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers, U.S. Geological Survey/Biological Resources Division, South Florida Water Management District, and St. Johns River Water Management District through the Florida Cooperative Fish and Wildlife Research Unit cooperative agreement No. 14-16-0007-1544, RWO90. We appreciate the field assistance from Lyn Bjork, David Boyd, Phillip Darby, Katie Golden, Hilary Maier, Steve McGehee, Scott Severs, and Patty L. Valentine-Darby. We appreciate the helpful comments of James Rodgers Jr., James D. Nichols, and Paul Sykes Jr. This paper is contribution No. R-06465 of the Florida Agricultural Experiment Station Journal Series, Institute of Food and Agricultural Sciences, University of Florida.

LITERATURE CITED

- BEISSINGER, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. *Ecol. Appl.* 5:618-631.
- BENNETTS, R. E. AND W. M. KITCHENS. 1997a. The Demography and Movements of Snail Kites in Florida. U.S. Geological Survey/Biological Resources Division, Florida Cooperative Fish & Wildlife Research Unit. Tech. Rep. No. 56. Gainesville, Florida.
- , AND ———. 1997b. Population dynamics and conservation of Snail Kites in Florida: the importance of spatial and temporal scale. *Colonial Waterbirds* 20:324-329.
- , M. R. SHANNON, AND W. M. KITCHENS. 1998. Causes of mortality of post-fledging juvenile and adult Snail Kites in Florida. *Florida Field Nat.* 26:84-87.
- , V. J. DREITZ, W. M. KITCHENS, J. E. HINES, AND J. D. NICHOLS. 1999. Annual survival of Snail Kites in Florida with comparisons between radio telemetry and capture-recapture data. *Auk* 116:435-447.
- CARY, D. M. 1985. Climatological factors affecting the foraging behavior and ecology of Snail Kites (*Rostrhamus sociabilis plumbeus* Ridgeway) in Florida. M.Sc. thesis, Univ. Miami, Miami, Florida. 58 pp.
- COX, D. R. 1972. Regression models and life tables. *J. R. Stat. Soc. B* 34:187-220.
- , AND D. OAKES. 1984. Analysis of survival data. *Monographs on Statistics and Applied Probability* 21. Chapman and Hall, New York. 201 pp.
- DARBY, P. C., P. L. VALENTINE DARBY, R. E. BENNETTS. 1996. Spatial relationships of foraging and roost sites used by Snail Kites at Lake Kissimmee and Water Conservation Area 3A. *Fla. Field Nat.* 24:1-9.
- FREIBURG, M. W., AND D. H. HAZELWOOD. 1977. Oxygen consumption of two amphibious snails: *Pomacea paludosa* and *Marisa cornuarietis* (Prosobranchia: Ampullariidae). *Malacologia* 16:541-548.
- HANNING, G. W. 1978. Aspects of reproduction in *Pomacea paludosa* (Mesogastropoda:Piliidae). M.S. thesis. Florida State Univ., Tallahassee. 149 pp.
- KAPLAN, E. L., AND P. MEIER. 1958. Nonparametric estimation from incomplete observations. *J. Amer. Stats. Assoc.* 53:188-193.
- LEE, E. T. 1992. Statistical methods for survival data analysis. 2nd ed. John Wiley and Sons, New York. 482 pp.
- LOERY, G., K. H. POLLOCK, J. D. NICHOLS, AND J. E. HINES. 1987. Age-specificity of Black-capped Chickadee survival rates: analysis of capture-recapture data. *Ecology* 68:1038-1044.
- MCCCLARY, A. 1964. Surface inspiration and ciliary feeding in *Pomacea paludosa* (Prosobranchia: Mesogastropoda: Ampullariidae). *Malacologia* 2:87-101.
- MECHLIN, L. M., AND C. W. SHAIFFER. 1979. Net firing gun for capturing breeding waterfowl. U.S.D.I. Fish & Wildlife Service. Northern Prairie Wildl. Res. Center. Jamestown, N.D. 14 pp.

- NICHOLS, J. D., G. L. HENSLER, AND P. W. SYKES JR. 1980. Demography of the Everglade kite: implications for population management. *Ecological Modelling* 9:215-232.
- , J. BART, R. J. LAMPERT, W. J. L. SLADEN, AND J. E. HINES. 1992. Annual survival rates of adult and immature eastern population Tundra Swans. *J. Wildl. Manage.* 56:485-494.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. *J. Wildl. Manage.* 53:7-15.
- RICKLEFS, R. E. 1973. Fecundity, mortality, and avian demography. Pp 366-435, in D. S. Farner, ed. *Breeding biology of birds: proceedings of a symposium on breeding behavior and reproduction physiology in birds*. National Academy of Sciences, Washington, D.C.
- SAVAGE, I. R. 1956. Contributions to the theory of order statistics—the two sample case. *Ann. Math. Stat.* 27:590-615.
- SAS INSTITUTE INC. 1988. SAS/STAT user's guide. Release 6.03. SAS Inst. Inc. Cary, N.C. 1028pp
- SNYDER, N. F. R., BEISSINGER, S. R., AND R. CHANDLER. 1989. Reproduction and demography of the Florida Everglade (Snail) Kite. *Condor* 91:300-316.
- SYKES, P. W., JR. 1984. The range of the Snail Kite and its history in Fla. *Bull. Florida State Mus.* 29:211-264.
- , J. A. RODGERS, JR., AND R. E. BENNETTS. 1995. Snail Kite (*Rostrhamus sociabilis*). No. 171 in A. Poole and F. Gill, eds. *The birds of North America*. The Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C. 32 pp
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press Inc., New York. 383 pp.

Received 20 Jan. 1998; accepted 9 Jul. 1998.