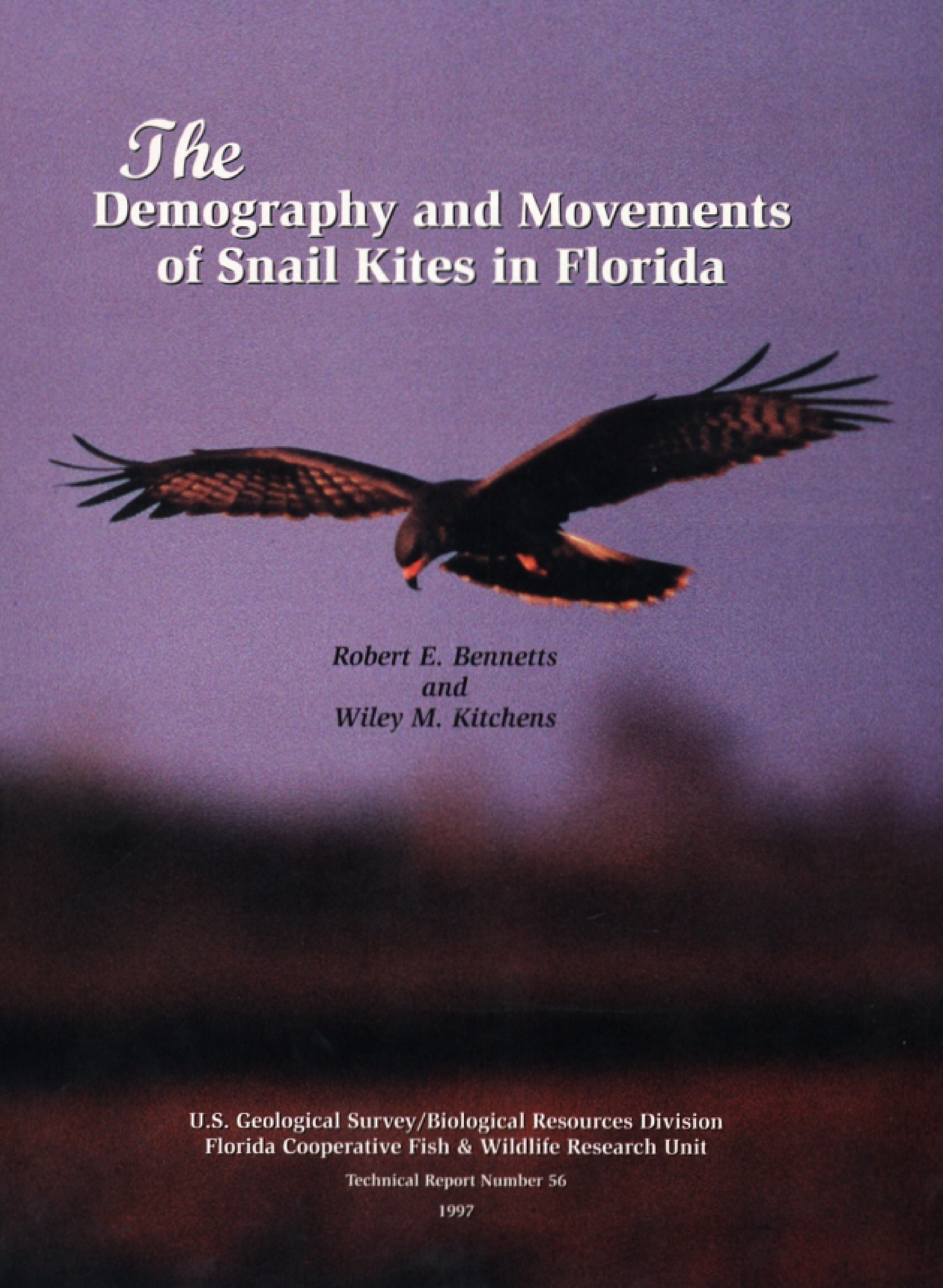
The
Demography and Movements of Snail Kites in Florida



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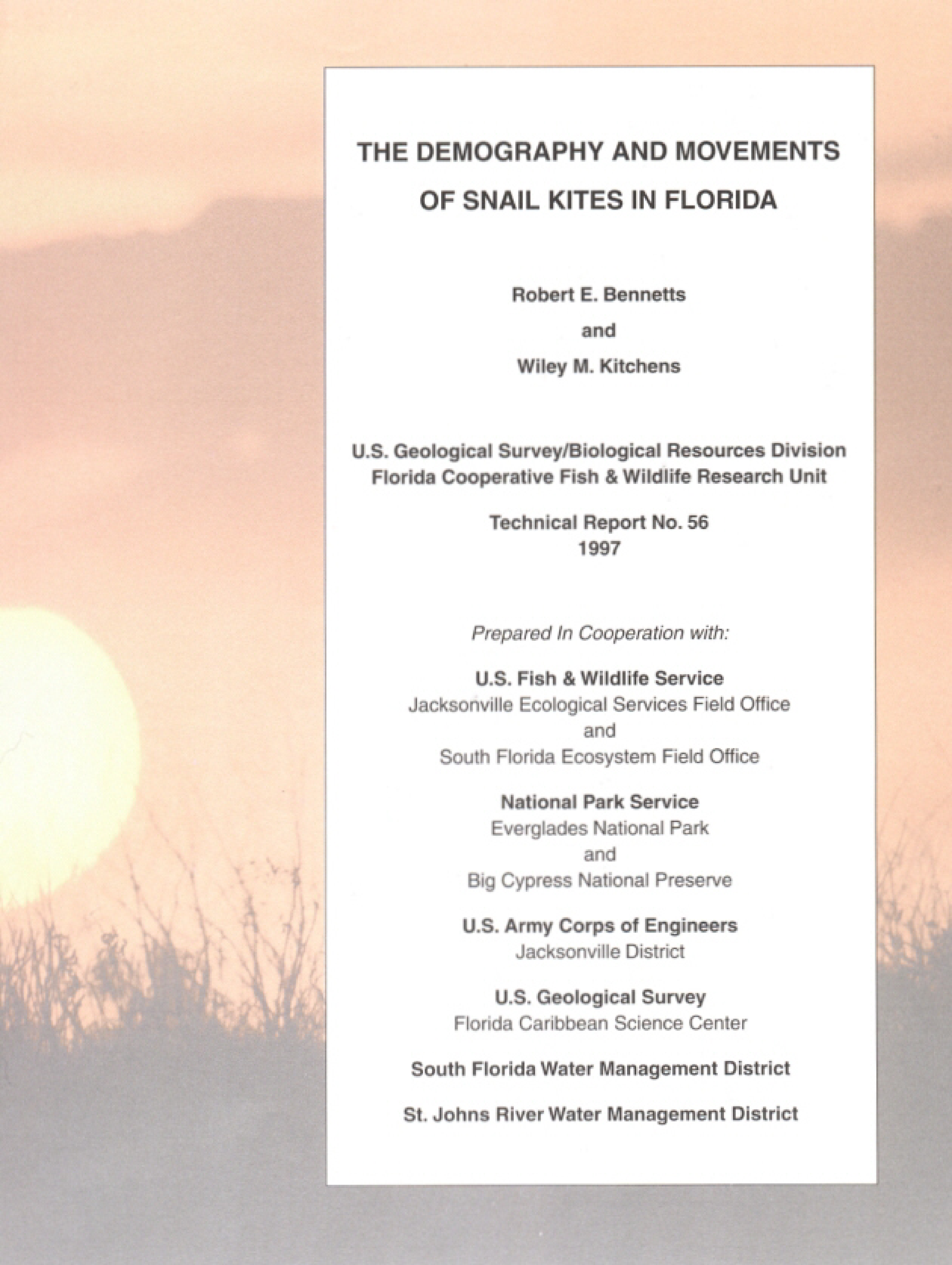

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Foreword

In preparing this report, we recognized that our audience consisted of both scientists and managers. We also recognized that there often is a significant gap in the information exchange between these disciplines. Consequently, the format and style of this report represent an attempt to bridge that gap. To this end, we have tried to provide sufficient detail of our methodology and results to enable the scientific community to evaluate the validity of our research or to incorporate our findings into a wide variety of potential models. At the same time we have also tried to provide "down to earth" explanations, and to frame our research in such a way as to enable managers to incorporate our findings into realistic management scenarios and planning. For those with a strong quantitative science background, we hope that our explanations do not border on being offensive. For those with a background of more applied biology, we hope that we have retained the essence of the biology within a potential myriad of statistics. Our goal is to make this report usable to all and that requires a balance in presentation. We hope that we have succeeded in our attempt.

We also realize that there often is some reluctance (and rightly so) on the part of scientists to make conclusions when they know that the temporal or spatial scale of their research precludes valid inferences beyond the scope of the conditions in which their research was conducted. At the same time, management agencies urgently need answers to questions that may be a long way from being answered. Hence, we are often forced to balance the need for answers with the validity of inferences derived from research conducted within a limited set of conditions. Again, we have attempted to bridge this gap through our interpretation and conclusions of the patterns we have observed. This occurs primarily in the *Management and Conservation* section of this report and we have tried to be very clear about what is speculative and what we have actually observed. We anticipate and welcome challenges to our ideas. That is part of the scientific process and how we advance in our knowledge.

Executive Summary

Florida's wetlands have undergone extensive anthropogenic change over the past century including drainage, impoundment, changes in water flow regimes, increased nutrient loadings, and invasion of exotic plants and animals. The Snail Kite (*Rostrhamus sociabilis*), like many other species, is potentially influenced by these environmental changes. Snail Kite populations during this century have changed considerably in number and distribution and several authors have suggested that changes in kite populations correspond with changes in environmental conditions, particularly hydrology. Our knowledge, however, of demographic processes and their influences has been far from complete. In addition to demographic parameters, movements of Snail Kites are poorly understood and have been the subject of recent controversy during the planning of wetland restoration (e.g., the Everglades) within Central and South Florida. The underlying purpose of this study was to better understand snail kite population and spatial dynamics and how they are influenced by environmental conditions. This understanding combined with reliable estimates of demographic parameters would enable a wide range of demographic modeling (e.g., viability analyses and risk assessments) with a higher degree of confidence. It also increases our predictive capability regarding the response of snail kites to changes in water management. The primary objectives of this study were to (1) estimate demographic parameters with an emphasis on survival, (2) evaluate the influences of environmental conditions (e.g., hydrology) on survival, (3) evaluate the movement patterns of snail kites in Florida including rates, locations, and what environmental conditions are correlated with these movements, and (4) develop a protocol for future monitoring of snail kites.

Radio telemetry and mark-resighting (banding) were the two primary field methods we used to obtain estimates of survival and movement probabilities. The combination of these two methods provided a comprehensive assessment of these parameters and was complimentary to each other. Radio telemetry enabled assessment of "within-year" patterns of both survival and movement. This allowed us to determine such things as the cause of death of an animal or what the environmental conditions were at the time an animal moved. Mark-resighting is intended to assess "between-year" patterns of these parameters. Our goal was to annually (for three consecutive years) capture and radio tag 100 snail kites of which 60% were adults and 40% juveniles. Our targeted ratio of adults to juveniles was intended to emphasize adult survival because demography of long-lived avian species (e.g., snail kites) tends to be more sensitive to adult rather than juvenile survival. Additionally, we targeted a 50:50 sex ratio of adults to keep our sample balanced. Our annual sample size of 100 was based on estimates of the statistical power to distinguish survival differences among groups (e.g., age or sex) or time periods.

We attached 282 radio transmitters on 271 individual Snail Kites. Eleven birds were recaptured and re-tagged in a subsequent year. We were short (82%) of our targeted sample size of 100 birds during 1992, but fully attained our targeted sample sizes in 1993 and 1994. We were very close to our targeted age and sex ratios for all years. Our total sample of individual banded birds for our mark-resighting analyses of survival was 913. Of this sample, 191 were adults at the time of addition to our sample and 722 were juveniles.

We estimated adult survival to be an average of approximately 0.90 using radio telemetry and 0.92 mark-resighting. Estimates of juvenile survival were not as consistent between methods and averaged 0.71 using radio telemetry and 0.50 using mark-resighting. We present evidence that the radio telemetry estimates may be biased high. Both sources of data indicated that survival was age-dependent and that survival differed among years for juveniles but not adults. Survival was high enough that within-year patterns would have been difficult to detect without enormous effort (i.e., too few individuals died to enable quantitative comparisons with those that survived) and probably not have been very insightful. Based on our results, we believe that between-year differences in survival would be more detectable and more insightful. From the outset of this study we realized that our scope of inference would be limited to those conditions encountered during our study. We encountered relatively high water conditions throughout this study. Consequently, we were unable to derive inferences about drought conditions. Fortunately, the mark-resighting program should enable a long-term evaluation of environmental correlates (e.g., hydrologic conditions) as variable conditions occur in the future.

Our data on movement indicated that Snail Kites frequently move among wetlands throughout their range. Overall probabilities of movement (per month) averaged approximately 0.25 for adults and 0.20 for juveniles. Our results also indicated that the probability of movement is influenced by age, time (yearly and seasonal differences), and location. Although relatively high water conditions persisted throughout this study, water levels (independently of location) did not appear to influence monthly movement probabilities. This does not imply that such an influence would not occur under low-water conditions. Some shifting of birds among regions within the state also may have been a result of a drought that preceded our study. Dispersal is generally thought to be favored when local resources (e.g., food) are low or better conditions exist elsewhere. In contrast, our results from both within-year and between year comparisons suggest that higher probabilities of movement occur when food resources are high. We also found that natal dispersal of juveniles was lower in areas where food resources were likely depressed. We suggest the hypothesis that this may be a reasonable strategy given the dynamic and unpredictable nature of a kite's environment. In years that food is not limiting, which for kites may be most years, high food resources may enable kites to "explore" their potential habitats with little risk. The resulting experience may then help kites to locate food resources faster during times (e.g., droughts) when food is limiting.

Prior to 1969 the statewide Snail Kite population was monitored only through sporadic and haphazard surveys. Numbers of Snail Kites in Florida since 1969 have been monitored via a quasi-systematic annual survey. Since these surveys began there have been numerous biological interpretations, often with little or no regard for the inherent sources of variation in these data that could influence the validity of subsequent interpretations. We examined several sources of variation inherent in the annual survey and discuss how this variation could influence the validity of data interpretations. Based on our results and on logic of valid scientific inference, we suggest the annual survey is not a valid estimator of population size; nor should year to year variation in the count be used to estimate demographic parameters (i.e., survival or recruitment). We do, however, believe that the annual count has some value for examining long term population trends provided that the sources of variation be incorporated into any analysis. We explore alternatives to the annual count and provide recommendations that are dependent on what parameters are being estimated.

There has been considerable discussion in the literature about the influence of drought on Snail Kite populations; however, few authors have even defined a drought sufficiently to enable an independent observer to designate a given year as a "drought year" based on objective criteria. We suggest that there are three essential characteristics of droughts (i.e., intensity, spatial extent, and temporal extent) that should be operationally defined for effective evaluation of droughts. We further suggest ways that these components can be measured such that they may be incorporated into demographic analyses.

Our data are consistent with previous views that the habitats used by Snail Kites in Florida are considerably more extensive than the currently-designated-critical habitat. We also believe that the protection of only the currently designated critical habitat would be insufficient to maintain viable populations of Snail Kites over the long term. We suggest that the use of habitats can be characterized as an extensive network and present a hypothesis of how the spatial and temporal patterns of this network might influence viability of Snail Kites in Florida. We believe that the general directions and goals of the South Florida Ecosystem restoration process are not in conflict with maintaining a viable population of Snail Kites; however, a broader spatial extent of habitat protection (i.e., outside of the Everglades and Okeechobee watersheds) probably is necessary for long-term viability of the Florida population.

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Chapter 1. INTRODUCTION

Florida's wetlands have undergone extensive anthropogenic change over the past century including drainage, impoundment, changes in water flow regimes, increased nutrient loadings, and invasion by exotic plants and animals. The Snail Kite (*Rostrhamus sociabilis*), like many other species, is potentially influenced by these environmental changes. Snail Kite populations during this century have changed considerably in number and distribution and several authors (e.g., Sykes 1984; Beissinger 1988; Bennetts et al. 1994, Sykes et al. 1995) have suggested that changes in kite populations correspond with changes in environmental conditions, particularly hydrology. Our knowledge, however, of demographic processes and their influences is far from complete (Bennetts and Kitchens 1994).

Changes in the size of all populations are a sum of births and immigration minus deaths and emigration. The Florida population of Snail Kites, however, is perhaps simpler in that all evidence suggests that this population is closed with respect to immigration and emigration. Snail Kites in Florida have long been known for their nomadic tendencies (Stieglitz and Thompson 1967, Sykes 1979, Bennetts 1993), leading to our previous suggestion that the Florida population is not comprised of discrete subpopulations, but instead, is one population that frequently shifts in distribution throughout the state (Bennetts and Kitchens 1992, 1993). There has been speculation about exchange between populations of the United States and Cuba (e.g., Sykes 1979, Beissinger et al.1983, Sykes et al. 1995); however, no evidence supporting this hypothesis has emerged. Thus, from a demographic perspective, we are concerned primarily with birth and death processes and the influences on those processes (Fig. 1-1).

The birth and death processes can be conceptualized as part of the demographic cycle represented by parameters for survival (ϕ_i) and fecundity (f_i) (Beissinger 1995, Legendre and Clobert 1995)(Fig. 1-2). Reliable estimates of these demographic parameters would enable a wide range of demographic modeling (e.g., viability analyses and risk assessments) with a higher degree of confidence. It also would

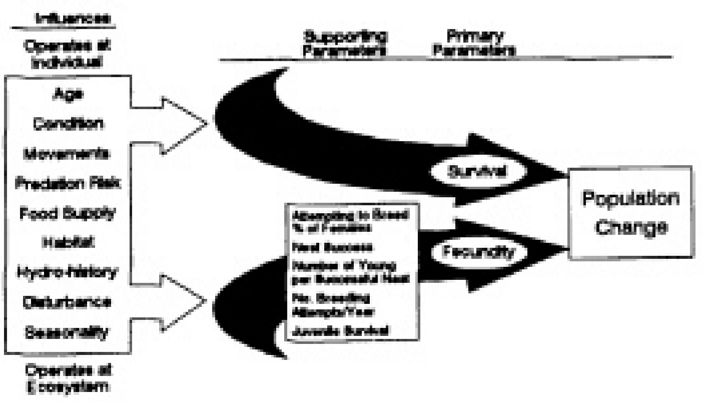


Figure 1-1. A conceptual model of the parameters and their influences that affect population change of Snail Kites in Florida.

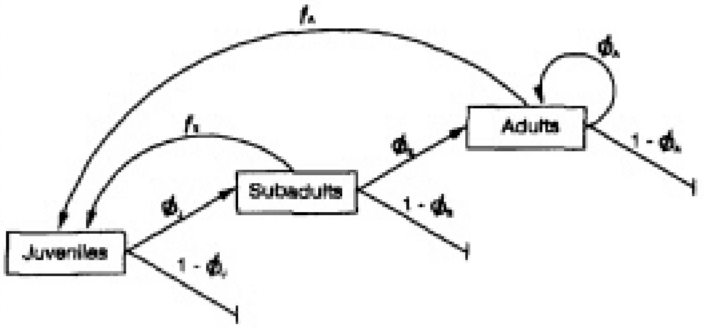


Figure 1-2. The demographic cycle of Snail Kites showing three age classes (Juveniles=J, Subadults=S, and Adults=A). Parameters for survival (ϕ) and fecundity (f) are shown for each age class. Adapted from Caswell (1989), Beissinger (1995) and Legendre and Clobert (1995).

increase our predictive capability regarding the response of Snail Kites to changes in water management. Given the scope of projects currently being planned or implemented (e.g., the Central and South Florida Project, the South Florida Ecosystem Restoration Initiative, Kissimmee River Restoration, Upper St. Johns River Basin Project, Kissimmee chain of Lakes Fishery Restoration) an improved predictive capability would be highly beneficial and would greatly reduce controversies.

The goal of this study was to better understand Snail Kite population and spatial dynamics and how they are affected by both natural and anthropogenic processes. We believe that demographic models play an important role in the refinement of our understanding of these dynamics. However, it is also our belief that reliable parameter estimates, particularly if a model is sensitive to those parameters, are an essential basis for reliable model outputs. Lastly, we believe that our models, as well as our knowledge, should be an iterative and adaptive process (Walters 1986). As we acquire new information or better parameter estimates, or if our predictions are falsified, we need to adjust our models, as well as our thinking, to adapt to new information (Fig. 1-3).

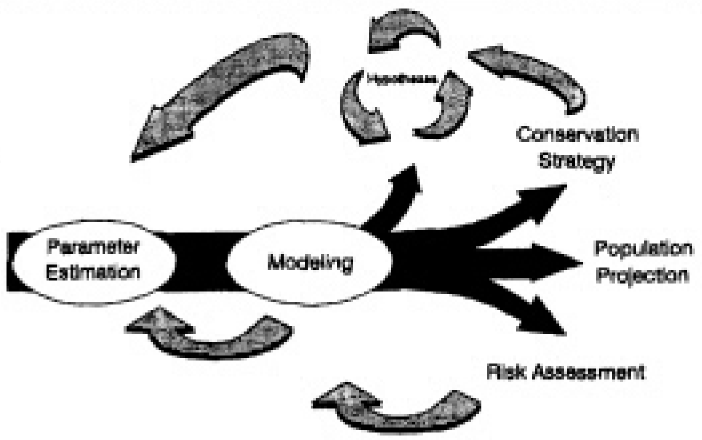


Figure 1-3. Conceptual framework for this study. Reliable estimation of parameters is the first step toward the development of a wide variety of demographic models.

Objectives

Most previous research on the demography of Snail Kites has focused on reproduction. Nesting success, in particular, has received considerable attention in recent years (e.g., Sykes 1987b, 1987c, Bennetts et al. 1988, 1994; Snyder et al. 1989a). There remains considerable debate about the what factors influences nesting success (Bennetts et al. 1994, Sykes et al. 1995); however, compared to other species, the relationship between nesting success of Snail Kites and environmental conditions is relatively well understood. Other reproductive parameters are less well known. Unsubstantiated estimates or speculation have been made regarding the proportion of birds attempting to breed each year and the number of nesting attempts per year (e.g., Snyder et al. 1989a, Beissinger 1995); however, reliable estimates for these parameters have been lacking.

In as much as there appears to be general agreement that changes in Snail Kite populations are more sensitive to survival than to reproduction (Nichols et al. 1980, Beissinger 1995, Sykes et al. 1995), data to estimate survival are very limited (Snyder et al. 1989a) and as a result, reliable estimates of survival are sorely lacking (Beissinger 1995). Consequently, the first objective of this study was to estimate adult and juvenile survival and to evaluate the influences of environmental conditions (e.g., hydrology) on survival. In addition to this primary goal, we also recorded supplementary information on reproductive parameters to the extent that it did not conflict with accomplishing our primary goals and in areas where such information was not already being collected.

In addition to demographic parameters, movements of Snail Kites also are poorly understood and have been the subject of recent controversy during the planning of marsh restoration within Central and South Florida. While long term changes in Snail Kite distribution tend to coincide with changes in hydrologic regimes, shorter term (e.g., annual and seasonal) shifts do not always coincide with local hydrologic conditions (Bennetts et al. 1994). It has been hypothesized that dispersal of kites may be in response to hydrologic conditions (Takekawa and Beissinger 1989), localized food depletion (Bennetts et al. 1988), or localized environmental conditions (e.g., dissolved oxygen in the water) that may influence apple snail (*Pomacea paludosa*) availability (Bennetts et al. 1994). To what extent movements reflect long-term changes in habitat quality versus short-term environmental dynamics is poorly understood, as is their ability to locate and re-colonize wetlands that have been, or will be, restored. Thus, movements are critical to understanding Snail Kite population dynamics leading to our second primary objective to evaluate the movement patterns of Snail Kites in Florida including rates, locations, and what environmental conditions are correlated with movements.

Because of the kites' endangered status and because there are a multitude of projects than have and continue to alter hydrologic regimes of southern Florida, there has been considerable interest in monitoring the Florida population of Snail Kites. Since 1969, Snail Kites in Florida have been monitored using an annual statewide survey. Unfortunately, there are serious questions regarding the inferences that can be reliably made from this data source. Consequently, our third primary objective was to evaluate the validity of existing monitoring and to provide recommendations for future monitoring of Snail Kites in Florida.


South Florida
1992
NORTH

Chapter 2. STUDY AREA

Study Population

Snail Kites within the United States occur only in Florida (Sykes 1984). It has been suggested (Bennetts and Kitchens 1992, 1993, 1994, Beissinger 1995) that Snail Kites comprise one population that shifts in distribution throughout the state, rather than there being separate subpopulations within the state. Data from studies on movements (this study) and genetics (Rodgers and Stangel 1996) support that there is considerable interchange of birds among wetlands in Florida. Consequently, it was deemed essential for the scope of this study to include the entire population of Snail Kites in Florida and our study area comprised a network of wetlands throughout Central and South Florida within the entire documented range of Snail Kites (Fig. 2-1).

Spatial Scales

Because the scale of our study is statewide, we did not focus on movements within individual wetlands. For the purpose of this study, we considered wetlands to be distinct if they were separated by a physical barrier (e.g., ridge or levee) and/or were under a different hydrologic regime either through natural or managed control. Thus, adjacent wetlands, which were once hydrologically continuous (e.g., WCA-2A and WCA-2B), were considered separate units if they were under different water regulation schedules.

Although we recorded locations of animals by specific wetland, for many analyses we had insufficient data to consider wetlands individually. For example, in the highly fragmented agricultural areas, there were more than 50 wetlands used by kites during this study. Consequently, some pooling of locations was required. For most analyses agricultural areas were pooled into a single class of wetlands. It was not uncommon for kites to frequent several such wetlands in immediate proximity, and we seldom (if ever) would have had sufficient data to support estimating parameters (i.e., survival or movement probabilities) for each of these wetlands. Other cases of pooling are described below, or are reported on a case specific basis based on model selection criteria (see methods).

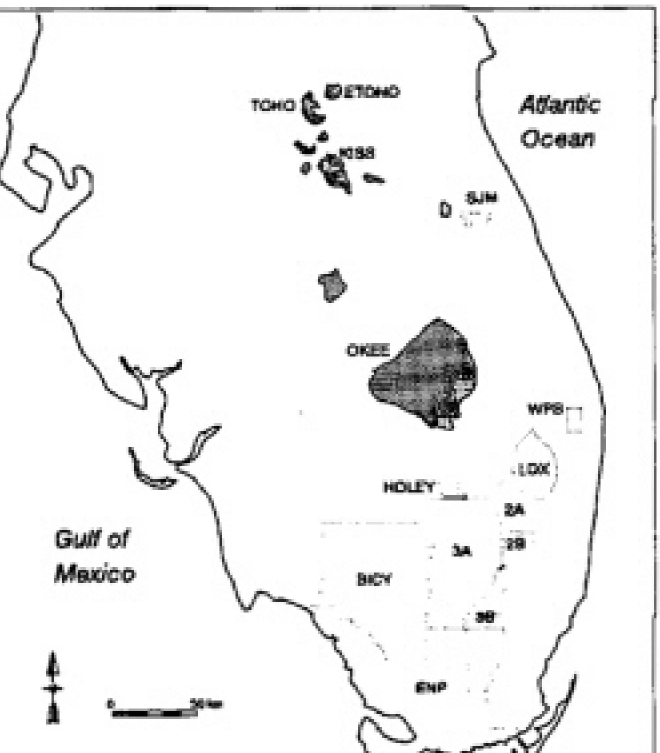


Figure 2-1. Major wetlands of South Florida referred to in this report. Wetlands are Everglades National Park (ENP), Big Cypress National Preserve (BICY), Water Conservation Areas 3A, 3B, 2B, 2A, Loxahatchee National Wildlife Refuge (LOX), Holey Land Wildlife Management Area (HOLEY), West Palm Beach Water Catchment Area (WPB), Lake Okeechobee (OKEE), Upper St. Johns [Blue Cypress] Marsh (SJM), Lake Kissimmee (KISS), Lake Tohopekaliga (TOHO), and East Lake Tohopekaliga (ETOHO).

REGIONS

For some analyses (e.g., survival) we treated location at a regional scale because it was infeasible to estimate separate parameters for all wetlands. Based primarily on watersheds, climatic factors, physiography, and management regimes we assigned each location to one of five primary regions (Fig. 2-2). Locations not included in these five regions (e.g., agricultural areas and isolated peripheral wetlands) were assigned to a sixth region we call the peripheral region. Undoubtedly, there are differences in the quantity and quality of habitats within this sixth "catch all" region (and within the 5 primary regions as well); however, the amount of data required to partition the effects of this within-region variability would be enormous and require significantly more effort that the scope of this study. However,

Figure 2-2. South Florida showing geographic regions used for some analyses in this report. All areas not within a region shown were assigned to a peripheral region.

whenever the data supported partitioning beyond a regional scale we did so.

The Everglades and Big Cypress Region is comprised of Water Conservation Areas 1,2, and 3, Everglades National Park, and Big Cypress National Preserve. The Loxahatchee Slough Region is comprised of wetlands in the drainage system of the Loxahatchee Slough and vicinity including the Corbitt Wildlife Management Area, Pal-Mar Water Control District, private wetlands owned by Pratt-Whitney Corp., and wetlands within the Loxahatchee Slough owned by the City of West Palm Beach (i.e., the West Palm Beach Water Catchment Area and vicinity). The Okeechobee Region is comprised of Lake Okeechobee within the Herbert Hoover Dike. The Kissimmee Chain-of-Lakes Region was comprised of all lakes within this chain including Lakes Kissimmee, Tohopekaliga, East Tohopekaliga, Marion, Marian, Tiger, Pierce, Jackson, and Hatchineha. The Upper St. Johns Region includes wetlands within the Upper St. Johns River Basin, but most *Snail* Kites used the Blue Cypress Marsh Water Conservation Area, Blue Cypress Water Management Area, and surrounding wetlands in private ownership. Agricultural areas (e.g., citrus groves, canals, agricultural fields, or agricultural retention ponds) within each of these regions, as well as all other areas not included in one of the above regions, were assigned to the peripheral region.

HABITAT TYPES

Snail Kites inhabit freshwater wetlands throughout central and south Florida. There is considerable variation in the physiographic characteristics and specific plant communities that comprise Snail Kite habitat (reviewed by Sykes et al. 1995). Our objectives did not warrant documentation of micro-habitat use by kites, nor was our sampling (often by aircraft) conducive to recording such data. However, for some analyses we wanted to incorporate the effects of at least a broad classification of habitats being used by kites. This classification had to be broad enough to enable assignment of locations obtained from aircraft to a given habitat type and sufficiently broad such that micro-habitat variation did not confound the assignment given normal daily movements of foraging birds. Consequently we assigned each location to one of five habitat types: (1) graminoid marsh, (2) cypress prairie, (3) Okeechobee, (4) northern lakes, and (5) miscellaneous peripheral. Graminoid marshes (Fig. 2-3) were generally slough and wet prairie communities (Loveless 1959). We distinguished cypress prairies (Fig. 2-4) in that a dominant feature of the landscape profile was comprised of cypress. This habitat occurred primarily in western WCA3A, and portions of the Big Cypress National Preserve and Loxahatchee Slough. The littoral zone of Lake Okeechobee is an extensive system of diverse marsh habitats, and consequently had elements of at least three of our other habitat types (*i.e.*, graminoid marsh, northern lake, and highly disturbed). Because of this high local diversity we were unable to assign locations to a particular type without extensive ground verification. Even then, birds often used more than one of these habitat types within a given day. Thus, we assigned locations at Lake Okeechobee (Fig. 2-5) to its own habitat type. The northern lake habitat type (Fig. 2-6) consisted primarily of lakes within the Kissimmee Chain-of-Lakes, but also included a few lakes along the Lake Wales Ridge. In contrast to Lake Okeechobee, this habitat type generally was comprised of a narrow littoral zone (usually < 200 m) on the periphery of these lakes. This littoral zone had a relatively steep elevation gradient compared to other habitat types; the zone used by foraging kites often was a band of < 100 m usually dominated by maidencane (*Panicum* spp) interspersed with patches of bulrush (*Scirpus* spp) or cattail (*Typha* spp). Primary nesting areas were often a zone of cattail and/or willow (*Salix* spp) in the shallower zone adjacent to foraging areas. The peripheral habitat type (Fig. 2-7) was comprised primarily of agricultural areas. These included retention ponds for citrus groves, agricultural ditches, and other miscellaneous, usually highly disturbed, habitats. Larger canals, not necessarily associated with agriculture, were also included in this habitat type.

For some analyses we had insufficient data to partition locations into each of these habitat types. Consequently, for some analyses we assigned locations to an even broader category of lakes (i.e., Lake Okeechobee, the northern lake habitat type, and permanently flooded canals [<0.01% of our locations]) and marshes (any non-lake habitat). This was intended to distinguish habitats that had a permanent water source component available (even if it was not used) with those that dried periodically.

Figure 2-3. Graminoid marsh habitat type.

Figure 2-4. Cypress prairie habitat type.

Figure 2-5 Lake Okeechobee habitat type.

Figure 2-6. Northern lakes habitat type.

Figure 2-7. Peripheral habitat type.

Chapter 3. METHODS

To provide sufficient detail of our methods and still keep it readable for general audiences we have split up some of the information between the text and appendices. In the text, we have tried to provide a more general description of our methods including the appropriate citations for analytical procedures. However, for some analyses we have provided a more detailed description, including the corresponding formulae in appendices. Because we also make use of extensive notation, which for readers not familiar with such notation, can be confusing, we have also provided a summary (Appendix 3-1) of notation used throughout this report.

Overview of Field Methods

Radio telemetry and mark-resighting (banding) were two primary field methods used to estimate survival and movement probabilities. The combination of these two methods provided a comprehensive assessment of these parameters and were complementary to each other. Radio telemetry enabled assessment of "within-year" patterns of both survival and movement. This allowed us to determine such things as the cause of death of an animal or what the environmental conditions were at the time an animal moved. Mark-resighting is intended to assess "between-year" patterns of these parameters. This approach was a much more cost efficient method for estimating annual survival. We are also exploring its potential to estimate population size of Snail Kites. Within-year patterns could not be determined using the mark-resighting approach; however, we had hypothesized that the primary factor that regulates Snail Kite populations is periodic drought (Takekawa and Beissinger 1989, Beissinger 1995), which is a between-year phenomenon. Thus, the ability to detect differences and to estimate survival for drought phenomena can therefore be assessed using mark-resighting methodology.

Capture and Marking of Animals

We captured adult snail kites primarily using a net gun (Mechlin and Shaiffer 1979). We initially tried to capture kites using a variety of noose carpets (Snyder et al. 1989b) and traps. These methods proved inefficient and indicated a relatively strong heterogeneity (catchability) among individuals that could have biased our sample. Some individuals would actively avoid perches or food that were associated with traps, while others showed no apparent avoidance. We decided to use the net gun after careful evaluation of the potential risks (i.e., injury, death, or nest abandonment) and apparent poor success and potential for bias in other techniques.

The net gun propels a 10-foot triangular nylon net using 22 caliber blank cartridges. The projectiles of the net gun were encased in foam rubber to reduce the chance of injury. Most captures were of adults while flying close during nest defense. We also captured some foraging birds although this was less effective. To further reduce the potential for injury, we did not shoot at birds that were: (1) closer than 7-8 m, (2) in a defense dive toward us, or (3) in a position where the vegetation below the bird posed a risk (e.g., too high to retrieve the bird). We almost always were able to retrieve the bird within 60 s of capture. In order to reduce the risk of nest abandonment, we did not attempt to capture birds in the early stages of nesting (e.g., courtship or egg laying). We attempted to capture birds primarily after eggs had hatched, although a some birds were inadvertently captured during the incubation period while engaged in group defense of an adjacent nest.

All adults captured and most nestlings encountered at fledging were banded with U.S. Fish & Wildlife Service bands as well as a uniquely-numbered-anodized aluminum band. The anodized-aluminum bands enabled an individual to be identified from up to 40 m (a distance not difficult to obtain with snail kites) using a spotting scope. The banding of nestlings was conducted in a cooperative effort with the Florida Game and Fresh Water Fish Commission (GFC). Biologists with the GFC were banding Snail Kites as part of other ongoing studies using colors to designate natal wetlands. Consequently, we provided GFC biologists our anodized numbered bands which enabled us to identify individuals in the field using colors needed for their respective studies.

In addition to leg bands, all adults and some juveniles (below) were equipped with radio transmitters. Radio tagging more than one juvenile per nest would have allowed us to explore some questions about the tendency for siblings to disperse together; however, it would have violated the assumption of independence required for our survival analysis. Consequently, a maximum of one juvenile per nest was equipped with a radio transmitter.

Male Snail Kite fitted with radio transmitter.

All radio transmitters were equipped with a mortality switch that upon prolonged lack of motion (= 6 h) altered the pulse rate such that we could remotely determine if a bird were dead or had dropped its radio. Radio transmitters were attached using a backpack harness. Harnesses were made of four separate pieces of 1/4" Teflon ribbon which were securely fastened at the transmitter, but were sewn together at the breast with a single cotton string. This cotton string attachment was intended as a "weak link" which would allow the transmitter to fall off cleanly as the string weakened and broke over time. The 15 g transmitters were approximately 3.5% of the body weight of adult snail kites ($\bar{x}_{AD} = 427$ g) and 3.9% of the body weight of juveniles at the time of fledging ($\bar{x}_{JUV} = 384$ g) (Darby et al., in press), which were within the 5% required by our permits.

Sampling Protocols

For our sample to be representative of the statewide population we targeted the sample from each location to be proportional to the preceding annual count made approximately 3 months prior to trapping. Our goal was to annually (for three consecutive years) capture and radio tag 100 snail kites of which 60% were adults and 40% juveniles. Our targeted ratio of adults to juveniles was intended to emphasize adult survival because demography of long-lived avian species (e.g., snail kites) tends to be more sensitive to adult rather than juvenile survival (Young 1968, Grier 1980, Beissinger 1995). Additionally, we targeted a 50:50 sex ratio of adults to keep our sample balanced. Our annual sample size of 100 was based on estimates of the statistical power to distinguish survival differences among groups (e.g., age or sex) or time periods (Fig. 3-1). We estimated power assuming a binomial distribution because we intended to use a binomial estimator for movement probabilities (below) and the Kaplan-Meier estimator for survival analyses (below) which is an extension of a binomial estimator that enables censoring and staggered entry of animals (White and Garrott 1990). Consequently, a binomial estimator was our best starting point from which to estimate power prior to actual collection of data. We used an initial survival estimate of 0.90 as a null hypothesis (H_o) based on previous speculation (Nichols et al. 1980, Snyder et al. 1989a). We then computed power for the alternative hypotheses (H_a) of 0.80, 0.70 and 0.60 using a range of potential sample sizes. This analysis indicated that substantially smaller sample sizes than those we targeted would have had little power to detect even large differences in annual survival.

Sample sizes needed for capture-recapture data are highly dependent on estimates of re-sighting probability for which we had no preliminary indication. Consequently, our goal was to band as many birds as logistically possible to evaluate whether this method had sufficient power given the sample sizes of banded birds and resightings we were able to obtain.

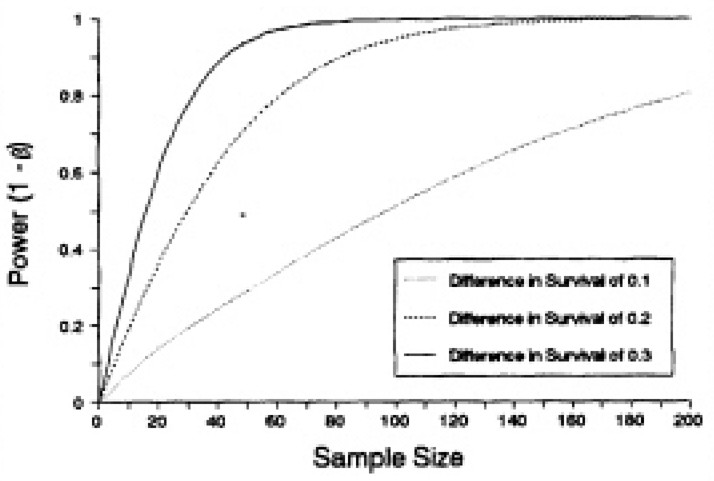


Figure 3-1. The probability (power) of detecting differences in survival based on using different sample sizes. We assumed a binomial distribution and an initial survival estimate of 0.9.

Monitoring Protocols

We attempted to locate all radio-tagged kites bi-weekly. At this frequency we were likely to detect most major movements and had a reasonable probability of finding most dead birds before they were too decomposed to determine cause of death. Given the size of our study area, more frequent locations would have required considerably more effort and expense. Also because of the size of our study area, searches were conducted most efficiently by aircraft. Even by aircraft, only a small portion of the potential habitat could be adequately covered during any given flight. Consequently, we flew approximately two times per week (for ≈ 4-5 h each flight) to obtain our bi-weekly locations. We also verified the status (i.e. alive or dead) and location of birds on the ground (i.e., by airboat or from levees) whenever we visited each area.

Mark-resighting was conducted from March through June of each year. Using this period enabled simultaneous estimates of survival along with recruitment through nest monitoring and created additional advantages. For example, the tendency for a bird to remain in proximity of its nest increased our ability to read band numbers (i.e., a resighting) of an individual. Nest visits were also required for the marking of individuals (i.e., fledglings), making for an efficient use of our effort by simultaneously monitoring nesting success. During nest monitoring we checked the adults at each nest for leg bands, in addition to other non-nesting birds observed, and attempted to read the bands of all birds encountered.

Estimation of Survival

THE KAPLAN-MEIER ESTIMATOR

We estimated survival (Φ) of radio-tagged kites using a staggered entry design (Pollock et al. 1989) of the Kaplan-Meier product limit estimator (Kaplan and Meier 1958). Detailed descriptions of the estimator and its properties can be found in Kaplan and Meier (1958), Cox and Oakes (1984), Pollock et al. (1989a), and White and Garrott (1990); formulae are provided in Appendix 3-2.

This estimator is preferred to other estimators because (1) no assumptions are required about the hazard function (e.g., constant survival over intervals)(White and Garrott 1990), (2) the estimator allows for staggered entry of radios (i.e., radios can be added to the population at any time)(Pollock et al. 1989), and (3) the estimator allows censoring (i.e., radio failure or loss)(White and Garrott 1990). We used an arbitrary starting date of 15 April for our survival estimates. At this time we had a reasonable sample (n = 16 during our 1st year) to allow estimation of survival. Birds captured after 15 April were included in the analysis in accordance with the staggered entry procedures described by Pollock et al. (1989) and annual survival each year was estimated from April 15 to April 14. All calculations were conducted in SAS (SAS Inc. 1988) using variations (for our specific data) of the program provided in White and Garrott (1990).

Comparison among groups-- For comparison among survivorship curves generated by the Kaplan-Meier estimator we used the log-rank tests (Savage 1956, Cox and Oakes 1984). For a log-rank test, each time step is treated as a 2 x 2 contingency table. Detailed descriptions of the test and corresponding formulae are provided in Appendix 3-3. While alternative tests are possible, the log-rank test is easily generalized to the staggered entry design (Pollock et al. 1989). Cox and Oakes (1984) describe three variations of the log-rank test based on slightly different procedures for estimating the variance for the number of deaths (d_{ij}). The tests differ slightly in their Type I error rate and corresponding power. Unless otherwise stated, we have reported only the results from the most conservative test (i.e., less likely to make a Type I error, but having lower power). However, when the significance levels were questionable (i.e., at or near $\alpha=0.05$) we reported all three test results for comparison. All of the variations assume conditional independence and asymptotic normality of d_{ij} (Cox and Oakes 1984, Pollock et al. 1989, White and Garrott 1990).

THE CORMACK-JOLLY-SEBER MODEL

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 an extremely flexible unified framework capable of handling a variety of models ranging from simple to complex models of survival including effects of individual characteristics (e.g., age and sex), environmental variables (e.g., weather), and the ability to incorporate transition probabilities and multiple states (e.g., exchange among geographically stratified populations)(Lebreton et al. 1992, Nichols 1992, Brownie et al. 1993, Nichols et al. 1993). This increased flexibility has shifted the emphasis of CJS models from primarily parameter estimation to a powerful tool for testing biological hypothesis about the life history parameters being estimated (Lebreton et al. 1992, Nichols 1992).

Unlike radio telemetry data, where survival is estimated on a relatively continuous-time basis (estimation is discrete at the interval of obtaining radio locations), survival from banding data is estimated for discrete time intervals, which are usually yearly. Our capture and resighting period corresponded with the peak time of fledging (March-June). Thus, survival estimates are not strictly annual, but rather can be roughly interpreted as survival from one breeding season to the next, regardless of whether a given animal was breeding.

The basic probabilistic framework for estimating survival lies in the estimation of two parameters. Let Φ_i denote the probability that an animal is alive and in the population at time $t + 1$ given that the animal was alive at time t, and let p_i denote the probability that an animal alive and in the population at time t is seen (i.e., recaptured or resighted). As such, the probabilities of survival (Φ_i) for each sampling occasion (for this study each occasion equals 1 year) can be described (Fig. 3-2). Unfortunately, without radio telemetry, we usually do not know if an animal survived over an interval; we only know whether or not it was observed. We summarize this knowledge in the form of capture (resighting) histories for each individual marked during the study (Fig. 3-3). For example, a capture history of {1 1 1} indicates that an animal was seen on each of 3 occasions for a 3-occasion study. Similarly, a capture history of {1 0 1} represents an animal that was seen on occasions 1 and 3, but not seen on occasion 2.

We can then represent each capture history in the form of a probablistic model using the parameters Φ and p (Table 3-1). From this probabilistic framework, parameters were estimated using maximum likelihood estimation. Maximum likelihood estimates (MLE) in the

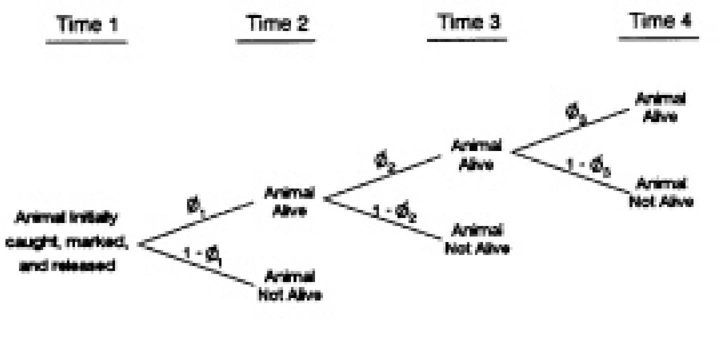


Figure 3-2. The probabilistic framework for estimating survival over 4 time periods. Adapted from Nichols (1992).

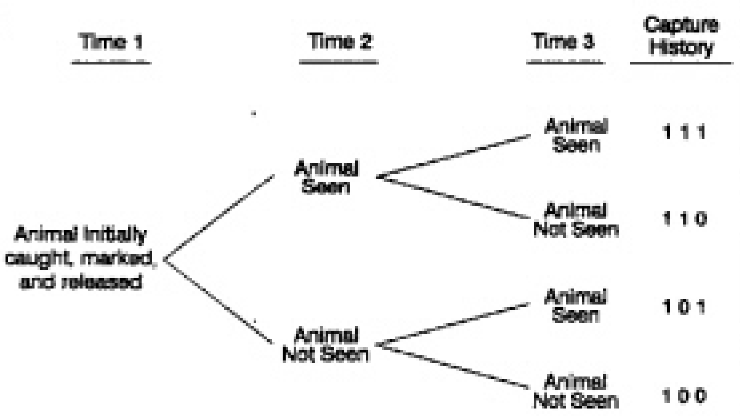


Figure 3-3. Diagram of events that result in each of 4 capture histories for animals released at time 1 in a 3-occasion Cormack-Jolly-Seber (CJS) model. Adapted from Nichols (1992).

context of survival analyses are described in considerable detail elsewhere (e.g., White 1983, Brownie et al. 1985, Pollock et al. 1990, Lebreton et al 1992); however, for our purposes, it is important to recognize that an MLE is asymptotically unbiased, normally distributed, and has minimum variance (White 1982, Brownie et al. 1985, Lebreton et al. 1992). These properties make MLE well suited for our purposes compared to other estimators. An additional advantage of MLE is that it enables the resulting models to be evaluated in the context of likelihood-ratio framework for hypothesis testing (White 1983, Lebreton et al. 1992)(see *Likelihood Ratio Tests* below). All parameter estimation of CJS models was conducted in either Program SURVIV (White 1983, White and Garrott 1990) or MSSURVIV (Hines 1994).

Table 3-1. Possible capture histories for animals released at time 1 and coresponding probabilities for a Cormack-Jolly-Seber model with 4 occasions. Capture histories and probabilities for animals released at times 2 and 3 of this model are not shown..

Capture History	Probability
1111	$\Phi_1 p_2 \Phi_2 p_3 \Phi_3 p_4$
1110	$\Phi_1 p_2 \Phi_2 p_3 (1 - \Phi_3 p_4)$
1101	$\Phi_1 p_2 \Phi_2 (1 - p_3) \Phi_3 p_4$
1100	$\Phi_1 p_2 [1 - \Phi_2 p_3 - \Phi_2 (1 - p_3) \Phi_3 p_2]$
1011	$\Phi_1 (1 - p_2) \Phi_2 p_3 \Phi_3 p_4$
1010	$\Phi_1 (1 - p_2) \Phi_2 p_3 (1 - \Phi_3 p_4)$
1001	$\Phi_1 (1 - p_2) \Phi_2 (1 - p_3) \Phi_3 p_4$
1000	1 - (all terms above)

MEAN LIFE SPAN

We estimated mean life span (MLS) for adults using the estimator introduced by Cormack (1964):

$$MLS_{ad} = -\frac{1}{ln(\hat{\Phi}_{ad})}$$

This approach assumes constant survival among years (Cormack 1964); however, when the above estimator is considered as an approximation, Brownie et al. (1985) suggest that this estimate is useful when computed from mean annual survival ($\hat{\bar{\Phi}}_s$). Our data also do not indicate a violation of the assumption of constancy for adults. Our data do indicate that juvenile survival is lower than adults for approximately the first 100 days post fledging after which it is similar to adult survival. Thus, our estimate of adult MLS$_{ad}$ is applicable to birds conditional upon their survival of the first 100 days. It has also been suggested by numerous authors (e.g., Sykes 1979, Beissinger 1986, Rodgers et al. 1988, Snyder et al. 1989a) that there is increased mortality associated with droughts. Beissinger (1995) estimated adult survival during droughts to be 0.60. This was based on the average difference in the annual count for drought years after 1973 (Beissinger 1995)(but see discussion in *Monitoring Snail Kite Populations in Florida*). Based on ancillary evidence (e.g., band sightings from known-age birds), we believe Beissinger's survival estimate for drought years is substantially low. To our knowledge, no reliable data exist for estimating survival during droughts (although we have a mark-resighting program in place to derive such estimates when future droughts occur). Consequently, we estimated MLS using a range of hypothesized estimates for drought-year survival ranging from Beissinger's (1995) estimate of 0.60 to estimates that we believe are more reasonable. Beissinger (1995) also suggested that survival in lag years (i.e., one-year after a drought) was 0.90 based on radio telemetry of eight adult Snail Kites that were radioed during the 1981 drought (7 of 8 survived and the fate of the other was unknown)(Snyder et al. 1989a, 1989b). We are unclear as to what extent this estimate applies to lag years versus drought years (the radios were attached in May and June when water levels were lowest) and the actual survival of these birds was $0.885 < \Phi < 1.00$. However, for lack of a better estimate, we also included this estimate as a hypothesized value for lag years.

Brownie et al. (1985) derived an analogous estimator for the expected life time $E(T)$ of juveniles as:

$$E(T)_{juv} = \frac{1}{-ln(\Phi_{juv})} + \frac{\Phi_{juv}}{-ln(\Phi_{ad})} + \frac{\Phi_{juv}}{-ln(\Phi_{juv})}$$

Thus, for our application this estimates the expected life time of a juvenile conditional upon it surviving to fledging (i.e., when birds are banded). It includes the first 100 days post fledging, but does not include the pre-fledging nestling period.

Estimation of Natal Dispersal of Juveniles

Natal dispersal of birds has been defined as the dispersal of juveniles from their natal site to the site of their first reproduction or potential reproduction (Greenwood and Harvey 1982). Unlike most species for which natal dispersal has been described, Snail Kites exhibit nomadic tendencies and may breed colonially or solitarily throughout their range (Sykes et al. 1995). Consequently, the assessment of whether or not a site is a potential breeding site is rather ambiguous. Thus, for the purposes of this study, we have defined natal dispersal as the initial dispersal of a bird from its natal wetland regardless of whether or not there was potential for breeding at the site to which it dispersed.

We estimated the cumulative probability of natal dispersal of radio-transmitted birds using the Kaplan-Meier product-limit estimator (see above). For this analysis, a juvenile was considered to have dispersed when it was located alive outside its natal wetland. The time of dispersal was estimated as the midpoint between its previous location (in its natal wetland) and the first location outside of its natal wetland. This analysis only relates to the initial dispersal from its natal wetland. Any movements subsequent to initial dispersal were ignored for this analysis, but were included in our estimation of movement probabilities (below). Birds were censored if either we were unable to locate their radio signal or if they were known to have died prior to dispersal from their natal area. For clarity, we report these results as the complement of our estimate (the actual estimate is the probability of not dispersing). Log-rank tests were used for comparisons among dispersal functions.

Estimation of Movement Probabilities

We estimated the conditional probability of radio-transmittered kites moving (ψ) or staying ($1 - \psi$) at a given location j over a finite time period t to $t + 1$ (one month) as a simple binomial parameter, conditional upon the animal being alive and its location known at t and $t + 1$ (Appendix 3-4). A one-month time interval was based on our sampling frequencies. Although the average time between consecutive locations was 13.5 days (our targeted interval was 14 d), there was considerable variability in this parameter. We estimated the upper limit of a 95% confidence interval for the time between locations as 29 days. Thus, we were reasonably certain to have located all birds within our study area every 29 days. For the ease of interpreting our results we used calendar months as the time step for these analyses.

There were alternative approaches to estimating movement probabilities that did not rely upon a fixed time interval (i.e., variations of the Kaplan Meier); however we chose a fixed time interval because it allows more straightforward interpretations of our results. The estimates derived from a variable-time estimator would have been confusing because each estimate would be associated with a different length of time. One problem with using a fixed time interval is that some birds may have moved more than once during our interval. However, this problem is inherent in our data regardless of what analysis approach was used because our sampling of radio locations was not continuous.

Model Selection as a Basis for Data Analysis

ANALYSIS PHILOSOPHY

Although the philosophy and statistical methods we used for much of our data analysis have become increasingly more common in ecological literature and are described in considerable detail elsewhere (e.g., Burnham and Anderson 1992, Lebreton et al. 1992, Brownie et al. 1993, Nichols et al. 1993, Anderson et al. 1994, Spendelow et al. 1995), some of the statistical tools we used may not be familiar to some readers. Consequently, we present a brief general discussion of our approach. A critical concept to our approach to data analysis is that a given amount of data will support only limited inference (Burnham and Anderson 1992). Given that premise, we treat data analysis as a problem of optimization, rather than strict elimination of alternative hypotheses based on arbitrary criteria (e.g., α level). We also recognize that data often will suggest more than one model as being appropriate (McCullagh and Nelder 1989), and that we must integrate biological common sense into our statistical inference.

The Principle of Parsimony-- We use the principle of parsimony as a basis for model selection. We begin with the recognition that all models are wrong (McCullagh and Nelder 1989). Given this recognition, our goal is to be able to make generalizations about the system we are trying to model that are supportable by the data. If we incorporate all possible effects (including their interactions) into our model, we will have the best fit of the data. The problem is that we will not have learned anything. As the number of parameters in a model is increased, the fit of the model to data will improve. The cost, however, for increasing the number of parameters in a model is that precision of the parameter estimates decreases (i.e., the confidence intervals increase)(Burnham and Anderson 1992, Lebreton et al. 1992)(Fig. 3-4). Thus, the goal of our analysis is to find a good balance between having enough parameters in the model to adequately describe the underlying patterns, but not so many so as to defeat the purpose of making generalizations. Thus, a parsimonious model is one which retains only those parameters that are warranted (judged using the tools such as likelihood ratio tests and Akaike's Information Criterion [AIC] described below) and eliminates excessive parameters (Lebreton et al. 1992).

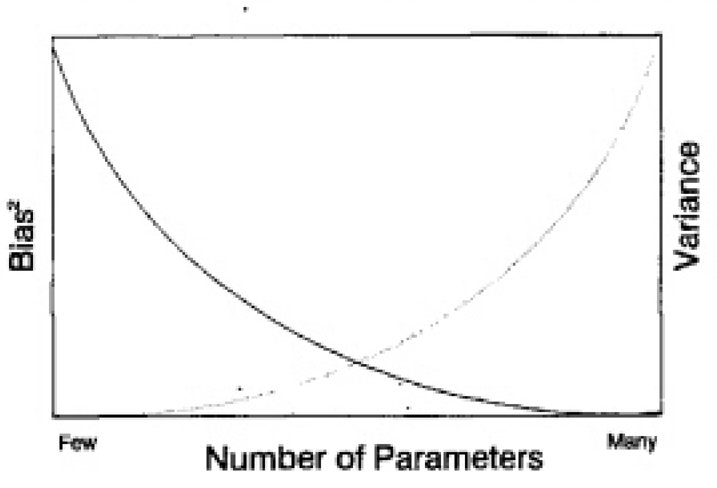


Figure 3-4. Conceptual tradeoff between precision (low variance)(dotted line) and bias (solid line) as a function of the number of parameters in a model (After Burnham and Anderson 1992).

Starting Point-- Whenever possible, we tried to evaluate a full spectrum of models. However, in some cases the number of parameters in more saturated models (i.e., with many main effects and interactions) was prohibitively large (e.g., >200). These more complex models also usually contained some parameters that were not identifiable or estimable (see discussion in parameter identifiability in Lebreton et al. 1992). Consequently, when we were unable to evaluate a full suite of models, we used the starting procedures described by Hosmer and Lemeshow (1989). Their approach begins with a univariate assessment of each main effect. Effects that are significant at a liberal $\alpha=0.25$ are retained for further evaluation. This liberal rejection criterion retains main effects that may have an influence in an interaction that might have been masked during initial tests. The next step was to evaluate a multivariate model with all of the retained main effects, but lacking interactions. Effects that were retained at this stage were further evaluated including their interaction effects. This approach enabled us to reduce the parameter space for more complex models down to a more manageable level, while retaining the integrity of the analysis.

THE LIKELIHOOD RATIO TEST

One of the advantages of maximum likelihood estimation (MLE) is that it enables a likelihood ratio testing framework. Likelihood ratio tests (LRT) allow testing hypotheses about whether the addition of parameters to a model significantly improves the fit of that model. The test statistic is:

$$-2ln\,\frac{(\mathcal{L}_1)}{(\mathcal{L}_2)} = -2\,[ln(\mathcal{L}_1) - ln(\mathcal{L}_2)]$$

where $\mathcal{L}$ is the likelihood for a given model evaluated at its maximum, and is distributed as χ^2 with $np_1 - np_2$ degrees of freedom, where np is the number of estimable parameters. The null hypothesis (H_0) is that the reduced model (i.e., the model with fewer parameters) fits equally well as the more general model (i.e., the model with more parameters). Thus, a failure to reject H_0 indicates that the additional parameters of the more general model are not warranted. A limitation of LRTs is that they are limited to pairwise comparisons and that the models being compared must be nested (i.e., one is a reduced subset of the other). Consequently, for non-nested models and for multiple comparisons we used Akaike's Information Criteria (AIC)(below) to compare models.

AKAIKE'S INFORMATION CRITERION

In contrast to using a LRT for hypothesis testing, where the intent (in the context used for our analysis) is to test whether the addition of a particular parameter(s) improves the fit of a model, the use of Akaike's

Information Criterion (AIC)(Akaike 1973, Sakamoto et al. 1986, Shibata 1989, Anderson et al. 1994) provides a systematic approach to the analysis of complex multidimensional data, and it removes the limitation of nested models required by LRTs (Burnham and Anderson 1992, Lebreton et al. 1992, Anderson et al. 1994).

Akaike's Information Criterion is defined as:

$$-2 \, ln(\mathcal{L}) + 2np$$

where $\ln(\mathcal{L})$ is the log-likelihood function evaluated at the maximum likelihood estimates (Akaike 1973). The first term of AIC (i.e., -2 $ln(\mathcal{L})$, called the relative deviance (Lebreton et al. 1992), is a measure of goodness-of-fit of the model and the second term (i.e., $2np$) can be viewed as a cost for adding excessive parameters (Lebreton et al. 1992). The properties and benefits of using AIC as a model selection tool have been extensively documented (Shibata 1989, Burnham and Anderson 1992, Anderson et al. 1994, Burnham et al. 1994).

We emphasize that the notion of finding one "true" model for complex biological data is unlikely, and often more than one model may be indicated as being appropriate for a given data set (Burnham and Anderson 1992). Anderson et al. (1994) suggest viewing model selection in the analogous context of confidence intervals, rather than point estimation, such that the selection process often indicates a range of models that are appropriate, rather than a single model. Thus, as the differences in AIC become smaller, so does the statistical basis for distinguishing among alternative models (Burnham and Anderson 1992). Sakamoto et al. (1986) suggests that AIC differences of >1-2 should be considered as statistically significant. Models within this range were consequently judged not to be more or less suitable based on AIC criteria alone.

ESTIMATING POWER

In the context of hypothesis testing, the results of a given statistical test can have only one of four possible outcomes with respect to "truth"; two that are correct (i.e., are consistent with truth) and two that are erroneous (Table 3-2). The Type I error rate (i.e., α) is reported as a standard protocol for reporting the outcome of statistical tests. Unfortunately, the Type II error rate (i.e., β) is often overlooked.

Table 3-2. Four outcomes with respect to truth of the null hypothesis H_o and their corresponding errors (After White et al. 1982).

Decision Based on Test Statistic	H_o True	H_o False
Reject H_o	Type I Error (α)	No Error
Fail to Reject H_o	No Error	Type II Error (β)

Power is defined as 1 - β, or the probability of not committing a Type II error. Estimation of power requires specifying the Type I error rate (α) and an alternative hypothesis (H_a) to the null hypothesis (H_o). We have attempted to report power for tests where we fail to reject a specified alternative hypothesis. If otherwise unspecified, all Type I error rates for power estimation were $\alpha = 0.05$. In most cases we have used more than one alternative hypothesis H_a and express these hypotheses in the form of a systematic departure (Δ) from the null hypothesis H_o, so that we may evaluate power over a range of hypothesized differences. We usually express these alternative hypotheses as:

$$H_a(\theta) = \Delta * \theta$$

where θ is a given parameter (e.g., survival or movement probability), and Δ is the departure from H_o imposed on that parameter. For example, if $\theta=0.8$ under our null hypothesis and $\Delta = 0.95$, then θ under our alternative hypothesis would be $0.95*0.8 = 0.76$

We evaluated the power of a given test by simulating an effect on the actual data (Lebreton et al. 1992). We generated expected count data under an alternative model H_a (as above) that included the differences (Δ) we intended to evaluate. These expected values were then analyzed as if they were real data (Drost et al. 1989, Lebreton et al. 1992). The resulting test statistic asymptotically has a non-central chi-square distribution and can be used to approximate the non-centrality parameter for an alternative hypothesis H_a to the null hypothesis H_o of no effect. The *probchi* function (SAS Inc. 1988) enables us to then estimate β (i.e., the Type II error rate) using this non-centrality parameter for a specified α (in this case α=0.05). Power is then estimated as 1 - β.

LOGISTIC REGRESSION AND LOG-LINEAR MODELS

For some analyses of the influences of survival and movement probabilities, we used a conditional logistic regression or log-linear models based on one month time intervals (see discussion of time interval under *Estimation of Movement Probabilities*). We used logistic regression in cases where there was a binary response variable (i.e., survival or movement)(Cox 1970, Cox and Oakes 1984, Hosmer and Lemeshow 1989). Because individual animals can move more than once, we are assuming conditional independence (e.g., that the probability of moving between times t and $t + 1$ is not dependent on whether that animal moved during the previous interval).

We used log-linear models for cases where there was no designated response variable, but rather, for exploration of interactions in multi-way cross tabulation (e.g., the probabilities of movements between specific locations)(Agresti 1990, Everitt 1992). We used MLE for the parameter estimation from both logistic and log-linear models (SAS inc. 1988) and consequently, could apply all of the model selection tools described above.

THE ANALYSIS OF RESIDUALS FROM CROSS-CLASSIFICATION MODELS

In some cases in our analysis of cross-classified models (e.g., contingency tables or log linear analyses) we make use of the residuals for exploring the contributions of individual cells to the overall test significance. We do not use this approach in a hypothesis testing or model selection capacity as described for LRTs or AIC; but rather, to further describe patterns already detected in our analysis. This is often done informally by inspection of deviations from expected values. A problem, however, with this approach is that a fixed deviation does not have the same importance across all sample sizes (Everitt 1992). Consequently we used standardized residuals (Agresti 1990, Everitt 1992) for evaluating the contribution of individual cells to the overall model significance from models in which the expected values were derived from an a priori hypothesis. Where expected values were derived from the marginal totals, we evaluated cell contributions using adjusted residuals (Haberman 1973). Adjusted residuals are normally distributed with a mean of zero and a standard deviation of one such that a residual of 1.96 corresponds with an α of 0.05.

MULTIPLE COMPARISONS

Throughout this report we have conducted numerous statistical analyses, often involving multiple comparisons of the same parameter. Multiple comparisons can result in an inflated alpha (α) level (Day and Quinn 1989, Fowler 1990); however, the complexity of many of our analyses would enable several approaches to correct for this inflation. Consequently, unless otherwise stated, we did not attempt to adjust the α level. Thus, the reader is cautioned to consider the number of multiple comparisons when interpreting our results.

Chapter 4. SURVIVAL AND MORTALITY

Longevity

Sykes (1979) observed known-age birds in Florida that were 7.2-8.8 years old. He suggested that the maximum life span of kites in the wild is probably at least 10 years. Beissinger (1986) later reported known-age birds of 10-13 years. Snail Kites from South America (*Rostrhamus sociabilis sociabilis*) have lived and been capable of reproduction in captivity to 15 years (G. Gee, National Biological Service, Patuxent Environmental Science Center, pers. comm.). Our observations suggest that Snail Kites in the wild are capable of living (and breeding) until at least 18 years of age and may commonly live 13-15 years. In 1993 we captured one bird that was banded as a juvenile by Paul Sykes in 1976. This bird successfully raised one brood at 17 years old and may have made a second nesting attempt that year. The bird was observed again at a nest with eggs during 1994. Thus, Snail Kites in the wild are capable of living and breeding to at least 18 years. In addition to this bird, we captured another bird in 1993 (also nesting) that was banded as a juvenile in 1978 by Noel Snyder. We read the USFWS bands of two other birds banded that same year. These birds were each 15 years old at the time of observation. We also observed several birds (=10) that had plastic color bands of a type not used since 1978. We were unable to read the USFWS band and, consequently, could not determine their exact age due to the potential of band loss and fading of colors. However, these birds had to be ≥15 years old. We also observed an additional 23 individual kites that were banded by Noel Snyder and Steve Beissinger in 1979. These birds had numbered PVC bands that enabled individual recognition without having to read the USFWS band (Snyder et al. 1989a). Given that our CJS models indicated that the probability of resighting a bird in any given year was low (overall $\hat{p} \approx 0.21$), there probably were several other birds from the 1979 cohort that were still alive but were undetected.

Table 4-1. Mean life span (MLS) for adult Snail Kites and expected life time E(T) for juvenile Snail Kites; given estimated parameter values for adult (ad) and juvenile (juv) survival (Φ) during high water and hypothesized parameter values for the drought interval (years), Φ_{ad} (drought), and Φ_{ad} (lag year).

Hypothesized Drought Interval	$\hat{\Phi}_{ad}$ (High Water)	Hypothesized Φ_{ad} (Drought)	Hypothesized Φ_{ad} (Lag Year)	$\hat{\Phi}_{juv}$	MLS_{ad}	$E(T)_{juv}$
5	0.91	0.6	0.9	0.58	6.0	4.2
5	0.91	0.7	0.9	0.58	7.0	4.8
5	0.91	0.8	0.9	0.58	8.3	5.6
5	0.91	0.9	0.9	0.58	10.1	6.6
6	0.91	0.6	0.9	0.58	6.5	4.5
6	0.91	0.7	0.9	0.58	7.4	5.1
6	0.91	0.8	0.9	0.58	8.6	5.7
6	0.91	0.9	0.9	0.58	10.2	6.7
7	0.91	0.6	0.9	0.58	6.9	4.7
7	0.91	0.7	0.9	0.58	7.7	5.3
7	0.91	0.8	0.9	0.58	8.8	5.9
7	0.91	0.9	0.9	0.58	10.3	6.7

Mean Life Span (MLS)

Beissinger (1986) suggested that the average adult life span of Snail Kites in the wild is 5-8 years. This suggestion was based on presumed mortality associated with droughts, based on differences in consecutive counts from the annual Snail Kite survey.

Our results, based on Cormack's (1964) estimator, suggests that, given a bird has survived 100 days post-fledging, mean life span (MLS) for adults ranges from 6.0 to 10.3 years (depending on the assumptions made about drought intervals and survival during droughts), and the expected life time *E*(*T*), based on the estimator of Brownie et al. (1985), for a newly-fledged juvenile ranges from 4.2 to 6.7 years (Table 4-1). Improvements on these estimates should be possible as data on drought-year and lag-year survival become available (a monitoring program is in place to obtain these data, provided that funding is available to maintain this effort). These estimates also do not take into account the potential for senescence (i.e., declines in survival rates as age increases).

Estimation of Survival from Radio Telemetry

We attached a total of 282 radio transmitters, representing 271 individual Snail Kites with 11 birds having been recaptured in a subsequent year and their radios replaced. We were slightly short (82%) of our targeted sample size of 100 birds during 1992 (Table 4-2); but fully attained our targeted sample sizes in 1993 (Table 4-3) and 1994 (Table 4-4). We were very close to our targets of age and sex ratios of our sample. The overall age distribution of our sample was 59% (165 of 282) adults and 39% (117 of 282) juveniles; our target was 60% adults and 40% juveniles. We had a total of 82 males (49.7%) and 83 females (50.3%); our target was 50% of each. We had a few minor discrepancies between the distribution of our samples each year and the preceding annual counts; however, most of these resulted from shifts in the distribution of birds, rather than an inability to sample from particular areas.

Table 4-2. The number of snail kites captured during 1992 and equipped with radio transmitters at each location of each age class and sex.

Location	Adult	Juvenile	Male[1]	Female[1]	Total 1992 Sample	% of Sample	% of 1991 Count[2]
WCA-2A	2	7	0	2	9	12	4
WCA-2B	1	0	1	0	1	1	3
WCA-3A	2	0	1	1	2	2	1
Holey Land W.M.A.	1	1	1	0	2	2	0
Loxahatchee Slough	2	2	1	1	4	5	7
Lake Okeechobee	19	14	12	8	34	41	40
Lake Kissimmee	7	0	5	2	7	9	13
Lake Tohopekaliga	3	7	1	2	10	12	1
St Johns Marsh	7	6	2	5	13	16	22
Total	45	37	24	21	82	100	91[3]

[1] *Applies to adults only, juveniles cannot readily be sexed in the field*
[2] *Percentage of kites in each area based on the 1992 annual survey*
[3] *Some peripheral areas included in the annual count were not sampled due to absence of birds at time of sampling.*

Table 4-3. The number of snail kites captured during 1993 and equipped with radio transmitters at each location of each age class and sex.

Location	Adult	Juvenile	Male[1]	Female[1]	Total 1993 Sample	% of Sample	% of 1992 Count[2]
Everglades N.P.[3]	0	2	0	0	2	2	9
WCA-2A	5	2	3	2	7	7	6
WCA-2B	1	1	0	1	2	2	0
WCA-3A	6	9	4	2	15	15	15
WCA-3B	2	2	1	1	4	4	2
Holey Land W.M.A.	2	1	0	2	3	3	2
Loxahatchee Slough	7	2	1	6	9	9	2
Lake Okeechobee	20	11	10	10	31	31	29
Lake Kissimmee	10	3	7	3	13	13	5
Lake Tohopekaliga	2	0	0	2	2	2	3
E. Lake Tohopekaliga	1	2	0	1	3	3	1
St. Johns Marsh	4	5	4	0	9	9	11
Total	60	40	30	30	100	100	85[4]

[1] *Applies to adults only, juveniles cannot readily be sexed in the field*
[2] *Percentage of kites in each area based on the 1992 annual survey*
[3] *Including the North East Shark River Slough addition lands.*
[4] *Some peripheral areas included in the annual count were not sampled due to absence of birds at time of sampling.*

Table 4-4. The number of snail kites captured during 1994 and equipped with radio transmitters at each location of each age class and sex.

Location	Adult	Juvenile	Male[1]	Female[1]	Total 1994 Sample	% of Sample	% of 1993 Count[2]
Everglades N.P.[3]	0	1	0	0	1	1	3
Loxahatchee N.W.R.	0	1	0	0	1	1	0
WCA-2A	0	0	0	0	0	0	0
WCA-2B	18	10	8	10	28	28	4
WCA-3A	11	11	4	7	22	22	41
WCA-3B	2	0	1	1	2	2	12
Lake Jackson	1	1	0	1	2	2	0
Loxahatchee Slough	0	0	0	0	0	0	4
Lake Okeechobee	10	4	5	5	14	14	13
Lake Kissimmee	9	6	5	4	15	15	5
Lake Tohopekaliga	4	1	1	3	5	5	0
E. Lake Tohopekaliga	2	4	2	0	6	6	3
St. Johns Marsh	3	1	2	1	4	4	1
Total	60	40	28	32	100	100	86[4]

[1] *Applies to adults only, juveniles cannot readily be sexed in the field*

[2] *Percentage of kites in each area based on the 1992 annual survey*

[3] *Including the North East Shark River Slough addition lands.*

[4] *Some peripheral areas included in the annual count were not sampled due to absence of birds at time of sampling.*

EFFECTS OF AGE ON SURVIVAL

Our estimates of survival for adults were generally higher than for juveniles in each year of this study (Fig. 4-1)(Appendix 4-1). Based on log-rank statistics, adult and juvenile survival estimates differed for study years (SY) 1992 and 1994, but not in SY 1993 (Table 4-5). In both years where they differed, estimates of adult survival were higher than estimates of juvenile survival (Table 4-6). However, in 1993 estimates of juvenile survival were slightly (but not significantly, $P = 0.869$) higher than adult survival. Ancillary evidence suggests that our estimates for juvenile survival during 1992 and 1993 were biased high (see discussion of *Assumptions, Bias, and Sources of Error*). Our data from banding (i.e., mark-resighting) also indicates an age effect on survival (below). Consequently, we believe that real differences exist between adult and juvenile survival and that differences were underestimated for 1992 and 1993.

Table 4-5. Results of log-rank tests between survivorship functions of adult and juvenile Snail Kites during each study year (April 15 - April 14).

Year	χ^2	df	Prob
1992	4.611	1	0.032
1993	0.027	1	0.869
1994	29.520	1	<0.001

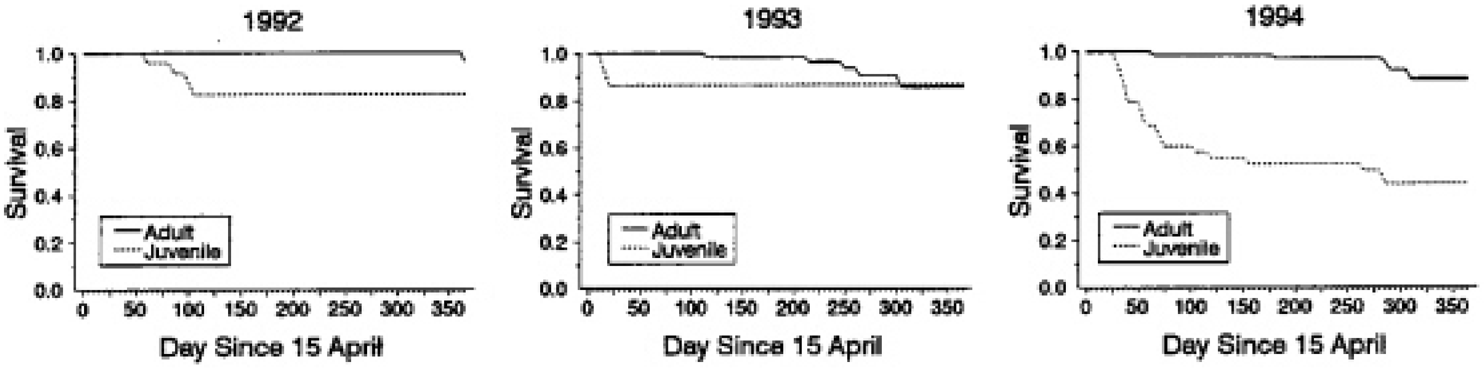


Figure 4-1. Estimates of survivorship functions of radio-transmittered adult and juvenile Snail Kites during study year (SY) 1992, 1993, and 1994. Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 4-1.

Table 4-6. Annual survival estimates ($\hat{\Phi}$) for adult and juvenile Snail Kites for 1992, 1993, and 1994. Survival is estimated from 15 April to 14 April (e.g., $\hat{\Phi}$ for 1992 is estimated from 15 April, 1992 to 14 April, 1993). Estimates are derived from Kaplan Meier estimator.

Age Class	Year	$\hat{\Phi}$	SE($\hat{\Phi}$)	95% CI($\hat{\Phi}$)
Adult	1992	0.962	0.038	0.888 - 1.000
Adult	1993	0.858	0.063	0.734 - 0.982
Adult	1994	0.883	0.042	0.801 - 0.965
Juvenile	1992	0.825	0.080	0.668 - 0.981
Juvenile	1993	0.867	0.088	0.695 - 1.000
Juvenile	1994	0.439	0.090	0.263 - 0.615

EFFECTS OF SEX ON SURVIVAL

In contrast to age, survivorship functions did not differ between adult male and female kites at $\alpha = 0.05$ (Table 4-7); although there was a slight divergence (significant at $\alpha = 0.1$) in these functions during SY 1994 (Fig. 4-2)(Appendix 4-2). We were unable to determine the sex of juveniles in the field and consequently have no information regarding survival differences between sexes for this age class.

TEMPORAL EFFECTS OF SURVIVAL

Annual Effects-- Our estimates of survivorship functions of adult Snail Kites did not differ among years at $\alpha = 0.05$; although, SY 1992 differed from SY 1993 at $\alpha = 0.10$ (Fig. 4-3)(Table 4-8). In contrast, our estimates of survivorship of juveniles during SY 1994 differed from both SY 1992 and SY 1993 (Table 4-9).

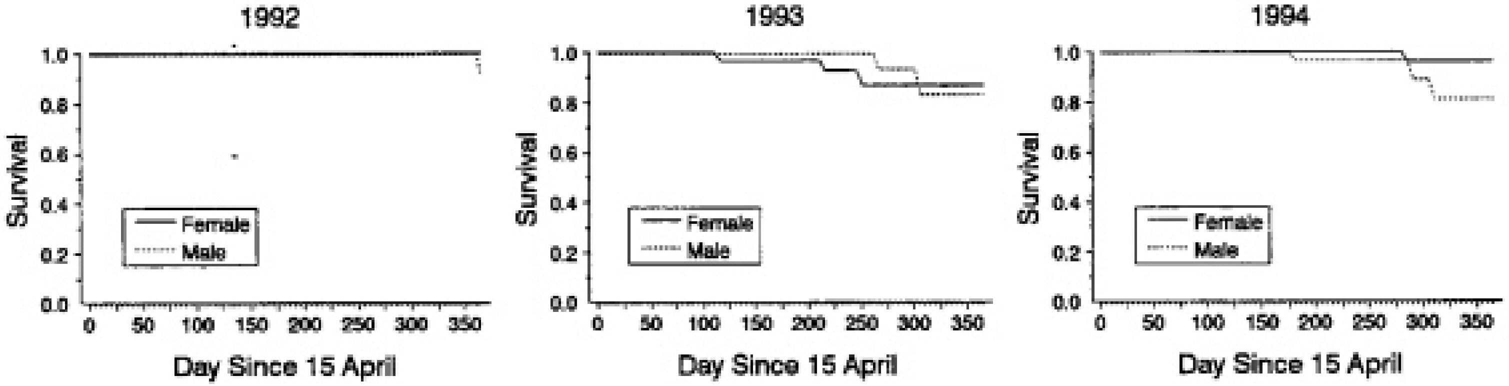


Figure 4-2. Estimates of survivorship functions of radio-transmittered adult male and female Snail Kites during study years (SY) 1992, 1993, and 1994. Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 4-2.

Table 4-7. Results of log-rank tests between survivorship functions of adult female and male Snail Kites during each study year (April 15 - April 14).

Year	χ^2	df	Prob
1992	1.667	1	0.280
1993	0.243	1	0.622
1994	2.753	1	0.097[1]

[1] *Using the altenative tests described by Cox and Oakes (1984)(Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated* $\chi^2=2.77$, $P=0.095$ *and* $\chi^2=2.75$, $P=0.097$ *for alternative tests 1 and 2, respectively.*

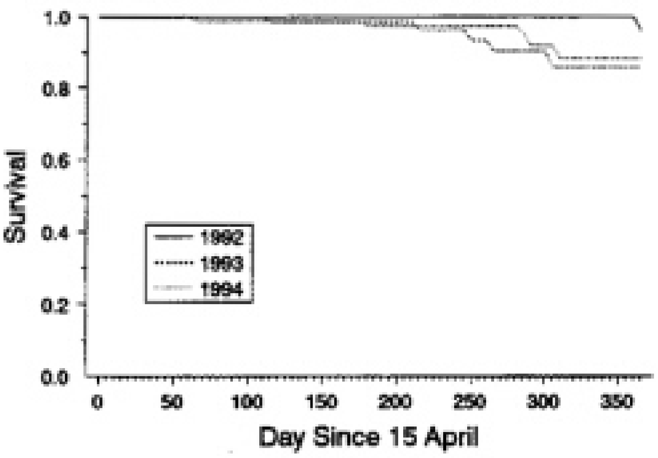


Figure 4-3. Kaplan-Meier estimates of survivorship functions of radio-transmittered adult Snail Kites during each study year (SY). Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 4-1.

Table 4-8. Results of log-rank tests between survivorship functions of adult Snail Kites during each study year (SY)(April 15-April 14).

Comparison	χ^2	df	Prob
1992 vs. 1993	2.836	1	0.092[1]
1992 vs. 1994	1.762	1	0.184
1993 vs. 1994	0.480	1	0.486

[1] *Using the altenative tests described by Cox and Oakes (1984) (Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated* $\chi^2=2.93$, $P=0.087$ *for both tests.*

Survival estimates for juveniles during SYs 1992 and 1993 were very similar, but were markedly higher than the estimate for 1994 (Fig. 4-4) (but see discussion of censoring below in section on *Assumptions, Bias, and Sources of Error*).

Table 4-9. Results of log-rank tests between survivorship functions of juvenile Snail Kites during each study year (SY)(April 15-April 14).

Comparison	χ^2	df	Prob
1992 vs. 1993	1.432	1	0.231
1992 vs. 1994	6.156	1	0.013
1993 vs. 1994	12.412	1	<0.001

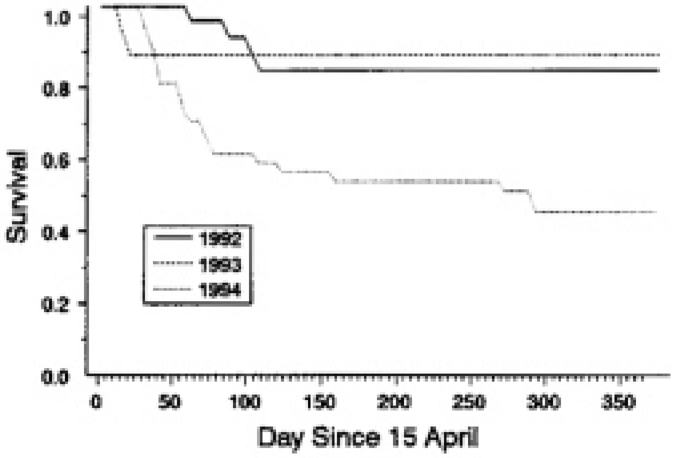


Figure 4-4. Kaplan-Meier estimates of survivorship functions of radio-transmittered juvenile Snail Kites during each study year (SY). Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 4-1.

Seasonal Effects-- It was apparent from survivorship functions that the risk of mortality (i.e., hazard function) was not constant over time. Compared to an expected value for the number of deaths being equal in each month, mortality of adults tended to be highest during the winter months ($\chi^2=18.00$, df=11, P=0.08), and juveniles during late spring and summer ($\chi^2=39.54$, df=11, P<0.001)(Fig. 4-5). The seasonal pattern of juveniles corresponds with the first few months post fledging (Fig. 4-6). Juveniles are becoming independent of their parents, beginning to forage on their own, and disperse into unfamiliar areas. Juveniles that survived the first few months post fledging appeared to be most vulnerable at the same time as peak mortality for adults (i.e., January). It is less clear why adult

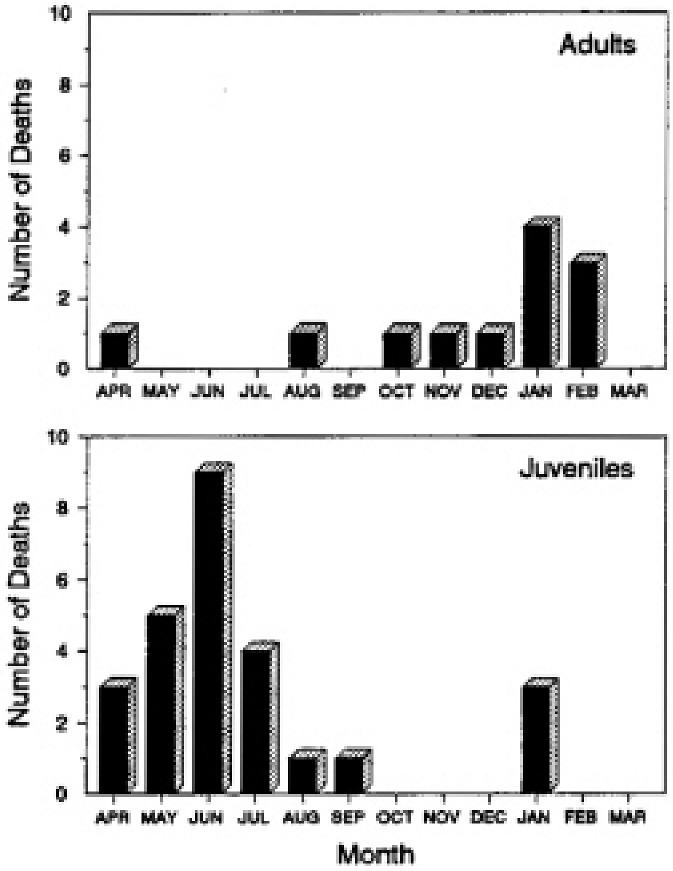


Figure 4-5. The number of radio-transmittered adult and juvenile Snail Kites found dead during each month.

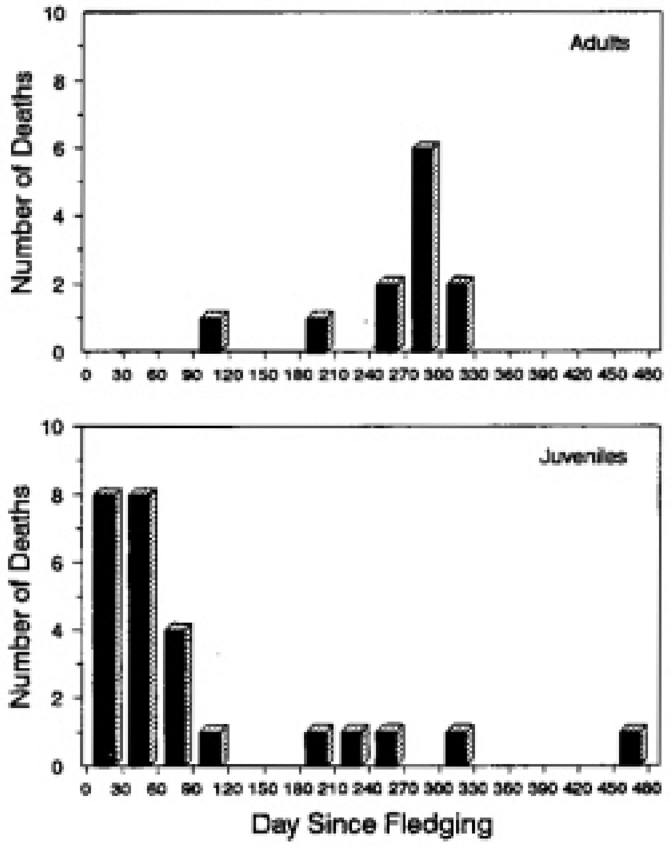


Figure 4-6. The number of radio-transmittered adult and juvenile Snail Kites found dead during each 30-day interval after fledging (juveniles) or capture (adults).

mortality was highest in winter; however, during this time cold temperatures tend to lower the availability of existing food resources (Cary 1983, 1985), and leaves are absent from willows, which is the most commonly used species for communal roosting (Sykes et al. 1995, Darby et al. 1996a). We offer this latter suggestion because predation was the most common cause of death of adults. Ancillary evidence suggests that Great-horned Owls (*Bubo virginianus*), which forage at night, were the most common predator. We emphasize, however, that our suggestions for why adult mortality tended to occur during winter is purely speculative. Other anecdotal evidence (i.e., approximately 6 to 10 birds without radios found dead at nests) suggested that adults can also be vulnerable to owl predation during nesting while incubating at night.

SPATIAL EFFECTS OF SURVIVAL

Regional Effects (By Region of Initial Capture)-- We approached regional differences in survival two ways. First we tested the hypothesis that differences in survival were attributable to differences in the region of initial capture. For this analysis, a bird was assigned to the region of its initial capture, regardless of whether it moved subsequent to capture. For juveniles, the region of capture represents their natal region; however, in most cases we do not know the natal origin of adults or their history of locations prior to capture. Consequently, this hypothesis is biologically more intuitive for juveniles than adults. Differences in survival could reflect several aspects of regional quality (e.g., food abundance).

Overall there were few differences in survival among regions of capture. Survival of adult birds captured in different regions did not differ among any regions during 1992 or 1993 (Table 4-10)(Fig. 4-7). During 1994, adult survival differed between the Everglades and Okeechobee regions and between the Everglades and Kissimmee regions but not among any other pairwise combinations. Juvenile survival differed between the Everglades and Okeechobee regions during 1992, but no other differences were detected in any year (Table 4-11)(Fig. 4-8).

We urge caution in interpreting these results. Partitioning survival into two age classes and five different regions (no animals were captured in the peripheral region) often resulted in the number of animals at risk for a given group (r_{ij}) being small. Although this does not impose bias, it can present misleading appearances (see discussion of small sample size in *Assumptions, Bias, and Sources of Error*).

Table 4-10. Results of pairwise log-rank tests between survivorship functions of adult Snail Kites captured from each region during each study year (SY).

	SY 1992			SY 1993			SY 1994		
Comparison[1]	χ^2	df	Prob	χ^2	df	Prob	χ^2	df	Prob
EVER vs. OKEE	0.650	1	0.420	0.021	1	0.885	5.014	1	0.025
EVER vs. KISS	--[2]	--	--	0.280	1	0.596	6.980	1	0.008
EVER vs. USJ	--[2]	--	--	0.231	1	0.631	--[2]	--	--
EVER vs. LOXSL	--[2]	--	--	0.140	1	0.708	--[2]	--	--
OKEE vs. KISS	0.600	1	0.439	0.229	1	0.632	0.227	1	0.634
OKEE vs. USJ	0.350	1	0.554	0.286	1	0.593	0.403	1	0.525
OKEE vs. LOXSL	0.300	1	0.584	0.230	1	0.631	--[2]	--	--
KISS vs. USJ	--[2]	--	--	0.388	1	0.533	0.621	1	0.431
KISS vs. LOXSL	--[2]	--	--	0.031	1	0.860	0.051	1	0.822
USJ vs. LOXSL	--[2]	--	--	0.333	1	0.563	--[2]	--	--

[1] Regions of comparison are Everglades (EVER), Okeechobee (OKEE), Kissimmee (KISS), Upper St. Johns (USJ), and Loxahatchee Slough (LOXSL).

[2] No deaths occurred of birds from this region during this year; however some sample sizes were quite small (Appendix 4-3).

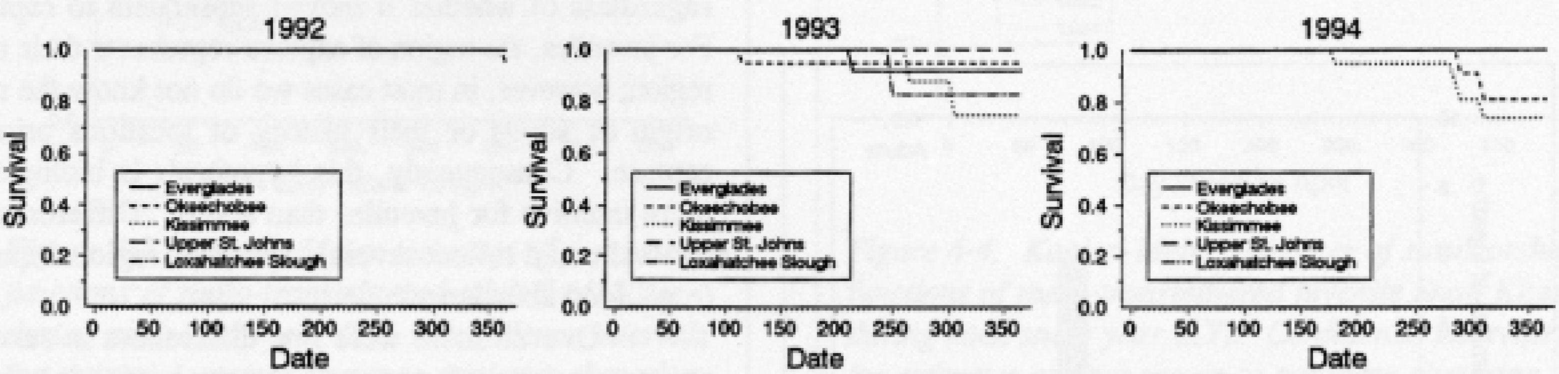


Figure 4-7. Estimates of survivorship functions of radio-transmittered adult Snail Kites that were captured from each region during each study year (SY). Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but can be easily estimated from information in Appendix 4-3.

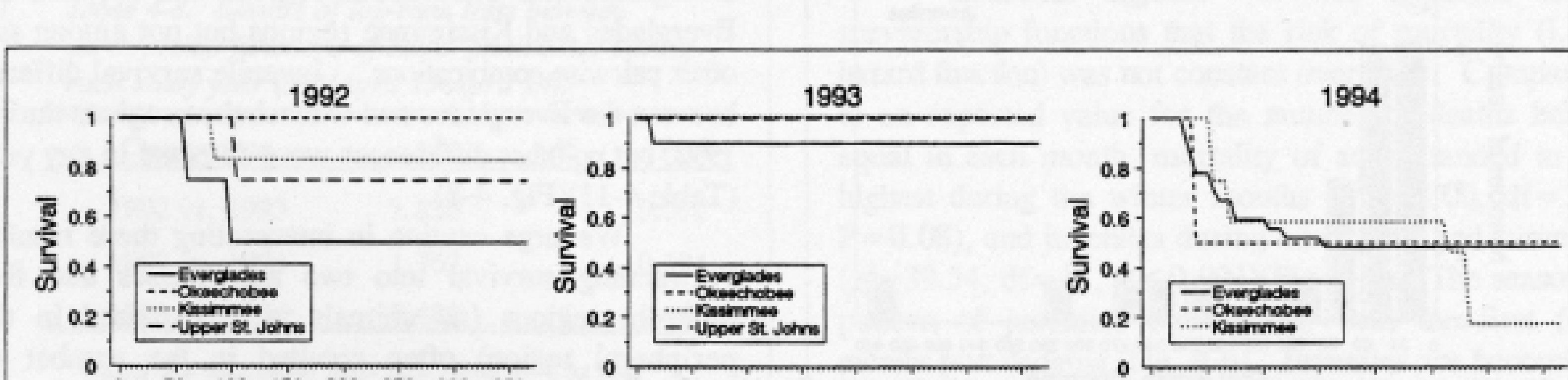


Figure 4-8. Estimates of survivorship functions of radio-transmittered juvenile Snail Kites that fledged from each region during each study year (SY). Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but can be easily estimated from information in Appendix 4-4.

Table 4-11. Results of pairwise log-rank tests between survivorship functions of radio-transmittered juvenile Snail Kites fledged from each region during each study year (SY).

	SY 1992			SY 1993			SY 1994		
Comparison[1]	χ^2	df	Prob	χ^2	df	Prob	χ^2	df	Prob
EVER vs. OKEE	4.582	1	0.032	0.300	1	0.584	0.095	1	0.758
EVER vs. KISS	1.138	1	0.286	--[2]	--	--	1.121	1	0.290
EVER vs. USJ	0.873	1	0.350	--[2]	--	--	--[2]	--	--
EVER vs. LOXSL	--[3]	--	--	--[3]	--	--	--[3]	--	--
OKEE vs. KISS	1.333	1	0.248	--[2]	--	--	0.655	1	0.418
OKEE vs. USJ	1.750	1	0.186	--[2]	--	--	--[3]	--	--
OKEE vs. LOXSL	--[3]	--	--	--[3]	--	--	--[3]	--	--
KISS vs. USJ	0.050	1	0.824	--[2]	--	--	--[3]	--	--
KISS vs. LOXSL	--[3]	--	--	--[3]	--	--	--[3]	--	--
USJ vs. LOXSL	--[3]	--	--	--[3]	--	--	--[3]	--	--

[1] *Regions of comparison are Everglades (EVER), Okeechobee (OKEE), Kissimmee (KISS), Upper St. Johns (USJ), and Loxahatchee Slough (LOXSL).*

[2] *No deaths occurred of birds from this region during this year; however some sample sizes were quite small (Appendix 4-4).*

[3] *There were insufficient data to estimate survival and to conduct corresponding log-rank test.*

Regional Effects (By Region of Current Location)-- The second approach we used for regional differences in survival reflected actual time spent in each region, rather than just focusing on the region of capture. Thus, we test the hypothesis that the survival of a bird is affected by its current location (e.g., predation risk). For this analysis, a bird that moved from a given region to another was censored from the number of animals at risk for that region (r_{ij}) at the midpoint of the interval, and added to the number of animals at risk in the region to which it moved. All deaths were assigned to the region where the dead bird was actually found.

Similar to region of initial capture, there was little indication of regional differences in adult survival. We found no differences during 1992 or 1993 although, as above, the number of birds at risk (r_{ij}) was often low (Fig. 4-9)(Table 4-12). Survival did differ between the Everglades and Okeechobee regions during 1994 at α = 0.05, and between the Everglades and both the Upper St. Johns and Peripheral regions at α = 0.10. We found no significant regional differences for juveniles among any regions during any year (Fig. 4-10)(Table 4-13).

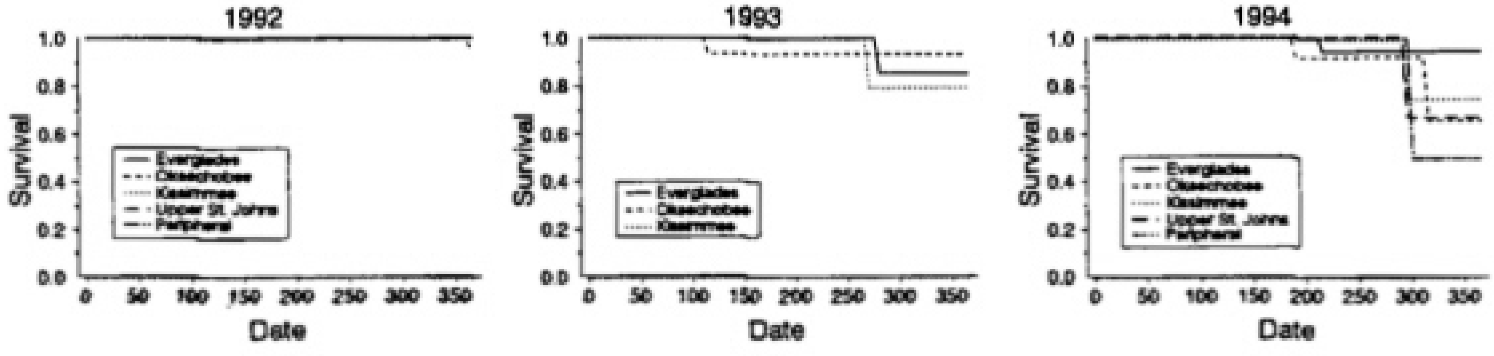


Figure 4-9. Estimates of survivorship functions of radio-transmittered adult Snail Kites while they were present in each region during each study year (SY). Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but can be easily estimated from information in Appendix 4-5.

Table 4-12. Results of pairwise log-rank tests between survivorship functions of radio-transmittered adult Snail Kites while they were present in each region during each study year (SY).

	SY 1992			SY 1993			SY 1994		
Comparison[1]	χ^2	df	Prob	χ^2	df	Prob	χ^2	df	Prob
EVER vs. OKEE	0.545	1	0.460	--[2]	--	--	4.061	1	0.044[3]
EVER vs. KISS	--[2]	--	--	0.377	1	0.539	1.358	1	0.244
EVER vs. USJ	--[2]	--	--	--[4]	--	--	2.842	1	0.092[5]
EVER vs. LOXSL	--[4]	--	--	--[4]	--	--	--[4]	--	--
EVER vs. PERI	--[2]	--	--	--[4]	--	--	2.768	1	0.096[6]
OKEE vs. KISS	0.364	1	0.546	0.1787	1	0.673	0.055	1	0.814
OKEE vs. USJ	0.136	1	0.712	--[2]	--	--	0.035	1	0.851
OKEE vs. LOXSL	--[4]	--	--	--[4]	--	--	--[4]	--	--
OKEE vs. PERI	0.045	1	0.831	--[4]	--	--	0.099	1	0.753
KISS vs. USJ	--[2]	--	--	--[4]	--	--	0.042	1	0.838
KISS vs. LOXSL	--[4]	--	--	--[4]	--	--	--[4]	--	--
KISS vs. PERI	--[2]	--	--	--[4]	--	--	--[2]	--	--
USJ vs. LOXSL	--[4]	--	--	--[4]	--	--	--[4]	--	--
UJS vs. PERI	--[2]	--	--	--[4]	--	--	0.020	1	0.887
LOXSL vs. PERI	--[4]	--	--	--[4]	--	--	--[4]	--	--

[1] *Regions of comparison are Everglades (EVER), Okeechobee (OKEE), Kissimmee (KISS), Upper St. Johns (USJ), Loxahatchee Slough (LOXSL), and Peripheral Wetlands (PERI).*

[2] *No deaths occurred while in this region during this year; however some sample sizes were quite small (Appendix 4-5).*

[3] *Using the altenative tests described by Cox and Oakes (1984)(Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated χ^2=4.210, P=0.040 and χ^2=4.149, P=0.042 for alternative tests 1 and 2, respectively.*

[4] *There were insufficient data to estimate survival for one or both groups and to conduct corresponding log-rank test.*

[5] *Using the altenative tests described by Cox and Oakes (1984)(Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated χ^2=2.847, P=0.092 for both alternative tests 1 and 2.*

[6] *Using the altenative tests described by Cox and Oakes (1984)(Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated χ^2=2.829, P=0.093 for both alternative tests 1 and 2.*

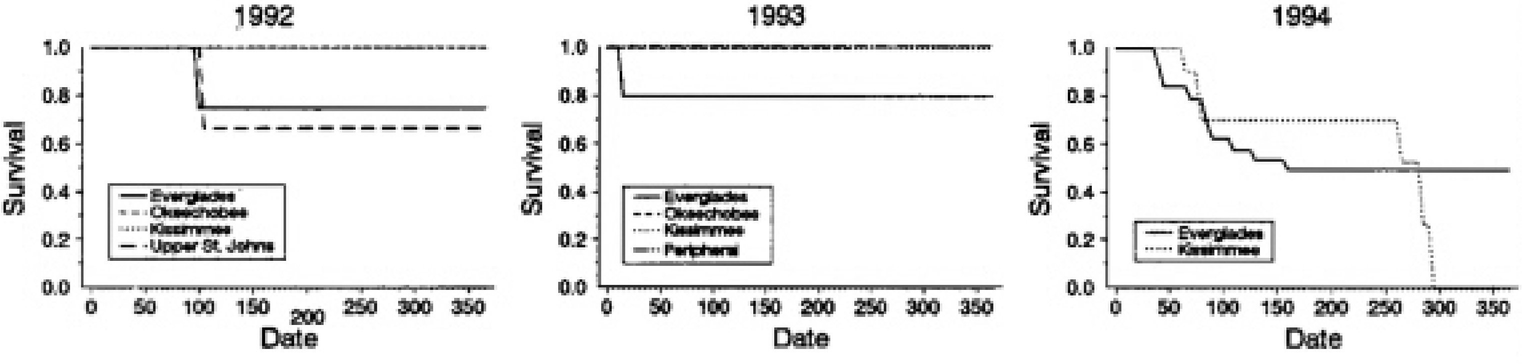


Figure 4-10. Estimates of survivorship functions of radio-transmittered juvenile Snail Kites while they were present in each region during each study year (SY). Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but can be easily estimated from information in Appendix 4-6.

Table 4-13. Results of pairwise log-rank tests between survivorship functions of radio-transmittered juvenile Snail Kites while they were present in each region during each study year (SY).

	SY 1992			SY 1993			SY 1994		
Comparison[1]	χ^2	df	Prob	χ^2	df	Prob	χ^2	df	Prob
EVER vs. OKEE	1.750	1	0.186	0.400	1	0.527	--[2]	–	--
EVER vs. KISS	1.000	1	0.317	--[3]	--	--	1.452	1	0.228
EVER vs. USJ	0.002	1	0.968	--[2]	--	--	--[2]	--	--
EVER vs. LOXSL	--[2]	--	--	--[2]	--	--	--[2]	--	--
EVER vs. PERI	--[2]	--	--	0.200	1	0.655	--[2]	--	--
OKEE vs. KISS	--[3]	--	--	--[3]	–	--	--[2]	–	--
OKEE vs. USJ	2.333	1	0.127	--[2]	–	--	--[2]	--	--
OKEE vs. LOXSL	--[2]	--	--	--[2]	–	–	--[2]	--	--
OKEE vs. PERI	--[2]	–	--	--[3]	--	--	--[2]	--	--
KISS vs. USJ	1.333	1	0.248	--[2]	--	--	--[2]	--	–
KISS vs. LOXSL	--[2]	--	--	--[2]	–	--	--[2]	--	--
KISS vs. PERI	--[2]	--	--	--[3]	--	--	--[2]	--	–
USJ vs. LOXSL	--[2]	–	--	--[2]	--	--	--[2]	--	--
UJS vs. PERI	--[2]	–	–	--[2]	–	–	--[2]	--	--
LOXSL vs. PERI	--[2]	--	–	--[2]	--	--	--[2]	--	--

[1] *Regions of comparison are Everglades (EVER), Okeechobee (OKEE), Kissimmee (KISS), Upper St. Johns (USJ), Loxahatchee Slough (LOXSL), and Peripheral Wetlands (PERI).*

[2] *There were insufficient data to estimate survival for one or both groups and to conduct corresponding log-rank test.*

[3] *No deaths occurred while in one or both of these regions during this year; however some sample sizes were quite small (Appendix 4-6).*

Habitat Effects--Because most of our radio locations were obtained from aircraft, we were sometimes unable to record the habitat type of a given animal's location. This, in combination with the intermittent use of some habitat types (e.g., cypress and disturbed habitats) precluded a meaningful analysis using a Kaplan-Meier estimator (i.e., the number of animals at risk $[r_{ij}]$ for these habitats was often too small, or zero). However, we did conduct a more cursory examination by testing whether the number of deaths that occurred in each habitat was proportional to the overall use of that habitat. This test gave us no indication of disparity between mortality and habitat type (χ^2=4.68, 4 df, P=0.68)(Fig. 4-11).

We were unable to detect any difference in survival of adults between lake and marsh habitats for any year (Table 4-14)(Fig. 4-12). In contrast, juvenile survival differed between these habitats during 1992 (Table 4-15), but not during 1993 or 1994 (Fig. 4-13). Although differences were not statistically significant when regions were compared, this is consistent with the survival estimates from different regions (i.e., estimates from the Everglades and Upper St. Johns regions [marsh habitats] were lower than from Okeechobee or Kissimmee regions [lakes]. This may, at least partially, reflect the conditions in the Everglades following an extended dry period from 1989 to 1991.

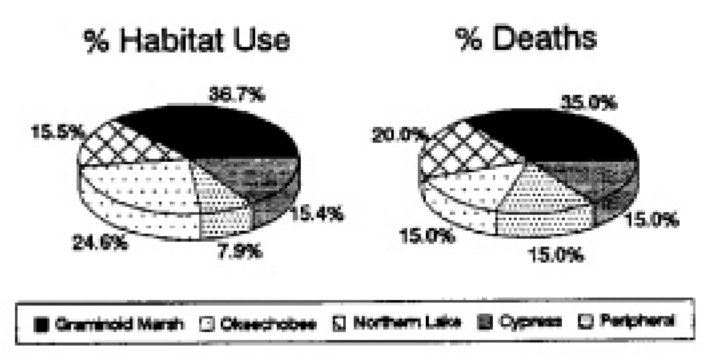


Figure 4-11. Percentage of total use by adult Snail Kites of each habitat type and percentage of the total number of birds that died in each habitat type.

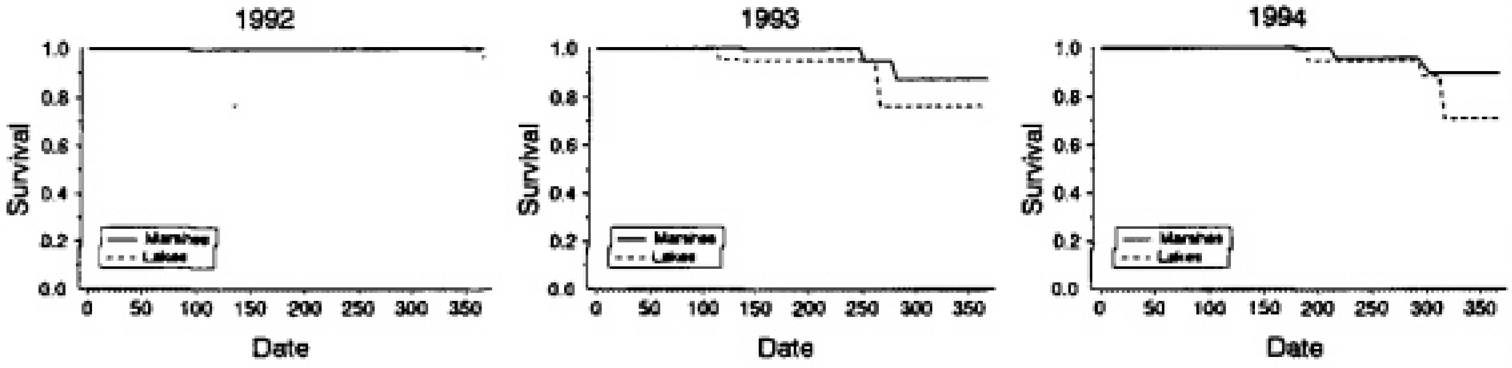


Figure 4-12. Estimates of survivorship functions of radio-transmittered adult Snail Kites while they were present in lake and marsh habitats during each study year (SY). Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 4-7.

Table 4-14. Results of log-rank tests between survivorship functions of adult Snail Kites while they were in lake and marsh habitats during each study year (SY).

Year	χ^2	df	Prob
1992	0.633	1	0.426
1993	1.367	1	0.242
1994[1]	2.028	1	0.154

[1] Using the altenative tests described by Cox and Oakes (1984)(Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated $\chi^2=2.075$, $P=0.150$ and $\chi^2=2.046$, $P=0.153$ for alternative tests 1 and 2, respectively.

Table 4-15. Results of log-rank tests between survivorship functions of juvenile Snail Kites while they were in lake and marsh habitats during each study year (SY).

Year	χ^2	df	Prob
1992[1]	4.353	1	0.037
1993	0.903	1	0.342
1994	0.559	1	0.455

[1] Using the altenative tests described by Cox and Oakes (1984)(Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated $\chi^2=4.383$, $P=0.036$ for alternative tests 1 and 2, respectively.

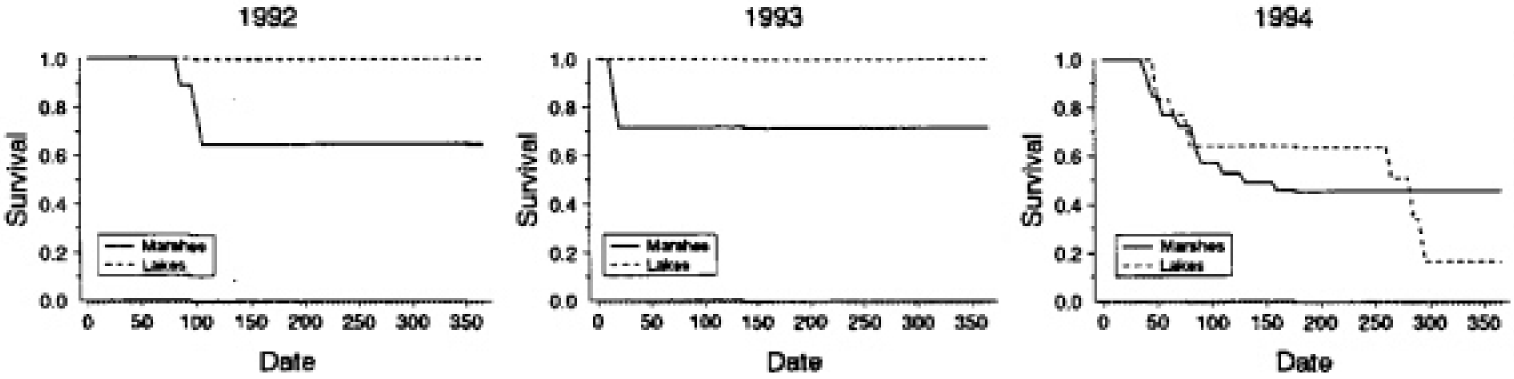


Figure 4-13. Estimates of survivorship functions of radio-transmittered juvenile Snail Kites while they were present in lake and marsh habitats during each study year (SY). Estimates were derived using a Kaplan-Meier estimator. Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 4-8.

MODEL SELECTION FOR EFFECTS ON SURVIVAL

Above we provided evidence for individual effects on survival based on relatively continuous time (data were discrete at the interval of telemetry locations) using a Kaplan-Meier estimator. While this approach has many advantages (e.g., no assumptions about the hazard function), it is not a convenient method for exploration of more complex models including the relative effects of multiple factors. Here we use a discrete-time approach (conditional logistic regression) to evaluate the probability that a bird survives to time $t + 1$, conditional on it being alive at time t. This approach enables us to better evaluate effects on survival in combination to determine effects most appropriately supported by our data in an overall survival model.

We began our analysis with a univariate examination of the sources of variation (Table 4-16). Because the potential for interaction effects to be masked at this preliminary stage, we followed the recommendation of Hosmer and Lemeshow (1989) and used 0.25 as a rejection criteria (α) for inclusion in further models. The effects due to region were the only source eliminated at this phase of our analysis. We also found little evidence for regional effects on survival using a Kaplan-Meier estimator. We were unable to estimate the effects of month because no deaths occured during some months. Consequently, we retained month as a potential source of variation at this stage of the analysis.

Table 4-16. Summary statistics for the univariate analyses (using conditional logistic regression) of effects on the conditional probability of an animal surviving to time $t + 1$, given that it was alive at time t. χ^2 is based on a Wald statistic (SAS Inc. 1988).

Source	df	χ^2	P
Age	1	18.29	<0.001
Sex	2	18.32	<0.001
Season	2	5.17	0.075
Month[1]	--	--	--
Year	2	8.59	<0.001
Region	5	3.06	0.691

[1] Because deaths did not occur in some months, estimation of these statistics were not reliable. We evaluated this source in a more comprehensive analysis (below) using model selection procedures.

Some of the parameters at this stage of the analysis were subsets of other parameters (e.g., season represents combinations of months). Next we evaluated which of these potentially redundant parameters to use in further models. For this analysis, we used 3 classes of sex (male, female, and unknown). Because we were unable to determine the sex of juveniles in the field, sex represents a combination of age and sex (i.e., all cases where the sex class is unknown are juveniles). Based on AIC (Table 4-17) sex provided no substantial gain in model fit at the cost of an additional parameter. Consequently, we used age, but not sex, in all subsequent models. Similarly, individual months provided no substantial gain in model fit over season at the cost of 9 additional parameters. Thus, we used season, but not month, in all subsequent models.

The remainder of our model selection invloved the comparison of models using different combinations of age, season, and year effects. Based on AIC, any of the models which did not include some combination of all three of these effects generally were less adaquate than models which included all three effects. Although model selection often indicates that more than one model is suitable (McCullagh and Nelder 1989) for a given data set, our analysis indicated (by a substantially lower AIC) that a model including the main effects of age, season, year, and the interaction effects of age*year, and age*season was the most appropriate model for our data. This conclusion is further supported by the goodness-of-fit ($P=0.806$) of this model compared to the fully saturated model.

EFFECTS OF HYDROLOGY

One objective of this study was to determine the environmental correlates of survival, particularly hydrology. However, as previously suggested (Bennetts and Kitchens 1993, 1994), survival was sufficiently high that within-year patterns would have been difficult to detect without enormous effort (i.e., too few individuals died to enable quantitative comparisons with those that survived) and probably would not have been very insightful. Rather, we now believe that between-year differences in survival will be more appropriate. Even though we encountered relatively high water conditions throughout this study, the mark-resighting phase of our study (below) was intended to detect these differences and will enable a long-term evaluation of environmental correlates (e.g., hydrologic conditions) as variable conditions occur.

Table 4-17. Summary statistics for conditional logistic regression model for the factors effecting the probability of survival to time t + 1 (at monthly time steps), given that an animal was alive at time t. Shown are the model description, number of estamable parameters (np), relative deviance (-2ln[$\mathcal{L}$]), Akiake's Information Criteria (AIC), and a measure of goodness-of-fit (GOF) for models with relatively low AIC values. GOF was derived using the probability of a LRT comparing a given model with a fully saturated model. The null hypotheses (H_0) of the GOF statistic is that the reduced model (with fewer parameters) fits tha data as well as the more general model (with more parameters). Thus, a failure to reject H_0, indicates a fit of the reduced model. The model with the lowest AIC (bold) would be selected if based only on this criteria.

Model[1]	*np*	-2ln($\mathcal{L}$)	AIC	GOF
Age	2	369.333	373.333	--
Sex	3	368.243	374.243	--
Seas	3	382.272	388.272	--
Mon	12	366.496	390.496	--
Yr	3	379.712	385.712	--
Reg	6	385.931	397.931	--
Age Seas	4	363.063	371.063	--
Age Seas Age*Seas	6	346.849	358.802	--
Age Yr	4	359.446	367.446	--
Age Yr Age*Yr	6	349.633	361.633	--
Seas Yr	5	372.513	382.513	--
Seas Yr Seas*Yr	9	363.101	381.101	--
Age Seas Yr Age*Seas Age*Yr	**10**	**324.142**	**344.142**	**0.806**
Age Seas Yr Age*Seas Seas*Yr	12	327.212	351.212	0.240
Age Seas Yr Age*Yr Seas*Yr	12	333.876	357.876	0.045
Age Seas Yr Age*Seas Age*Yr Seas*Yr	14	322.120	350.120	0.665
Age Seas Yr Age*Seas Age*Yr Seas*Yr Age*Seas*Yr	18	318.039	354.039	1.000

[1] Term abbreviations: Season (Seas), Month (Mon), Year (Yr), and Region (Reg).

Estimation of Survival from 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 (GFC). This sample was also supplemented by resighting of individually marked birds banded on previous studies that were observed during this study (REB, J. Rodgers unpubl. data). Our total sample of individual banded birds for analyses of survival was 913 (Table 4-18); although birds banded in 1995 will only contribute to estimates following subsequent resighting periods (i.e., in future years). Of this sample, 191 were adults at the time of addition to our sample and 722 were juveniles; however, resightings of juveniles after their fledging year then re-enter our sample as adults (although resightings were not included in our sample size reported above).

EFFECTS OF AGE AND TIME

Estimates of survival from banding data differ from those obtained via radio telemetry in that they are discrete at the interval of sampling periods. In this case we measured survival from one breeding season to the next (i.e., approximately annually, see methods). This precludes the ability for testing some of the effects that we tested using radio telemetry data. For example, we

Table 4-18. Number of banded birds from each age class, location, and year obtained through a cooperative banding effort with the Florida Game and Fresh Water Fish Commission or through resighting of birds banded on previous studies. Individual birds are only shown at the time and location that they entered our sample.

	1992		1993		1994		1995[1]	
Location	AD	JUV	AD	JUV	AD	JUV	AD	JUV
Everglades N.P.[2]	--	--	--	2	--	1	--	8
Big Cypress N.P.	--	--	--	--	--	--	--	18
Loxahatchee N.W.R.	--	--	1	2	--	2	--	--
WCA-2A	3	13	6	15	--	--	--	4
WCA-2B	1	--	1	2	16	45	--	87
WCA-3A	4	1	8	24	11	23	2	40
WCA-3B	1	--	1	6	3	--	--	--
Holey Land W.M.A.	2	2	2	6	--	--	--	--
Loxahatchee Slough	3	3	6	10	1	--	--	--
Lake Okeechobee	27	61	20	96	9	6	--	15
Lake Kissimmee[3]	8	14	9	31	11	19	--	--
Lake Tohopekaliga	4	21	1	7	4	8	1	15
East Lake Tohopekaliga	1	1	1	18	1	14	1	--
Upper St. Johns Marsh	12	43	6	33	3	1	--	5
Total	**66**	**159**	**62**	**252**	**59**	**119**	**4**	**192**

[1] *Birds newly marked in 1995 do not contribute to survival analyses until subsequent resighting periods are completed.*

[2] *Includes the Northeast Shark River Slough addition lands*

[3] *Includes nearby Lake Jackson*

are unable to test seasonal differences in survival without having had a sampling (i.e., capture and/or resighting) period in each season of interest.

We began our assessment using the testing sequence of models described by Pollock et al. (1990) as Models A, B, and D. Model A assumes that both survival and resighting probabilities are time dependent (i.e., that separate estimates for each year are warranted). Model B assumes that survival is constant over time (i.e., that a single estimate can be applied to all years), but that resighting probability is time dependent. Model D assumes that both survival and resighting probabilities are constant over time. Each of these models was generated with and without separate parameters for each age class.

In this set of models juveniles are assumed to become adults at the beginning of their first resighting period after their fledging year (this assumption is tested below). Juveniles are capable of breeding at nine months of age (Snyder et al. 1989a) and our radio telemetry results suggest that, for our data, survival of juveniles was similar to adults following an initial period of about 3-4 months of high post-fledging mortality. Thus, in these models, one resighting probability is used for both juveniles and adults (because juveniles become adults at the beginning of their first resighting period); but, a separate estimate of juvenile survival is initially generated (because juvenile survival is measured from the time of fledging to their first resighting period), but may be later deemed unnecessary through model selection procedures.

The results from this initial sequence (Table 4-19) indicated that model A with 2 age classes was the most suitable. The AIC (114.811) from this model was substantially lower than the alternative models. Likelihood ratio tests (LRTs) reinforced the selection of Model A as being the most appropriate with regard to time dependency. LRTs between models B and A with

Table 4-19. Model selection statistics for initial set of Cormack-Jolly-Seber (CJS) models with and without age and time dependency. The model with the lowest AIC (bold) would be selected if based only on this criteria.

Model	Model Description	No. Age Classes	$-2ln(\mathcal{L})$	*np*	AIC	GOF
A	$\Phi_i\ p_i$	1	141.657	6	153.657	<0.001
A_{age}	$\Phi_i\ p_i$	**2**	**96.811**	**9**	**114.811**	**0.167**
B	$\Phi.\ p_i$	1	152.344	4	160.344	<0.001
B_{age}	$\Phi.\ p_i$	2	116.161	5	126.161	0.004
D	$\Phi.\ p.$	1	154.412	2	158.412	<0.001
D_{age}	$\Phi.\ p.$	2	118.595	3	124.595	0.004

and without age effects both strongly rejected the more reduced model (Table 4-20), as did the comparisons between models A and D with and without age effects. This indicates that constraining survival (Φ) and/or resighting probability (p) to be constant among years was not justified (i.e., these data support a year effect). Similarly, a LRT between models A with and without an age effect (Models A and A_{age}) strongly rejected ($\chi^2 = 44.846$, 3 df, $P < 0.001$) suggesting that constraining parameter estimates to be equal for adults and juveniles also was not justified (i.e., these data also support an age effect). The goodness-of-fit (GOF) test also failed to reject the null hypothesis (H_0) that this model adaquately fits the data (GOF tests for all of the alternative models strongly rejected H_0.

In order to test the assumption (above) that a separate estimate for juvenile resighting probability was not warranted, we generated an alternative model structure in which we assumed that juveniles became adults at the end (rather than the beginning) of their first resighting period in the post fledging year. This enabled separate estimation for juvenile resighting, as well as survival, probabilities. We then tested the assumption using an analogous model to Model A_{age} from above by comparison of models where resighting probability is constrained and unconstrained to be equal for juveniles and adults. The AIC of the model in which resighting probability was constrained to be equal (which is equivalent to Model A_{age} from above) for the two age classes was lower than for the unconstrained model (Table 4-21). A LRT between these models also failed to reject the more reduced model ($\chi^2 = 1.808$, 3 df, $P = 0.613$) indicating that the additional parameters for a separate resighting probability for each age class were not warranted for these data.

Table 4-20. Resulting statistics from Likelihood Ratio Tests (LRT) between Cormack-Jolly-Seber (CJS) models "A", "B", and "D" with and without separate estimates for each age class.

General Model	Reduced Model	χ^2	df	$P > \chi^2$
A	B	10.687	2	0.005
A_{age}	B_{age}	19.350	4	<0.001
A	D	12.756	4	0.013
A_{age}	D_{age}	21.783	6	0.001

Based on the results from our radio telemetry, which indicated greater differences in survival among years for juveniles than adults, we generated one additional model to test this hypothesis (i.e., that survival was time dependent for juveniles, but not for adults). This model (Model $A_{juv\text{-}\Phi}$) had a lower AIC than model A_{age} (Table 4-22). A LRT between these models also failed to reject the null hypothesis (H_0) that the reduced model (Model $A_{juv\text{-}\Phi}$) fit the data equally well as the more general model (Model A_{age}) ($\chi^2 = 0.290$, 2 df, $P = 0.865$). The goodness-of-fit for this model also failed to reject the null hypothesis (H_0) that this model adequately fits the data.

Thus, these data support a model that survival differs among years for juveniles, but not adults. Parameter estimates for the most parsimonious model (Model $A_{juv\text{-}\Phi}$) are provided in Table 4-23.

Table 4-21. Model selection statistics for model A_{age} in which the assumption of equal resighting probabilities between adults and juveniles is relaxed or constrained. The model with the lowest AIC (bold) would be selected if based only on this criteria.

Model	Model Description	Resighting probability (p) equal for age classes	$-2ln(\mathcal{L})$	np	AIC	GOF
A_{age_p}	$\Phi_i\ p_i$	No	95.004	12	119.004	0.106
A_{age}	$\Phi_i\ p_i$	Yes	**96.811**	**9**	**114.811**	**0.167**

Table 4-22. Model selection statistics for variations of models in which survival is time dependent for both adults and juveniles (Model A_{age}), and is constrained to be constant for adults, but not juveniles (Model $A_{juv\text{-}\Phi}$). The model with the lowest AIC (bold) would be selected if based only on this criteria.

Model	Model Description	$-2ln(\mathcal{L})$	np	AIC	GOF
A_{age}	$\Phi_i\ p_i$	96.811	9	114.811	0.167
$A_{juv\text{-}\Phi}$	$\Phi_{juv,i}\ p_i$	**97.101**	**7**	**111.101**	**0.253**

Table 4-23. Parameter estimates for the selected Cormack-Jolly-Seber (CJS) Model (Model$A_{juv\text{-}\Phi}$), in which adults and juveniles differ in survival, survival is constant among years for adults, and survival is variable among years for juveniles. Resighting probability in this model differs among years, but is the same for adults and juveniles (i.e., juveniles are considered adults at the beginning of their first resighting period after their fledging year).

Age	Year	Φ_i	95% C.I.(Φ)	p_i	95% C.I.(p_i)
Adult	1992	0.840	0.637 - 1.000	0.142	0.073 - 0.210
Adult	1993	0.840	0.637 - 1.000	0.255	0.150 - 0.359
Adult	1994	0.840	0.637 - 1.000	0.217	0.095 - 0.336
Juvenile	1992	0.451	0.281 - 0.620	0.142	0.073 - 0.210
Juvenile	1993	0.163	0.071 - 0.256	0.255	0.150 - 0.359
Juvenile	1994	0.620	0.177 - 1.000	0.217	0.095 - 0.336

EFFECTS OF SEX

Most banded birds in this study were banded as juveniles, which cannot be sexed in the field. Thus, a large segment of our sample was of unknown sex. Consequently, we did not attempt any analysis from banding data on survival differences attributable to sex.

REGIONAL EFFECTS

To test for regional effects of survival and resighting probabilities, we generated a suite of multi-state models (Brownie et al. 1993, Nichols et al. 1993) analogous to the base models described above as models A, B, and D by Pollock et al. (1990) except that they include a multi-state component that enables parameters to be estimated for multiple strata (Brownie et al. 1993, Nichols et al. 1993)(in this case strata = 5 of the 6 regions of capture -- no captures occurred in the peripheral region). Regional effects were tested based only on the region of capture since banding data do not provide information regarding where a given bird has been between resightings. These models are also the default models generated by program MSSURVIV (Hines 1994) used for this analysis. As above, we generated models with and without age dependency, enabling us to test hypotheses that survival (Φ_i) and/or resighting probabilities (p_i) were affected by age, time, and region, simultaneously.

For this set of models, the AIC was lowest for Model B with no age effect; however, Model B_{age} with an age effect was sufficiently similar (a difference of 1.36– less than our criteria for exclusion) to be retained as a reasonable alternative (Table 4-24). LRTs reinforced the selection of Model B as being the most appropriate with regard to time dependency. LRTs between models B and A with and without age effects both failed to reject (Table 4-25), indicating that separate estimates of survival (Φ) for each year were not warranted. Similarly, LRTs between models B and D were highly significant, indicating that constraining resighting probability (p_i) to be constant among years also was not justified.

Because AIC was similar for models B and B_{age}, we used a LRT to specifically test the null hypothesis that an age effect for Model B was not warranted (i.e., that the fit of the 1-age model was equal to the fit of 2-age model). This test (Model B vs. Model B_{age}) strongly rejected the null hypothesis (χ^2 =48.638, 25 df, P=0.003) indicating that separate parameter estimates for each age class were warranted (i.e., there was an age effect). Thus, from this set of models we selected Model B with 2 age classes (Model B_{age}) as the most appropriate model for our data.

Using Model B_{age} as a base model, we generated another set of models in which (1) survival was constrained to be constant for all regions (Model $B_{age\_r\Phi.}$), (2) resighting probability was constrained to be constant for all regions (Model $B_{age\_rp.}$), and (3) both survival and resighting probability were constrained to be constant for all regions (Model $B_{age\_r\Phi.p.}$).

Based on AIC, these results indicated that Model $B_{age\_r\Phi.}$ was an improvement (i.e., had a lower AIC) over the base model but the other two regional models were worse than the base model (Table 4-26). Thus, our data do not support regional differences in survival but do support differences in resighting probability among regions.

As above we also wished to test the hypothesis that juvenile survival was time dependent but adult survival was not. To test this hypothesis, we used model $B_{age\_\Phi.p.}$ as our base model and relaxed juvenile survival to be time specific. The resulting model (Model $B_{ad.\_r\Phi p}$) had a lower AIC than alternative models (Table 4-27) indicating a time effect for juvenile, but not adult, survival. A LRT between Model $B_{age\_r\Phi.p.}$ (the reduced model) and Model $B_{ad.\_r\Phi p}$ (the more general model) also strongly rejected (χ^2 =10.204, 2 df, P=0.006), indicating that the additional parameters for year-specific survival of juveniles were warranted.

Parameter estimates using the model selected from above (Model $B_{ad.\_r\Phi p}$) are provided in Table 4-28.

Table 4-24. Model selection statistics for initial set of multi-state (regional) models with and without age and time dependency. The model(s) in bold text were selected as being the most appropriate (parsimonious) for these data.

Model	Model Description	No. Age Classes	$-2ln(\mathcal{L})$	*np*	AIC
A	Φ_i p_i	1	420.679	89	598.679
A_{age}	Φ_i p_i	2	338.447	164	666.447
B	$\Phi.$ p_i	**1**	**448.420**	**42**	**532.420**
B_{age}	$\Phi.$ p_i	**2**	**399.781**	**67**	**533.781**
D	$\Phi.$ $p.$	1	473.808	32	537.808
D_{age}	$\Phi.$ $p.$	2	429.037	57	543.037

Table 4-25. Resulting statistics from Likelihood Ratio Tests (LRT) between multi-state (regional) models "A", "B", and "D" with and without separate estimates for each age class.

General Model	Reduced Model	χ^2	df	$P > \chi^2$
A	B	27.740	47	0.989
A_{age}	B_{age}	61.335	97	0.998
B	D	25.389	10	0.005
B_{age}	D_{age}	29.256	10	0.001

Table 4-26. Model selection statistics for set of models which constrained survival and/or resighting probability to be constant for all regions. The base model for comparison was Model B_{age}. Model(s) in bold text were selected as being the most appropriate (parsimonious) for these data.

Model	Model Description for time dependency	Parameters constrained to be constant across regions[1]	$-2ln(\mathcal{L})$	np^2	AIC
B_{age}	$\Phi_{.}\ p_t$	--	399.781	67	533.781
$B_{age\_r\Phi.}$	**$\Phi_{.}\ p_t$**	**Φ**	**409.749**	**59**	**527.749**
$B_{age\_rp.}$	$\Phi_{.}\ p_t$	p	490.202	55	600.202
$B_{age\_r\Phi p.}$	$\Phi_{.}\ p_t$	Φ & p	455.231	47	549.231

[1] *One parameter estimate is used for all regions. For example Model $B_{age\_r\Phi.}$ has one estimate of survival for each age class that is used for all regions, but a separate estimate of resighting probability for each age class and each region.*

[2] *Includes parameters for transition probabilities (i.e., the probability of being in a different strata [region] between times t and t + 1. These probabilities are better estimated using radio telemetry and consequently not reported [see methods]).*

Table 4-27. Model selection statistics for set of models which constrained survival to be constant for adults, variable for juveniles. The base model for comparison was Model B_{age}. Model(s) in bold text were selected as being the most appropriate (parsimonious) for these data.

Model	Model Description for time dependency	Parameters constrained to be constant across regions[1]	$-2ln(\mathcal{L})$	np^2	AIC
B_{age}	$\Phi_{.}\ p_t$	--	399.781	67	533.781
$B_{age\_r\Phi}$.	$\Phi_{.}\ p_t$	Φ	409.749	59	527.749
$B_{age\_r\Phi p}$	$\Phi_{.}\ p_t$	Φ & p	455.231	47	549.231
$B_{ad\_r\Phi p}$	**$\Phi_{(a,j)}\ p_t$**	**Φ & p**	**389.717**	**61**	**511.717**

[1] *One parameter estimate is used for all regions. For example Model $B_{age\_r\Phi.}$ has one estimate of survival for each age class that is used for all regions, but a separate estimate of resighting probability for each age class and each region.*

[2] *Includes parameters for transition probabilities (i.e., the probability of being in a different strata [region] between times t and t + 1. These probabilities are better estimated using radio telemetry and consequently not reported [see methods]).*

Table 4-28. Parameter estimates for the selected multi-state model (Model $B_{ad\_r\Phi p}$), in which adults and juveniles differ in survival, survival is constant among years for adults, and survival is variable among years for juveniles. Resighting probability in this model differs among years and regions, but is the same for adults and juveniles (i.e., juveniles are considered adults at the beginning of their first resighting period after their fledging year).

Age	Year	Region	Φ_i	95% C.I.(Φ_i)	p_i	95% C.I.(p_i)
Adult	1992	EVER	0.996	0.715 - 1.000	0.126	0.000 - 0.377
Adult	1992	OKEE	0.996	0.715 - 1.000	0.099	0.000 - 0.213
Adult	1992	KISS	0.996	0.715 - 1.000	0.293	0.076 - 0.510
Adult	1992	USJ	0.996	0.715 - 1.000	0.766	0.000 - 1.000
Adult	1992	LOXSL	0.996	0.715 - 1.000	<0.001	0.000 - 0.321
Adult	1993	EVER	0.996	0.715 - 1.000	1.000	0.999 - 1.000
Adult	1993	OKEE	0.996	0.715 - 1.000	0.119	0.000 - 0.250
Adult	1993	KISS	0.996	0.715 - 1.000	0.416	0.156 - 0.678
Adult	1993	USJ	0.996	0.715 - 1.000	0.298	0.000 - 1.000
Adult	1993	LOXSL	0.996	0.715 - 1.000	0.005	0.000 - 0.018
Adult	1994	EVER	0.996	0.715 - 1.000	0.967	0.378 - 1.000
Adult	1994	OKEE	0.996	0.715 - 1.000	0.082	0.000 - 0.199
Adult	1994	KISS	0.996	0.715 - 1.000	0.170	0.026 - 0.314
Adult	1994	USJ	0.996	0.715 - 1.000	1.000	0.000 - 1.000
Adult	1994	LOXSL	0.996	0.715 - 1.000	<0.001	0.000 - 0.237
Juvenile	1992	EVER	0.709	0.228 - 1.000	0.126	0.000 - 0.377
Juvenile	1992	OKEE	0.709	0.228 - 1.000	0.099	0.000 - 0.213
Juvenile	1992	KISS	0.709	0.228 - 1.000	0.293	0.076 - 0.510
Juvenile	1992	USJ	0.709	0.228 - 1.000	0.766	0.000 - 1.000
Juvenile	1992	LOXSL	0.709	0.228 - 1.000	<0.001	0.000 - 0.321
Juvenile	1993	EVER	0.302	0.036 - 0.568	1.000	0.999 - 1.000
Juvenile	1993	OKEE	0.302	0.036 - 0.568	0.119	0.000 - 0.250
Juvenile	1993	KISS	0.302	0.036 - 0.568	0.416	0.156 - 0.678
Juvenile	1993	USJ	0.302	0.036 - 0.568	0.298	0.000 - 1.000
Juvenile	1993	LOXSL	0.302	0.036 - 0.568	0.005	0.000 - 0.018
Juvenile	1994	EVER	0.731	0.000 - 1.000	0.967	0.378 - 1.000
Juvenile	1994	OKEE	0.731	0.000 - 1.000	0.082	0.000 - 0.199
Juvenile	1994	KISS	0.731	0.000 - 1.000	0.170	0.026 - 0.314
Juvenile	1994	USJ	0.731	0.000 - 1.000	1.000	0.000 - 1.000
Juvenile	1994	LOXSL	0.731	0.000 - 1.000	<0.001	0.000 - 0.237

[1] *Region abbreviations: Everglades (EVER), Okeechobee (OKEE), Kissimmee (KISS), Upper St. Johns (USJ), and Loxahatchee Slough (LOXSL).*

CONCLUSIONS ABOUT THE EFFECTS OF SURVIVAL FROM BANDING DATA

Our overall conclusion from both the CJS models and the extension to multi-state models support (1) an age effect on survival, (2) annual differences in survival of juveniles, but not adults, and (3) regional differences in resighting probability, but not survival. Both the CJS models and the multi-state models ended up with the same model with respect to age and time dependency; although they arrived there in different ways. The CJS model indicated Model A_{age} (i.e., age and time dependency for both survival and resighting probabilities) of the initial set of models was most parsimonious. However, when survival was constrained to be constant among years for adults (but not juveniles), it improved the model. In contrast, the multi-state models initially resulted in the selection of Model B_{age} (i.e., survival was constant among years but resighting probabilities differed among years). However, when juvenile (but not adult) survival was relaxed to vary among years, it likewise improved the model. Thus, both the CJS and multi-state models ended up with selection of models in which (1) adult and juvenile survival differed, (2) adult survival was constant among years, (3) juvenile survival differed among years, and (4) resighting probability differed among years. The multi-state models also supported the hypothesis that resighting probabilities differed among regions but survival probabilities did not.

A Synthesis of the Effects of Survival

EFFECTS OF AGE

The results from radio telemetry and banding data were generally consistent. Both sources of data indicated that survival was dependent on age. Log-rank tests between survivorship functions of radio-transmittered adults and juveniles were significant for 2 of 3 years. Model selection from a conditional logistic model of survival of radio-transmittered birds also indicated an age effect on survival; as did LRTs of banding from both (CJS) and multi-state models. In all cases, where significant differences occurred adult survival was higher than juvenile survival. The exception to that pattern was the radio telemetry data for 1993 in which juvenile survival (0.87) was estimated to be slightly (and not significantly, $\chi^2=0.243$, 1 df, $P = 0.622$) higher than adult survival (0.86).

EFFECTS OF SEX

As explained above, we did not attempt any analysis from banding data to evaluate differences in survival that were attributable to the sex of the bird. Our Kaplan-Meier estimates and our logistic regression analyses of radio-telemetry data generally did not support differences in survival attributable to sex of the bird. However; survivorship functions from Kaplan-Meier estimates did indicate a difference between males and females for one of three years (1994) at $\alpha = 0.10$.

TEMPORAL EFFECTS

Survival estimates from both radio telemetry and banding data generally indicated annual differences in survival among juveniles but not adults. However, survivorship functions of adults did differ between 1992 and 1993 at $\alpha = 0.10$. Although both sources of data indicated differences among years for juvenile survival, the parameter estimates from these two data sources were not consistent in their relative ranking among years. The Kaplan-Meier estimates for juveniles were 0.83, 0.87, and 0.44 for 1992, 1993, and 1994, respectively. In contrast the CJS estimates were 0.45, 0.16, and 0.62 for 1992, 1993 and 1994, respectively.

Assumptions, Bias, and Sources of Error for Survival Estimators

Although it is often not explicitly stated, virtually all estimators require making assumptions. Estimators are often robust to violation of some assumptions (i.e., violation of the assumption does not strongly affect its performance) but not to others. Some of the readers of this report may not be familiar with particular estimators we have used or their corresponding assumptions. We have attempted to summarize here what we believe are the major factors that could produce spurious or misleading results regarding our estimates of survival and discuss what influence these factors may or may not have on interpreting our results.

ASSUMPTIONS INHERENT IN THE STUDY DESIGN FOR VALID INFERENCES FROM SURVIVAL ANALYSES

Study Animals are Representative of Population-- Random sampling within a population is usually intended to assure that the scope of inference from a study can validly be applied to the population of interest. Our design was intended to systematically accomplish that same goal. Our study area encompassed the entire range of Snail Kites in Florida. We then stratified our sample to be proportional to the annual count and balanced our sample with respect to age and sex. Thus, we believe that we have a representative sample from the entire Florida population. We cannot be sure that there was an equal probability of capturing any given individual; however, we believe that heterogeneity of catchability played only a minor role in determining our final sample.

Study Conditions are Representative of the Conditions of Interest-- There is considerable variability in the environmental conditions that may influence Snail Kite populations. We recognized from the outset of this project that our inference would be limited to the conditions encountered during our study (Bennett and Kitchens 1992, 1993, 1994). Most notably, drought has been reported as a major influence on kite populations (Sykes 1983b, Takekawa and Beissinger 1989, Beissinger 1995), and we did not encounter drought conditions during this study. Consequently, valid inference from our study cannot be extended to drought conditions. Although speculation has often been made concerning survival during drought conditions (e.g., Snyder et al. 1989a, Beissinger 1995), we know of no valid estimation of survival during such conditions.

Survival Is Independent of Other Animals-- An assumption shared by both radio telemetry and banding studies is that the fate of one marked animal is not influenced by the fate of another. This assumption is likely to be violated when being in a group of animals results in exposure to some common risk (e.g., predation at a roost site). Although we were unable to explicitly test for independence, violation of this assumption does not cause bias in the estimates of survival. Rather, it will artificially reduce the variance of the resulting estimates (Burnham et al. 1987, Pollock et al. 1989). We do not believe that any severe violation of this assumption occurred. Only once during this study did we find mortality of more than one individual at the same time and place. Two banded siblings, one of which was radio transmittered, were found dead at the same site in Loxahatchee National Wildlife Refuge at what was believed to be the feeding site of a Great-horned Owl.

ASSUMPTIONS OF THE KAPLAN-MEIER ESTIMATOR

Carrying a Radio Transmitter Does Not Affect Survival-- A critical assumption of studies using radio telemetry to estimate survival is that the radio transmitter does not affect survival. There has been substantial evidence in recent years to suggest that, for some species, radio transmitters may influence the behavior, weight gain, reproduction, or survival of study animals (e.g., Marks and Marks 1987, Hooge 1991, Paton et al. 1991, Foster et al. 1992).

We tested for the effect of carrying a radio transmitter on survival using both CJS and multi-state CJS models from our banding data. These data consisted of animals both with and without radio transmitters, thus allowing us to specifically test for radio effects. Because our previous analyses using CJS models had indicated Model $A_{juv-\Phi}$ (see above) as the most parsimonious, we used it as a base model for testing radio effects. We maintained the constraints of this model for constant adult survival among years but variable juvenile survival; however, we derived separate parameter estimates (for survival, resighting probability, or both) for birds with and without radio transmitters. The resulting models all had a higher AIC than the previously selected model (Table 4-29). This indicates that using separate parameters for birds with and without radio transmitters was not supported by our model selection procedures (i.e., there is no radio effect). This conclusion was further supported by LRTs between models with separate estimates for birds with and without radio transmitters and our base model in which parameters among these groups were equal (Table 4-29). In addition to model selection and LRTs, the actual parameter estimates from these models were higher for birds with radio transmitters than for birds without radio transmitters. Of course, we **do not** mean to imply that radio transmitters somehow improved the chances for survival (our procedures above suggest survival of birds with and without radio transmitters does not differ); but rather, that our parameter estimates also support the conclusion that radio transmitters did not lower the probability of survival.

We also explored the effects of radio transmitters on survival using a link function (Lebreton et al. 1992) in our multi-state models. Rather than use a separate parameter for survival of birds with and without radios for each group of animals (e.g., age class), a link function (*f*) links the parameters to an external variable (e.g., radios) via a linear formula.

Table 4-29. Variations of base (most parsimonious) model (Model $A_{juv\text{-}ad}$) in which separate estimates for birds with and without radio transmitters were derived for survival (Φ), resighting probability (p), or both.

Parameter(s)[1]	$-2ln(\mathcal{L})$	*np*	AIC	LRT[2]	df	$P > \chi^2$
none	97.101	7	111.101	--	--	--
Φ	92.697	11	114.697	4.404	4	0.354
p	89.755	13	115.755	7.345	6	0.290
Φ and p	87.478	14	115.478	9.623	7	0.211

[1] *Parameter(s) for which separate estimates are derived for birds with and without radio transmitters.*

[2] *Compared to base model where parameter estimates are equal for birds with and without radio transmitters.*

In this case we modeled survival of birds with and without radios as:

$$\Phi_{nonradio} = \Phi_{radio} * f(\Phi_{radio})$$

and

$$p_{nonradio} = p_{radio} * f(p_{radio})$$

Thus, the values of the link functions $f(\Phi)$ and $f(p)$ are the only two additional parameters estimated and a test of a radio effect is whether or not the confidence intervals of these link functions cover 1 (i.e., a value of 1 shows no effect from the parameter).

As above, we used the most parsimonious model from our previous analysis of multi-state CJS models (Model $B_{ad.\_r\Phi p}$) as a base model for testing radio effects. For both survival and resighting probability the confidence intervals of the link functions covered 1 (Table 4-30). In both cases the estimated link-function values were < 1, which would imply that our survival estimate for birds with radio transmitters was higher than for those without radios. We concluded this assessment by simulating a radio effect ($\Delta[\Phi]$) on the actual data and estimating the power to detect differences in survival attributable to that effect. This analysis showed that we had relatively low power to detect small differences attributable to radio transmitters, but had reasonable power to detect substantial radio effects (Fig. 4-14). Although our tests for an effect of radios on survival were not completely conclusive, all evidence that we had indicated that radios had no negative effect on survival during this study.

Table 4-30. Parameter estimates, standard error (SE), and 95% confidence intervals (C.I.) for link functions $f(\theta)$ of radio effects on survival and resighting probability from the most parsimonious multi-state CJS model (Model $B_{ad.\_r\Phi p}$).

Parameter	Estimate	SE	95% C.I.
$f(\Phi)$	0.977	0.053	0.873 - 1.081
$f(p)$	0.848	0.240	0.377 - 1.319

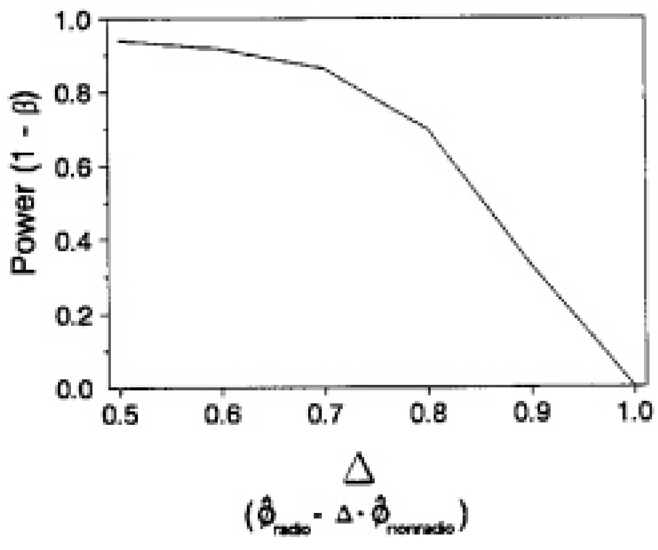


Figure 4-14. Estimated power for detecting differences (Δ) in survival of birds with and without radio transmitters. Differences in survival were simulated using Model $B_{ad.\_r\Phi p}$ as a base model from which differences were imposed.

***Censoring Is Random*–** Censoring is the removal of radio-transmittered animals from a sample when the radio transmitter signal can no longer be detected. An important assumption of the Kaplan-Meier estimator is that the censoring mechanism is random (Pollock et al. 1989). This means that the probability of a bird being censored is not related to its fate (i.e., censored and uncensored animals have the same survival probability). In the case of simple radio failure (a common reason for censoring) this assumption probably is valid. In cases where a radio is destroyed in the process of an animal dying (e.g., a radio is destroyed during predation or scavenging), or a radio-transmittered animal leaves the study area (e.g., through migration, or having been hunted or poached) this assumption may not be valid. When the probability of a censored animal dying is higher than an uncensored animal the resulting survival estimate will be biased high (i.e., survival will be over estimated).

We believe that there are 3 likely reasons animals were censored on this study: (1) simple radio failure, (2) when Snail Kites die they likely end up in water which reduces the life of the radio and/or decreases its range (i.e., they were harder to detect), and (3) some birds left the study area.

We defined simple radio failure as the failure of a radio transmitter that resulted from manufacturer defects, exhausted batteries, or electronic deterioration resulting from normal exposure to environmental elements. We did not include in this category, radios that had been damaged as a result of traumatic encounters (e.g., predation or vehicle collisions) or radios that had been exposed to conditions not normally encountered by living birds (e.g., prolonged submersion in water). Given the above definition, we had no reason to suspect that the rate of simple radio failure should differ between adults and juveniles. Consequently, the expected rate of censoring of radio-transmittered adult and juvenile Snail Kites due to simple radio failure also should not have differed. An examination of the distribution of "times to censoring" revealed a departure from this expectation (t=3.77, df=179, $P<0.001$)(Fig. 4-15). Juveniles had a substantial surge in censored animals that occurred within the first 60 days after radio attachment that was not apparent for adults. This surge also coincided with the period of high mortality of juveniles. Some of this censoring was likely the result of post-fledging dispersal into peripheral areas where our searches were less intensive. Banded juveniles have been occasionally recovered (usually dying or dead) outside of the usual range of adults. Our radio telemetry also revealed that juveniles will sometimes wander throughout peripheral areas and later return to more typical habitats (i.e., temporary emigration). However, some of the censoring probably was undetected mortality. Birds that wander into atypical habitats are likely to have encountered food shortages if apple snails were not abundant. In addition, the risk of predation by more terrestrial predators (e.g., Great-horned Owls) also probably increased in these habitats compared to the contiguous marshes usually inhabited. Search efficiency for the radio signal would also decrease if either the birds were in habitats not normally used by adults (i.e., we spent less time in areas where birds were usually not present), or if mortality resulted in the radio being on the ground (as opposed to up on a perch or flying) or submerged in water.

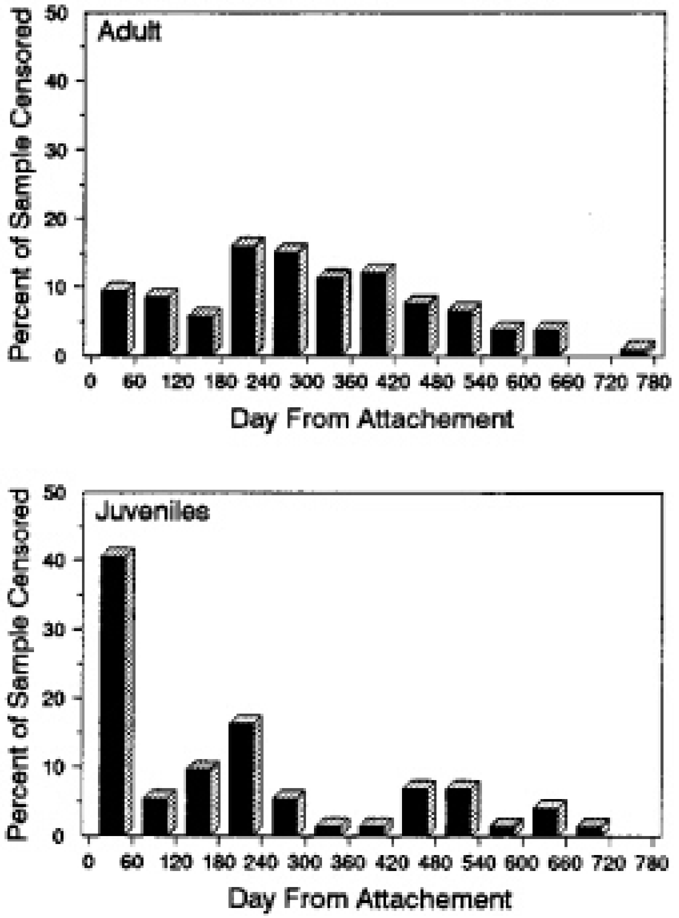


Figure 4-15. The percentage of radio-transmittered adult and juvenile Snail Kites that were censored in each 60-day time interval from the time of attachment.

Because we suspected that we may have been failing to detect some mortality, we increased our search effort during SY 1994 by hiring an additional field biologist whose primary responsibility was aerial searches for missing birds. Additional evidence that some of the censoring of juveniles was actually undetected mortality resulted from this increased effort. We examined the proportions of censored and dead birds during the first few months after attachment (i.e., < 1 September of each year) before radio batteries were likely to have been exhausted; consequently, simple radio failure from that cause was less likely. For adults, the proportions of censored birds and birds confirmed dead remained relatively constant for each year including 1994 when effort was increased (Fig. 4-16). In contrast, the proportions for juveniles remained relatively constant for SY 1992 and 1993, but showed a dramatic departure from this pattern during SY 1994. During SY 1994 the proportion of birds confirmed dead substantially increased and the proportion of censored birds substantially decreased. The proportion of censored juveniles during 1994 also closely matched the proportion of censored adults, which it had not during 1992 or 1993. This suggests that we were finding dead birds during 1994; whereas a substantial number of dead birds may have gone undetected during 1992 and 1993.

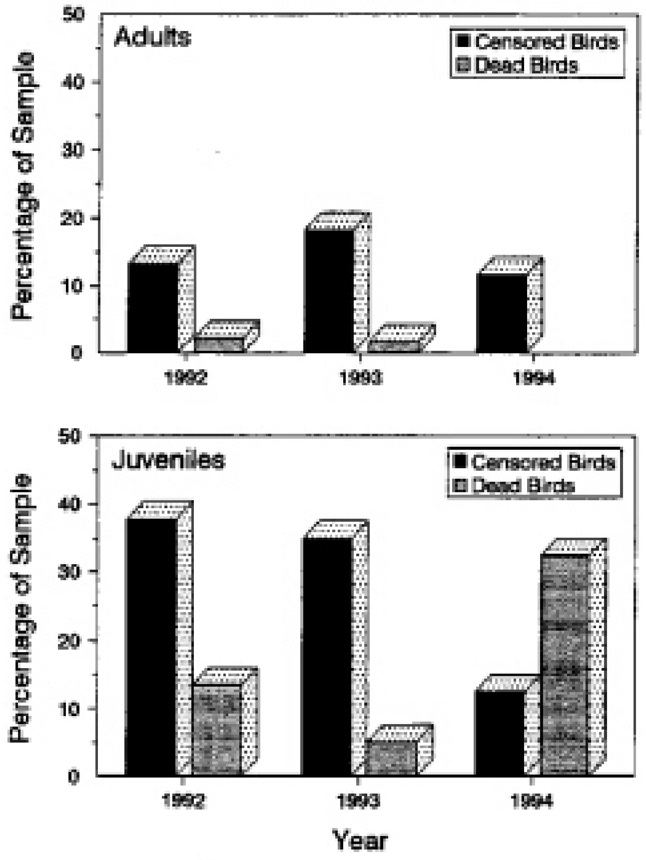


Figure 4-16. The percentage of adult and juvenile Snail Kites from each sampling cohort (i.e., the year that they fledged or were captured) which were censored or which died between the time of capture and 1 September in each year. Since all birds remaining in the sample will ultimately be censored due to radio battery failure, we used 1 September as a cutoff point which enabled comparability among years, without the confounding of battery failure.

Based on this evidence, we believe that we may have overestimated survival of radio-transmittered juveniles during SY 1992 and 1993. Although some undetected mortality of both adults and juveniles was certainly possible, even during 1994, the risk of biased estimates probability was less during 1994. Our estimates of juvenile survival from an independent data source (i.e., banding data using either CJS or multi-state CJS models) also were lower than the Kaplan-Meier estimates for 1992 and 1993, but not during 1994. In contrast estimates of adult survival from banding data did not differ among years and the average estimates from CJS and multi-state CJS models ($\Phi_s = 0.92$) were very similar to the average of the annual estimates derived from the Kaplan-Meier estimator ($\Phi_s = 0.90$). Thus, while we believe that survival of radio-transmittered juveniles was overestimated for 1992 and 1993, we have no evidence to support a similar conclusion for adults.

Small Sample Effect on Staggered Entry Design– Small sample sizes can produce misleading, but unbiased, estimates of survival. The Kaplan-Meier product-limit estimator is a simple extension of a binomial estimator (Kaplan and Meier 1958, White and Garrott 1990). One of the characteristics of this estimator is that the resulting product (i.e., the cumulative estimate) is equivalent to a binomial estimate over the interval of study (White and Garrott 1990). For example, if we start with a total of 10 animals and during the course of the study 2 animals die at different times, the final estimate derived from the Kaplan-Meier estimate will (9/10=0.9) x (8/9= 0.88) = 0.80 (Fig. 4-17); exactly the same as 8/10 from a binomial estimator for the overall interval. However, when using a staggered entry design the estimates for any given time interval will be equivalent to a binomial estimate, but the cumulative estimate (i.e., the product) will not necessarily be the equivalent to a binomial estimate for the overall interval (Fig. 4-17). For example, if only 2 animals are at risk over an interval, estimates of survival can have only 3 possible outcomes: 1.0 (both lived), 0.5 (1 died and 1 lived), or 0.0 (both died). The **expected value** (i.e., the mean of $\hat{\theta}$ from a very large number of repeated experiments) of the estimate may still reflect the "true" estimate, but the individual outcomes for intervals with a low number of animals at risk may be an inadaquate reflection of the expected value. For an estimate to be biased, the expected value of the estimate, not the outcome of any particular trial, must differ from the true parameter value.

In this study, we tried to circumvent this problem by beginning our estimation at a time when a sufficient sample size was established (i.e., April 15 of each year). There is always a balance that must be established between having sufficient sample size to "trust" the results and not missing potentially "real"

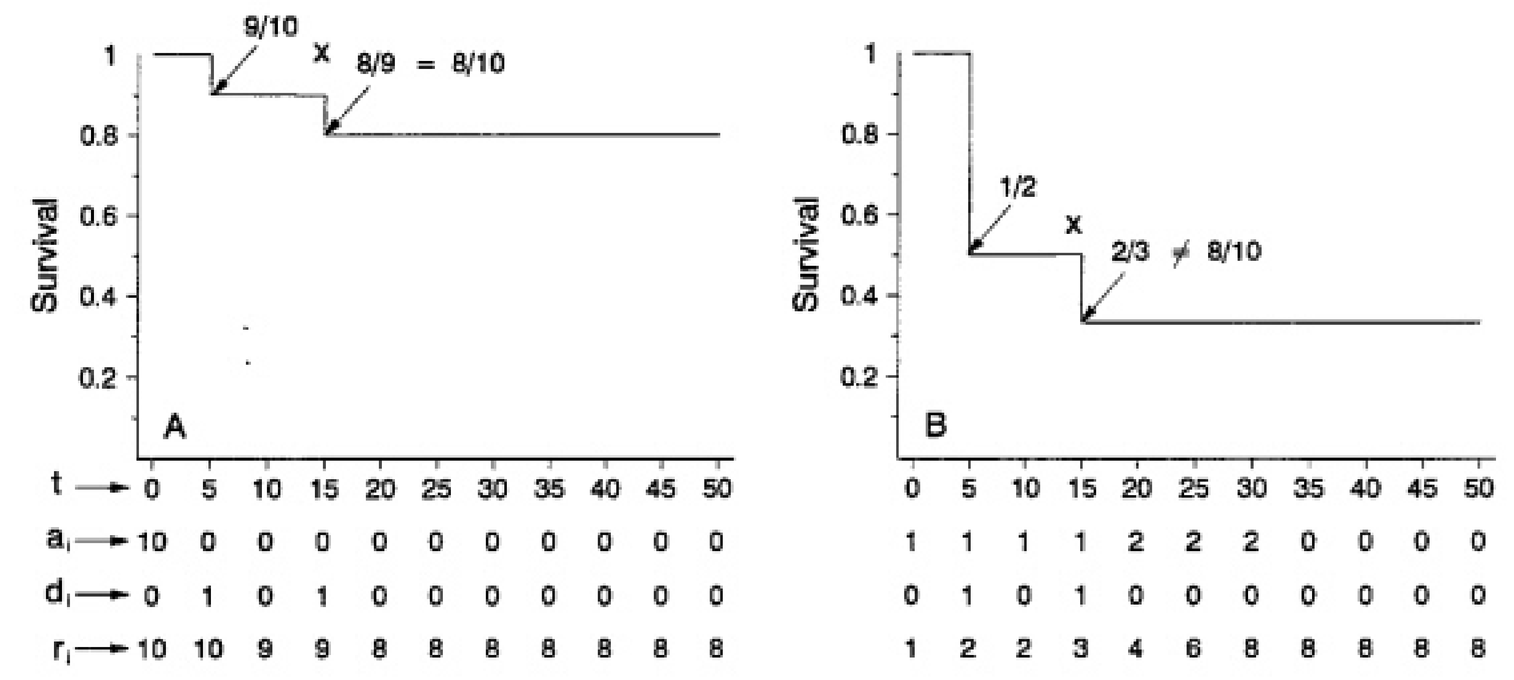


Figure 4-17. Hypothetical estimates of survival derived from Kaplan-Meier estimator where animals are entered into the sample all at once at the beginning of the study (A) and with staggered entry over the first 30 days of the study (B). In each case the total sample size was 10 animals and in each case 2 of the 10 animals died; however, the cumulative survival estimates were not equal. To illustrate how the estimates were derived we have also shown the number of animals added to the sample (a_i) at time t, the number of animals that died (d_i), and the number of animals at risk (r_i).

effects that may exist early in the sample interval. This was less of a problem for adults after the first year because our sample from the previous year is retained; and newly captured animals merely supplement the existing sample. However, juveniles from the previous year could not be retained for our sample of juveniles because they are no longer juveniles (they were added to the adult sample after their first year). However, when animals are partitioned into multiple groups for comparison (e.g., region effects), the number of animals at risk at any given time (even for adults) may have been very low. Thus, we urge caution in interpreting our Kaplan-Meier estimates without taking into account the confidence intervals or number of animals at risk (r_i) at a given time. We have provided the details from each Kaplan-Meier analysis (including r_i) in appendices.

ASSUMPTIONS OF CORMACK-JOLLY-SEBER MODELS

Capture and Release Occurs Over Brief Time Interval– When this assumption is met all animals in the study should have been exposed to the risks of mortality for the same time (Burnham et al. 1987). This assumption also enables a clear definition of the interval over which survival is measured. The life history of Snail Kites makes this assumption difficult to meet. Snail Kites have a relatively long breeding season and are not particularly synchronous in their breeding attempts. Consequently, the time span over which fledging, and therefore banding, occurs can be relatively long. We have tried to minimize the violation of this assumption by limiting our resighting period to the peak four months of fledging (March-June). We do not believe that violation of this assumption caused substantial bias to our estimates. For adults, the highest risk of mortality appears to be during the fall and winter. Thus, animals within a given study year all experience the same period of high risk. For juveniles, the highest risk of mortality occurs over the first few months post fledging and again all juveniles within a given cohort were exposed to that period of high risk. Violation of this assumption does, however, present some ambiguity about the period of time over which survival is estimated. As described in our methods section, we have defined our estimates of survival from banding data roughly as survival from one breeding season to the next.

There is No Band Loss or Misreading of Bands– The loss of bands in studies of marked birds can produce a serious negative bias in survival estimates (Pollock 1981, Nichols and Hines 1993). We believe that the problem of band loss was negligible on our study because almost all (859 of 913= 94.1%) birds were marked with riveted aluminum bands that were virtually assured of remaining on the bird. The other 5.9% were made of PVC and anecdotal evidence suggests that band loss from these bands also was extremely low. There have been bands used on previous studies of Snail Kites that were made from other materials (e.g., plastic and Lynnply) more likely to have been lost (e.g., Bennetts et al. 1988, Snyder et al. 1989a); however, we had no birds with bands of these types in our sample. Thus, we believe the potential for band loss effects on our results was minimal.

We probably had greater potential for misreading bands than for loss of bands. The misreading of bands does not necessarily result in bias (unless there is some systematic pattern to the misreading) but may have an effect on the variance (G.C. White, Pers. Comm.). We tried to minimize this potential effect two ways. First, the numbering sequence of bands was controlled by the manufacturer (ACRAFT Sign and Nameplate Co. LTD) to minimize duplication errors. For example, numbers that can be read as a different number if the band were accidentally put on upside down (e.g., 6S and 9S) were not used in a combination that would allow accidental duplication of number combinations. For example the number "19" could be misread as "61" if the band were upside down. Thus, only one of these two numbers would have been used. Secondly, we did not record any band resighting until the observer was virtually certain that the number had been read correctly. Whenever possible, we also had a second observer verify the number. This carefulness in recording probably resulted in a lower overall resighting probability because some bands that the observer wasn't reasonably sure of went unrecorded; however, we were reasonably assured that errors from misreading bands were minimized.

Statistical Analyses are Based on Correct Model-- This assumption is the essence of all statistical inference and its violation can seriously affect parameter estimates (Burnham et al. 1987). In the strictest sense, this assumption is always violated; however, our model selection procedures and subsequent goodness-of-fit tests help to ensure that violations are within acceptable limits; however, when the reported model does not fit the data then concern about bias of the estimator is warranted (Lebreton et al. 1992).

Capture and Release Does Not Influence the Subsequent Resighting of Animals-- This is a common and long-recognized problem for studies requiring recapturing or resighting of animals (Pollock 1981, White et al. 1982). We had some evidence of minor violation of this assumption from our radio telemetry. A few radio-transmittered birds (i.e., <5%) would depart the immediate vicinity upon our approach after having been captured. However, these birds usually just move to a new perch a short distance away. We were usually able to still read the bands through a slow careful approach. In addition, many birds were nesting and would consequently return to the nest vicinity within a few minutes. There were a few (≈ 1%) non-nesting individuals, however, that upon our approach, would leave the vicinity and we would be unable to read their bands. There were also occasionally unmarked individuals that would depart the vicinity upon our approach, suggesting that some birds are inherently more wary, regardless of previous capture history. Because radio-transmittered birds often had a more traumatic capture experience (i.e., many were captured with a net gun) than birds that were merely banded as nestlings, we believe that our observations of radio-transmittered birds overestimates the extent of avoidance as a result of having been banded. Consequently, although our ability to relocate birds was probably influenced by birds having been captured, our observations of radio-transmittered birds suggests that this influence is not substantial.

Causes of Mortality

Although our sample size of dead birds was not large, it was sufficient to provide an indication of the relative frequencies of different causes of death. Predation appears to have been the most frequent cause of death for both adults and juveniles (Fig. 4-18). We caution, however, that without finding each carcass while it is still fresh and conducting a necropsy, it is impossible to distinguish predation form post-mortality scavenging. However, we usually had ancillary information, in addition to the carcass having evidence of having been eaten (e.g., >1 carcass at the site or the location inconsistent with a site normally used by Snail Kites), when predation was assigned as the probable cause of death (Table 4-31).

Emaciation was the second most frequent cause of death for juveniles, but was not an observed cause of death for adults during this study. Here we caution that our data were collected during non-drought years. During widespread droughts, when food may be scarce, emaciation may be a more frequent cause of death for both age classes. Emaciation may also have been underestimated in our sample. For example, we suggested that some juvenile deaths may have been included as "censored" birds as a result of birds dispersing to habitats atypical of adults and subsequently, less adequately searched. These areas may also be more likely to have less predictable food resources. Two of the emaciated birds were found in marine environments where apple snails are completely lacking.

Other causes of death included vehicle collisions, disease, and one probable gunshot. Vehicle collisions were observed for both age classes and one additional death from this cause was observed for an unbanded or radio-tagged adult (i.e., it is not included in this sample). Deaths from vehicle collisions may be more likely when nesting or foraging concentrations occur adjacent to roadways. One adult female died of an infection of the coelomic cavity. One juvenile may also have had an intestinal disease, but severe autolysis precluded conformation. The skeletal remains of one juvenile had a probable gunshot (shotgun) hole through its sternum, but we were unable to confirm if this was the cause of death.

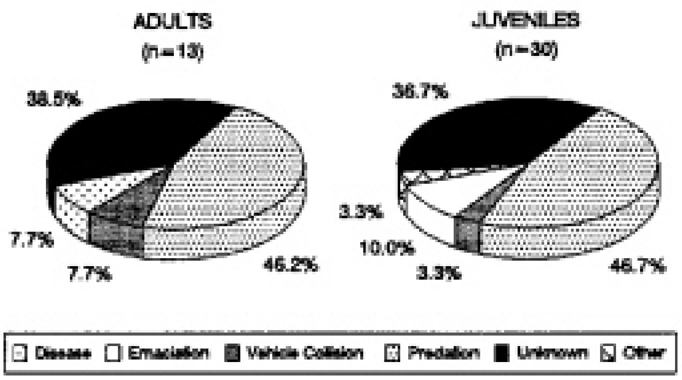


Figure 4-18. The percentage of mortality of adult and juvenile Snail Kites in each of 6 mortality classes. Particularly for causes of death in which a necropsy was not performed (e.g., predation), we can never determine the cause of death with certainty. However, we assigned mortality to each class only when ancillary evidence supported our conclusion. In the absence of such evidence, we assigned mortality to the unknown class.

Table 4-31. Known mortality of snail kites banded or radio-tagged during this study.

Year	Age	Location of Mortality	Probable Cause of Death
1992	JUV	WCA-3A	Predation[1]
1992	JUV	St Johns Marsh	Predation[1]
1992	JUV	Holmes Beach, FL	Emaciation[2]
1992	JUV	Florida Bay	Emaciation[2]
1992	JUV	Everglades Agricultural Area	Vehicle Collision[3]
1992	JUV	WCA-2A	Unknown[4]
1992	JUV	Agriculture Area (Collier Co.)	Unknown[4]
1993	JUV	West Palm Beach W.C.A.	Predation[1]
1993	JUV	Everglades National Park	Predation[1]
1993	AD	Lake Okeechobee	Predation[1]
1993	AD	Lake Okeechobee	Predation[1]
1993	AD	WCA-3A	Infection of Coelomic Cavity[5]
1993	JUV	Coquina W.C.D.	Unknown[6]
1993	AD	West Palm Beach W.C.A.	Unknown[5,7]
1994	JUV	WCA-3A	Predation[1]
1994	JUV	WCA-3A	Predation[1]
1994	JUV	WCA-3A	Predation[1]
1994	JUV	WCA-3A	Predation[1]
1994	JUV	Everglades National Park	Predation[1]
1994	JUV	Lake Kissimmee	Predation[1]

cont.

Table 31. Continued

1994	JUV	Loxahatchee N.W.R.	Predation[1]
1994	JUV	Loxahatchee N.W.R.	Predation[1]
1994	AD	Lake Kissimmee	Predation[1]
1994	AD	Lake Okeechobee	Predation[1]
1994	JUV	Everglades Agricultural Area	Unknown (not predation)[8]
1994	JUV	WCA-3A	Unknown (not predation)[8]
1994	JUV	Big Cypress National Preserve	Unknown (not predation)[8]
1994	AD	WCA-2A	Unknown (not predation)[8]
1994	AD	Lake Okeechobee	Unknown (not predation)[8]
1994	JUV	Lake Kissimmee	Unknown[4]
1994	JUV	Everglades National Park	Unknown[4]
1994	JUV	East Lake Tohopekaliga	Unknown[4]
1994	JUV	Lake Okeechobee	Unknown[4]
1994	JUV	C-111 Basin	Unknown[4]
1994	AD	East Lake Tohopekaliga	Unknown[4]
1995	AD	Lake Okeechobee	Predation[1]
1995	AD	Oesceola Co. (private land)	Predation[1]
1995	JUV	Lake Marion	Predation[1]
1995	JUV	East Lake Tohopekaliga	Predation[1]
1995	JUV	Lake Marian	Emaciation[2,9]
1995	AD	Glades Co. (State Highway 78)	Vehical Collision[2]
1995	AD	St. Johns Marsh	Unknown (not predation)[8,10]
1995	JUV	Lake Marian	Unknown[4]

[1] *Carcass showing clear signs of having been eaten (e.g., feathers plucked, bones broken) with additional ancillary evidence supporting having been taken by a predator (e.g., other carcasses found at the site, feathers of predator [Great-horned Owl], and location or conditions under which the carcass was found [e.g. on limbs of trees]). However, we can never be certain that some of these were not a result of scavenging after death.*

[2] *Based on necropsies performed by the National Wildlife Health Research Center.*

[3] *Bird found still alive along farm road with broken wing.*

[4] *Carcass too decomposed for evaluation.*

[5] *Based on necropsy performed by the University of Florida Laboratory of Wildlife Disease Research.*

[6] *Skeletal remains of bird banded by Jon Buntz (GFC) found at base of fence post. Small hole in sternum was consistent with shotgun pellet.*

[7] *Bird was in excellent nutritional health and had 3 snails in esophagus. No external signs of trauma.*

[8] *Carcass was completely intact (i.e., no sign of predation or scavenging), but was too decomposed for further evaluation.*

[9] *Bird was severely emaciated; however, some evidence of intestinal disease which may have contributed to death.*

[10] *Decomposition was too severe to determine cause of death, but bird was emaciated.*

Previous Estimates of Survival

There have been several previous reports of estimated survival (e.g.,Snyder et al 1989a, Beissinger 1995). To our knowledge these estimates emerged primarily from 3 sources of information: (1) the annual count, (2) a study by Snyder et al. (1989a) with banded birds, and (3) a study by Snyder et al. (1989a, 1989b) using radio transmittered birds.

Snyder et al. (1989a) reported the results of resighting birds banded from 1968-1978. They did not use standard capture-recapture methodology (i.e., CJS models) presumably because of a lack of sufficient data for most years. They point out that only a fraction of the birds were checked for bands in any given year. Consequently, they estimated a range for **minimum** annual survival, taking into account all possible band loss. Thus, actual survival estimates from these data would range from their lower minimum estimate to 1.0. All of the resightings they report were from 1979 when their resighting effort was most intensive. Consequently, their estimates of minimum annual survival also confound adult and juvenile survival since all birds, except those banded in 1978, were banded as nestlings and resighted as adults. The estimate for birds banded in 1978 would not confound adult and juvenile survival, since the estimates were only for minimum survival of their first year (i.e., the estimate was for juveniles only). For 4 of 10 years their lower estimate was 0 (i.e., actual survival ranged from 0.0 to 1.0) and the average of their lower estimates was 0.47 (i.e., survival ranged from 0.47 to 1.00). They suggested that adult survival probably exceeds 0.9 under good conditions, but did not present any estimation procedure to support this suggestion. Beissinger (1995) later reported adult survival during high-water years was 0.95 (±0.03 SD). He reported that these estimates were projected from the studies by Snyder et al. (1989a, 1989b); however, he reported no estimation procedure for either survival or its standard deviation; nor could we find such procedures in the sources cited. Beissinger later informed us (S. Beissinger, pers. comm.) that these were estimates in the sense of approximations and were not derived using a statistical estimator (e.g., maximum likelihood), and that the standard deviations were intended as a way of dealing with the uncertainty of the survivorship information in his stochastic model.

Estimates of survival during droughts, particularly the 1981 drought, have been frequently reported based on changes between years in the annual count (e.g., Beissinger 1986, 1988, 1995, Takekawa and Beissinger 1989). The count in 1980 (before the 1981 drought) was 652 birds (Sykes et al. 1995)(reported as 654 by Rodgers et al. [1988]). The count made in December of 1981 (after the drought) was 109 birds (an 83% decline in the count)(Rodgers et al 1988, Sykes et al 1995); although an alternative count for 1981 of ≈ 250 (done independently by Beissinger [1982, 1984] in March of 1982) is often substituted for the state-conducted count, implying a population decline of 60% (e.g., Beissinger 1984, 1986, 1988, 1995, Takekawa and Beissinger 1989). We suggest that using the annual count for estimating survival is not scientifically valid because it is subject to multiple sources of error that are inconsistent among years (discussed in detail in chapter on *Monitoring Snail Kite Populations in Florida*). Estimating survival from the annual survey during a drought is particularly suspect because it is well known that Snail Kites disperse in large numbers to peripheral wetlands during droughts, where counts are not conducted (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989) and this dispersal has not been taken into account in these survival estimates. Snyder et al. (1989a, 1989b) reported that at least 7 of 8 (one was of unknown fate) radio transmittered birds survived from May 1981 (just prior to the peak of the 1981 drought) until their study period of 1982. Although their sample size was small, this implies an estimate of survival during droughts as 0.875 (rather than the 0.17 - 0.40 inferred from the annual count). If these data are considered as following a binomial distribution (and assuming that the unknown bird was dead), then a 95% confidence interval would be 0.65 - 1.00 and does not even include the estimates inferred from the annual count. Beissinger (1995) later suggests that these data are more applicable as lag-year (the year following the drought) estimates because radios were attached toward the latter part of the actual drought after these birds had survived some of the dropping water levels and the risks associated with dispersal to Lake Okeechobee. We disagree for several reasons. First, our data show that the risks associated with dispersal are encountered on a regular basis (i.e., approximately 25% of the population disperses every month) whether there is a drought or not. We do agree that the risks of predation may be greater in peripheral habitats because of increased proximity to upland habitats and their associated predators (particularly Great-horned Owls); however, dispersal to these habitats is not likely to be extensive until alternative wetlands have dried (i.e., at the peak of the drought). We also suggest that much of the mortality associated with droughts will occur during the peak of the drought and during the first winter after a drought, when depressed food levels are compounded by cold temperatures, which decrease food availability even further (Cary 1983, 1985). Both of these periods of high risk were included in their sample of radio-transmittered birds and therefore should better represent drought-year, rather than lag-year, conditions. However, regardless of how these data are interpreted, there still remains a need for credible estimates of drought-related survival.

Chapter 5. REPRODUCTION

Because the focus of this report is on demography, we have concentrated our attention in this chapter on estimates of reproductive parameters. There are numerous papers on other aspects of reproduction (e.g., behavioral ecology) which we have given less attention but encourage interested readers to seek out (e.g., reviewed by Beissinger 1988, Sykes et al. 1995).

Reproduction of Snail Kites has been well studied; although significant gaps remain in our knowledge. There also exist several areas of disagreement among researchers regarding interpretation of existing data and literature. Here, we present a combination of original data and a synthesis of the existing literature on reproduction. We have attempted to explicitly point out any areas where disagreement among researchers exists, and to provide detailed explanations for our interpretations.

From a demographic perspective, what is ultimately of interest is the mean fecundity rate of females in each age class (Caughley 1977); that is, the mean number of young (or sometimes just the mean number of female young) produced per female of each age class in the population. Unfortunately, for many species, including Snail Kites, we cannot estimate this parameter directly. Rather, it is derived from the proportion of birds attempting to breed (α_i), the proportion of breeding attempts that are successful (S_i), and the number of breeding attempts per year (β_i). For successful nesting attempts, we also need to know the number of young produced (Y_i) and the sex ratio of the young produced (R_i) (Brown 1974, Caughley 1977)(Fig. 5-1). In this chapter we review the information that has been previously reported on each of these parameters, as well as present estimates based on new data.

SEMANTICS

Misunderstandings about measures of reproduction can frequently be attributable to a lack of clear definitions of what is being measured and/or to what is appropriate to be measured. We will address the latter type of misunderstanding in our discussions below; however, to avoid the former type, we will begin our

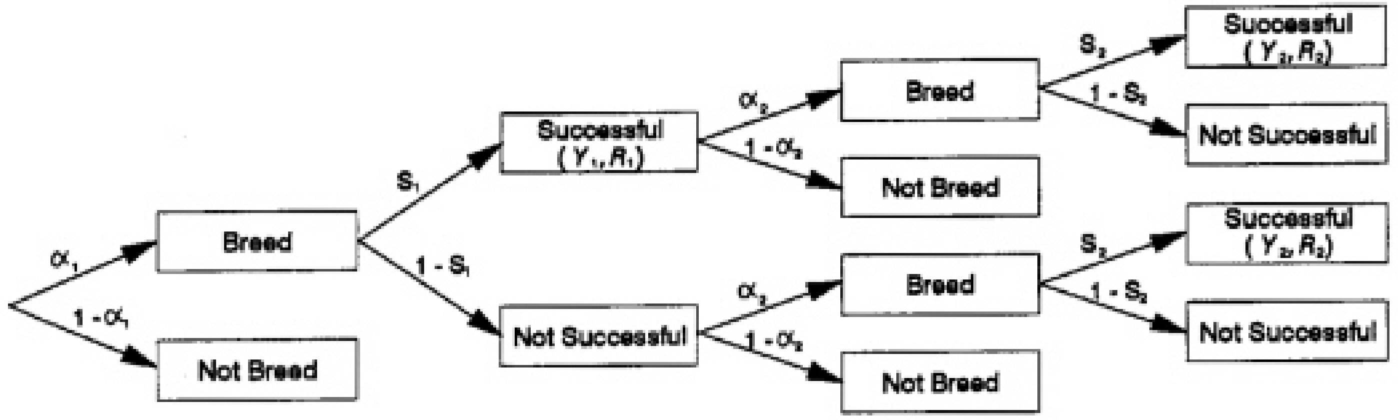


Figure 5-1. Conceptual diagram of reproductive parameters used to estimate fecundity. Show here for simplicity is model for 2 nesting attempts; although more attempts are possible within a given year.

assessment of reproduction by providing operational definitions for terms discussed below.

Breeding Attempt– There has been considerable disagreement among researchers regarding what constitutes a breeding attempt. For the purposes of this report, we consider a breeding attempt to begin with the laying of the first egg Steenhof (1987). Snyder et al. (1989a) considered a breeding attempt to begin with nest building, prior to the laying of the first egg. They suggested that to ignore the period before egg laying in analyses of reproductive success would be ill-advised because of the high proportion (>0.33) of nests they observed that failed prior to egg laying. We agree entirely with Snyder et al. (1989a) that, for many questions, the failure of nests prior to egg laying may have important biological implications. These failures may provide insight as to environmental conditions at the time of egg laying and also may provide information regarding behavioral aspects of mate choice. However, we disagree that nests during the nest-building stage for this species should be considered as a nesting attempt for estimation of reproductive parameters. We have several reasons for this conclusion.

First, inclusion of "pre-laying" failures may include nests in which a pair bond has not even been established between a male and female. Nest building is initiated by the male as part of courtship (Beissinger 1988, Bennetts et al. 1988) and more than one male may direct courtship toward a single female (Beissinger 1987, pers. obs.). Thus, if two males initiated nest building as part of the courtship toward a single female, this would be considered as two nesting attempts using the definition of Snyder et al. (1989a), even though only one of these nests may produce young. Similarly, our observations indicate that a single male may exhibit courtship behavior, including nest building, towards several females in succession. This behavior may last as little as a few hours or may last several days and may then be redirected to a new female if a pair bond is not established. We observed a single radio-tagged male direct courtship to as many as five different females before a pair bond was established that resulted in egg laying. Using the definition of Snyder et al. (1989a), each of these courtship attempts would have been interpreted as a failed breeding attempt. In contrast, we view this as part of the mate selection (courtship) process rather than as a demographic parameter.

Second, the passage of cold fronts and corresponding temperature change often results in reduced food availability (Cary 1985). Consequently, courtship is often terminated with the passage of cold fronts and resumed (often at a new location) when temperatures return to pre-front conditions (Beissinger 1988, Bennetts et al. 1988). Thus, if two cold fronts passed before eggs were actually laid, the pair would have been considered to have made three separate breeding attempts (with two failures) even if the pair successfully raised a brood. For demographic purposes, we view these postponements as courtship interruptions, rather than multiple breeding attempts with each interruption being considered as a breeding failure. Third, because nest building begins with the placement of the first stick and many more courtship nests are probably initiated than are ever detected, it creates a substantial bias in the estimate of success if these early starts are not detected (Mayfield 1961, Miller and Johnson 1978, Johnson 1979, Hensler and Nichols 1981).

Finally, it is well known that nesting raptors tend to be considerably more sensitive to disturbance early in the nesting cycle (Grier and Fyfe 1987, Steenhof 1987). Although previous investigators have reported a high proportion of nest abandonment by Snail Kites prior to egg laying (e.g., Beissinger 1986, Snyder et al. 1989a), we have seen no accounting for how much of this abandonment might be attributable to disturbance by the investigators themselves. In contrast, abandonment of eggs or young by Snail Kites is extremely rare (Bennetts et al. 1994, Sykes et al. 1995). Thus, measuring nesting success after the first egg has been laid can reduce this potential source of confounding and minimize disturbance to this endangered species.

Based on these concerns, we define a breeding attempt to begin with the laying of the first egg. Thus, unless otherwise stated, references to nests in this report implies the presence of eggs or young.

Successful Nest-- For the purposes of this report, a successful nest is one in which at least one young reaches fledging age (Steenhof 1987). Because birds after fledging may or may not be present at the nest, we defined fledging age as 80% of the average age of first flight (Steenhof and Kochert 1982). Snail Kites are capable of first flight at approximately 30 days of age (Chandler and Anderson 1974, Beissinger 1988, Bennetts et al. 1988); thus, we considered a nest as having been successful if it produced young that survived to at least 24 d (Bennetts et al. 1988). At this age, animals are reasonably assured of still being at the nest and mortality for most raptors between this time and fledging is minimal (Milsap 1981, Steenhof 1987). In addition, we banded birds at the time they were determined to be of fledging age. Consequently, any mortality that occurred after this age would have been included in our estimates of juvenile survival from our mark-resighting program.

The Breeding Season

The initiation of nests (i.e., egg laying) has been documented in all months of the year (Sykes1987c); although, for any given year, Snyder et al. (1989a) observed a maximum breeding season (interval over which nests were initiated) of 31.7 weeks (7.9 months) during an 18-year study in Florida. Although Snail Kites in Florida can potentially lay eggs in all months of the year, there is a very distinct seasonal distribution of nest initiations (Table 5-1) (Fig. 5-2). Nest initiations begin as early as November, but in most years widespread initiations usually do not begin until January or February. Peak initiations usually occur in March, but are often several weeks later, peaking in April, in the northern habitats (Toland 1994).

Table 5-1. The number of nest initiations reported in each month during studies from 1966 through 1995.

Month	Sykes (1987c)	Snyder et al. (1989a)[1]	Snyder et al. (1989a)[2]	Bennetts et al. (1988)[3]	Toland (1994)[4]	This Study[5]	Total[6]	Proportion of Total
OCT	5	0	0	--	0	0	5	0.00
NOV	9	9	8	--	0	0	17	0.01
DEC	5	35	35	--	0	7	47	0.04
JAN	26	90	81	14	3	74	184	0.16
FEB	35	98	78	102	22	66	201	0.17
MAR	36	147	119	125	49	106	310	0.26
APR	21	114	103	102	53	40	217	0.18
MAY	10	64	56	32	19	17	102	0.09
JUN	5	44	38	0	16	0	59	0.05
JUL	1	27	25	0	5	0	31	0.03
AUG	2	1	1	--	0	0	3	0.00
SEP	1	0	0	--	0	0	1	0.00
Total	156	629	544	375	167	310	1177	

[1] *Includes all years reported by Snyder et al. (1989a).*

[2] *Includes only years reported by Snyder et al. (1989a) to have wide seasonal coverage (1970-1982).*

[3] *Unpublised data from nests reported by Bennetts et al. (1988). Seasonal coverage was limited to January through July.*

[4] *Unpublished data courtesy of B.R. Toland from nests reported by Toland (1994).*

[5] *Based on data from 1994 and 1995.*

[6] *Based only on data with wide seasonal coverage (Sykes 1987c, Snyder et al. 1989a [1970-1982 only], Toland 1994, and this study.*

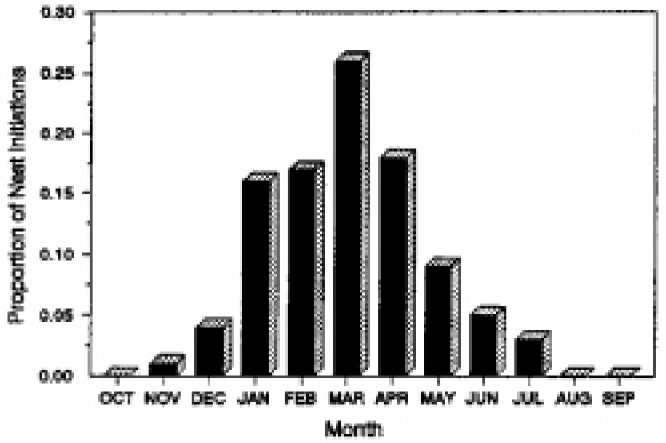


Figure 5-2. The proportion of nest initiations for each month of the year based on cumulative data reported by Sykes (1987c), Snyder et al. (1989a)(1970-1982 only), Toland (1994), and this study.

The Breeding Population

AGE OF FIRST REPRODUCTION

Sykes (1979) reported that Snail Kites are capable of breeding at 3 years of age. However, Sykes (1979) suggested that some birds possibly breed at a younger age. Beissinger (1986) later reported both male and female birds breeding at one year of age and Snyder et al. (1989a) reported one female breeding at nine months. Our data are consistent with Beissinger (1986) and Snyder et al. (1989a). During this study, we commonly observed yearling Snail Kites attempting to breed.

PROPORTION OF BIRDS ATTEMPTING TO BREED

Adults- Nichols et al. (1980) suggested that the proportion of birds that attempted to breed during favorable conditions was quite high. They suggested that there was no reason to suspect that it was not 1.0 and, consequently, assumed that value for their demographic model. They reported, however, that this was a crude estimate for lack of a better one. Beissinger (1995) similarly reported that the proportion of adult Snail Kites attempting to breed during high-water years was 1.0, but also provided no empirical evidence. Although our data for this parameter are very limited, they are consistent with these earlier estimates. During 1995, we closely monitored 25 radio-transmittered adult Snail Kites for breeding activity in order to assess the proportion attempting to breed and the number of breeding attempts per year. Of these 23 adults, 14 were females and 9 were males. During the 1995 nesting season, we located each bird on the ground approximately bi-weekly to determine its breeding status (e.g., a nest, courtship, not breeding). Birds in which no breeding activity was detected were generally observed for ≥2 hrs and subsequent visits, usually within 10 days, were required to confirm a non-breeding status and to confirm any nests for birds exhibiting courtship. During 1995 (a relatively high water year throughout the kite's range), all 23 (100%) adults attempted to breed at least once. Our estimate is based on a relatively small sample (N=23) and on only one year; however, it does provide an empirical basis that most, if not all, adults may attempt to breed in some years.

Sykes (1979) reported that he observed no nesting attempts during 1971 (a widespread severe drought; see *Management and Conservation*). Based on this observation, Nichols et al. (1980) assumed that no birds nested during 1971 for their demographic modeling effort. Beissinger (1986) reported that during the 1981 drought 80-90% of the kites did not attempt to nest, and Beissinger (1995) later reported that only 15% of adult Snail Kites attempt to breed during drought years. However, no empirical evidence was presented in support these estimates. Based on anecdotal evidence, we believe that the proportion of birds attempting to breed during drought years may be highly variable depending on the spatial extent of the drought (see discussions on *Water Management and Snail Kites* in *Management and Conservation*). We agree that during a severe widespread drought, most birds probably do not attempt to breed. However, in cases of more localized droughts, where portions of the kite's range may not be experiencing dry conditions, the proportion of birds attempting to breed may remain very high. For example, during 1991, the Everglades region was at the end of a 2-3 year drought (whether it was a 2 or 3 year drought depends on how a drought is defined). During this year almost no nesting activity was observed in the Everglades region (J.A. Rodgers Jr., pers. comm.). This would appear consistent that a small proportion of birds had attempted to breed. However, during this year, record numbers of birds were nesting on Lake Tohopekaliga (J.A. Rodgers and J. Buntz, pers. comm.) and in the upper St. Johns Marshes (B. Toland, pers. comm.), areas not influenced by the drought conditions in the Everglades. Our data on movement strongly suggest that the Florida population is one population that moves frequently throughout its range, rather than a meta-population of quasi-isolated subpopulations (see *Movements*). Thus, in years where drought is not widespread, birds may merely shift the location of nesting activities. Consequently, we suggest that this parameter may be quite variable and needs to take into account the severity and spatial extent of a given drought.

Sykes (1979) observed relatively few (n=6) nests during 1972, the lag year following the 1971 drought. The average number of nests per year that Sykes (1979) reported from 1968-1976, excluding 1971, was 23. Based on this observation of reduced nesting during this lag year, Nichols et al. (1980) assumed a proportion of 0.5 adults attempted to nest during 1972. Beissinger (1995) reported that a proportion of 0.8 adults attempt to breed during lag years, although we could find no empirical support for this estimate in any of the sources cited. We suspect that, similarly to drought years, this parameter may be highly variable depending on the specific drought. Thus, we view this parameter as also being unknown and subject to high variability.

Subadults-- Snail Kites have been reported to breed as young as 9 months old (Snyder et al. 1989a); thus, by a calendar-year definition Snail Kites are capable of breeding as juveniles (i.e., < 1 year old). However, these cases are ones in which the birds attempted to breed during the nesting season following the nesting season of their hatch year. Thus, this parameter should be defined as the proportion of birds attempting to breed during their second breeding season (the first is the one in which they hatched).

Based on data from Snyder et al. (1989a), Beissinger (1995) reported that 25% of subadults attempt to breed during high water conditions. Snyder et al. (1989a) observed 8 banded subadults breeding during 1979 out of a minimum of 74 that had survived from their hatching year of 1978. Because Snyder et al. (1989a) only checked 50.8% of the nests for bands, they estimated that there were probably 16 subadult breeders out of a minimum of 74 banded subadults (22%). Of course, this estimate assumes that only the 74 subadults observed alive in 1979 had survived and that there was an equal probability of detecting a banded subadult that was breeding in the sample of nests that were checked and those that were not checked.

During 1992, we estimated a similar percentage of 17% of the subadult birds attempting to breed (Bennetts and Kitchens 1992). Our estimate was based on only 2 breeding birds of 12 banded yearlings that we observed during the 1992 breeding season. Consequently, our estimate requires similar assumptions that we suggested above for Snyder et al. (1989a).

During 1995 (a high water year throughout the kite's range), we also closely monitored 9 radio-transmittered juvenile Snail Kites for breeding activity (as described above). Of these 9 birds 3 (33%) attempted to breed. All of the estimates derived from the data of Snyder et al. (1989a), as well as from our own data, are very limited (i.e., small samples each from one year); however, they do consistently suggest that a relatively small proportion of subadults do attempt to breed during some years.

Beissinger (1995) also reported that the proportion of subadults attempting to breed during drought years and lag years was 0.15. We could find no empirical basis for this estimate in any of the sources cited; but we agree with Beissinger that the average percentage would probably be lower when conditions are poor in part or all of their range.

Nest Success

Nest success has been among the most widely estimated parameters of reproduction of Snail Kites. However, it has probably also been among the most confusing. There are several areas of disagreement among researchers regarding estimation of nest success. The disagreements center primarily on which nests should be included in the sample and what estimator should be used. Consequently, nest success has been difficult to compare because different researchers have used different estimators and have included or excluded different categories of nests within their respective data sets. We have attempted to summarize below the major issues of contention. We have also summarized the literature on nest success and explicitly pointed out which estimator was used and what categories of nests were included or excluded in the sample. Thus, readers can make comparisons among studies and decide for themselves which estimates are most appropriate for their particular needs.

AREAS OF DISAGREEMENT REGARDING ESTIMATION OF NEST SUCCESS

Inclusion or Exclusion of Nests Found at Different Stages- At what stage a given nest is found can greatly influence its probability of success. Nests found late in the nesting cycle have a higher probability of success because they have less observation time during which they are at risk. A Snail Kite nest requires at least 57 days to fledge young (27 days of incubation and 30 days for nestlings to reach fledging age). Thus, a nest found during egg laying will have potentially >50 days "at risk" (provided it does not fail earlier) to be considered successful. In contrast, a nest found close to the time of fledging may have only a few days "at risk" to be considered successful. Consequently, estimates of nest success that were derived using nests found late in the nesting cycle tend to be biased high (Mayfield 1961, 1975, Miller and Johnson 1978, Hensler and Nichols 1981, Hensler 1985).

Nests at different stages also are vulnerable to different risks. For example, rat snakes (Elaphe obsoleta) are believed to be one of the major predators of Snail Kite nests (Bennetts and Caton 1988). Rat snakes will readily take eggs or young that are less than one week old; however, the larger size of older nestlings largely precludes predation by rat snakes. Consequently, nests found when young are > 1 week have an inherently lower risk of predation by rat snakes.

Some researchers (e.g., Beissinger 1986, Snyder et al. 1989a) also have included nests prior to eggs having been laid (i.e., during nest building) in deriving estimates of success. We disagree with this practice for the reasons previously discussed (see definition of *Breeding Attempt* in earlier section of this chapter on *Semantics*).

Because of these biases, estimates of nest success can be substantially influenced by what nests (i.e., found at what stage) are included or excluded for deriving a given estimate. This makes comparison of previous estimates of nest success for Snail Kites difficult because researchers have not used the same criteria for inclusion or exclusion of nests found at different stages when deriving their estimates. Steenhof and Kochert (1982) suggested three ways to minimize this type of sampling error for estimating nest success. First, they suggest estimating success based on a pre-determined sample of territorial pairs. However, because Snail Kites do not maintain nesting territories from one year to the next, this solution is not feasible for this species. Secondly, they suggested using estimates derived only from nests that were found during incubation (by definition, they considered a breeding attempt to have begun after they laying of the first egg). This suggestion is feasible for kites; but of the previously reported estimates, only Snyder et al. (1989a) reported estimates using this criterion (but they also included manipulated nests for which some strong assumptions were made; see discussion of *Manipulated Nests* below). Their third suggestion was to use the Mayfield Estimator (see discussion of *Mayfield vs Conventional Estimators* below), which is intended to account for the bias imposed by not finding all nests during early stages. Of the previously reported estimates, only Bennetts et al. (1988) reported estimates using this estimator.

Given the differences in what nests were included or excluded in previous studies, we urge caution in making comparisons among previous studies. We also agree with Steenhof and Kochert (1982) that estimates of success should be derived either using only nests that were found during incubation or using the Mayfield estimator. Of these two approaches we prefer the latter (discussed below in section on *Mayfield vs Conventional Estimators*), although there remains disagreement among researchers regarding this conclusion.

Manipulated Nests- Nests that occur in cattails may have a tendency to collapse under conditions of high winds or waves (Sykes and Chandler 1974). This led to a previous practice of placing nests that were subject to this type of failure in artificial nest baskets (Chandler and Andeson 1974, Sykes and Chandler 1974). Because this may influence the outcome of a given nest, whether to include or exclude these nests has been the subject of some debate (e.g., Beissinger 1986, Snyder et al. 1989a). Similarly, when these nests have been included in samples from which estimates of nest success were derived, there have been differences among researchers (e.g., Sykes 1979, Snyder et al. 1989a) as to how these nests were treated in the derivation of nest success.

Sykes (1979, 1987b) included 43 nests that were placed in artificial nest baskets in his sample for estimating success. These nests were not treated differently than other nests. Snyder et al. (1989a) later criticized this use of manipulated nests. They suggested that the success of manipulated nests was higher than if they had not been manipulated, and that this would have biased Sykes's estimate of success upward. Snyder et al. also presented estimates of nest success using 94 manipulated nests. They argued that because these nests were in imminent danger of collapse, they considered them all as failures. They suggested that to exclude them, as was done by Beissinger (1986) and Beissinger and Snyder (1987), would have also biased success upward because these manipulated nests were not a random sample with regard to their probability of success (i.e., that they would have failed). In contrast to their suggestion, we have observed collapsed nests containing older (> 10 d old) nestlings that have been successful. Although we agree with Snyder et al. (1989a) that exclusion of these nests probably would have biased success upward, we also believe that including them all as failures probably would have biased their estimate slightly downward. Our tendency is to agree with the solution of Snyder et al. (1989a), but to accept that there might be a slight bias toward underestimation of success.

An additional concern that has not been addressed by previous authors is that the susceptibility of nests to collapse may be influenced by the investigators themselves. The vulnerability of nests to collapse can be greatly influenced by the paths of airboats while conducting nests visits, particularly in cattails (Bennetts 1996). Airboat trails are often wide enough to allow increased susceptibility to wind damage and/or to weaken the structural support provided by the cattails adjacent to the nest. This type of damage can be minimized, if not eliminated, by maintaining a substantial distance from the nest during an approach and either wading in to nests or using a mirror pole from a distance to check them (Bennetts 1996). Nest baskets have not been used in recent years and we do not anticipate (or advocate) a recurrence of their use. Although some nest collapse still occurs in some areas, particularly on lakes (J.A. Rodgers, pers. comm.), we do not believe that the benefits of nest baskets warrant the effort or disturbance for their use as a general management tool. They may, however, be warranted for isolated special circumstances. Previous use of nest baskets had been initiated when numbers of Snail Kite probably were much lower than are currently found. We do, however, advocate that researchers must exercise extreme care to avoid influencing the outcome of nests being monitored.

Mayfield vs Conventional Estimator- Mayfield (1961, 1975) proposed an estimator for nest success that was based on daily exposure (risk) such that a daily probability of success was derived using only those days in which a given nest was under observation. Overall success is then derived by applying the daily success over the length of the interval being estimated. This approach provides an estimate of success that is unbiased with respect to when a given nest was found, but requires an assumption that the probability of success is constant over the period (e.g., incubation) being estimated. Hensler and Nichols (1981) later showed, using Monte Carlo simulations, that this estimator was superior to the conventional estimator under a wide variety of conditions.

Bennetts et al. (1988) used the Mayfield estimator for nest success of Snail Kites and found it to perform favorably for this species. They found some violation of the assumption of constancy (e.g., success differed between incubation and nestling stages); however, this assumption can be overcome by using separate estimates for periods that differ (Hensler and Nichols 1981). Snyder et al. (1989a) later argued that the Mayfield estimator was inappropriate for Snail Kites because the interval length for nest building was too variable to apply this estimator. We agree with Snyder et al. (1989a) that the Mayfield estimator would be inappropriate for estimation of success during the nest building stage. However, we also believe that the nest-building period is inappropriate to include in estimates of nesting success for this species (see discussion of *Breeding Attempt* in earlier section of this chapter on *Semantics*). Consequently, we disagree with Snyder et al. (1989a) that the Mayfield estimator is inappropriate for estimating nesting success of Snail Kites. Rather, we agree with Hensler and Nichols (1981), Miller and Johnson (1978), Steenhof and Kochert (1982), and Steenhof (1987), that this estimator is preferable to conventional estimates of nesting success because of its ability to produce unbiased estimates of nesting success.

ESTIMATES OF NEST SUCCESS AND ITS PROCESS VARIANCE

Given the wide disagreement among researchers regarding nesting success, we suggest that future researchers be specific about what is being included or excluded, and that consideration be given to reporting success both by conventional and Mayfield estimators so readers have the ability to compare their results. We have also provided a summary of the previously reported estimates, showing what nests (i.e., found at what stage) were included in each estimate, whether or not manipulated nests were included, and which estimator was used (Table 5-2).

We estimated the mean annual nest success $(\hat{S}_x)$ as 0.32 based on reported nest success from each year using estimates that were based on nests (in which at least one egg has been laid) that were found during the egg stage (Table 5-3). However, some years had extremely low sample sizes, which may have precluded a reliable estimate for that year. If we had excluded estimates for those years with < 10 nests, we would have estimated mean annual nest success $(\hat{S}_x)$ as 0.28.

Estimate of Process Variance-- It is important to recognize that there are several distinct variance components associated with demographic parameters (White et al. 1982, Burnham et al. 1987). A demographic parameter (e.g., survival) may vary over time (temporal variation) or among locations (spatial variation). There is also likely to be heterogeneity among individual (individual variation) in their probability of survival due to genetic or phenotypic variation (DeAngelis and Gross 1982). Each of these sources of variation are a type of population variation (Burnham et al. 1987). There is also variation attributable to sampling populations. Unlike these previous sources of variation, sampling variation is not a measure of population variability, but rather is a measure of sampling error. This latter source of variation is important because it provides a measure of the certainty for a given parameter estimate. However, for demographic modeling, what is important is the actual variability of parameter over time, space, and

Table 5-2. Mean annaul nest success from major studies conducted since 1968. A successful nest is considered a nest in which at least one young fledged. Also shown are the estimator used to estimate success, whether or not nests placed in nest baskets were included in the estimate, and whether or not nests found in each of 3 stages were included in the estimate.

$\bar{x}$ Annual Success	Range	Years	Location(s)[a]	N	Estimator	Includes Baskets	Stage Found: Nest Building	Stage Found: Inc.	Stage Found: Nestling	Source
54%	17-85%	68-76	1,2,3,4,5,6	175[b]	Conv[c]	Yes[d]	No	Yes	Yes	Sykes (1979)
56%	17-85%	68-78	1,2,3,4,5,6	204	Conv[c]	Yes[d]	No	Yes	Yes	Sykes (1987b)
21%	0-41%	78-83	2,3,4,5,6,7	331	Conv[c]	No	Yes	Yes	No	Beissinger (1986)
30%	23-36%	86-87	4	367	Mayfield[e]	No	No	Yes	Yes	Bennetts et al. (1988)
38%	30-46%	86-87	4	367	Conv[c]	No	No	Yes	Yes	Bennetts et al. (1988)
31%	21-40%	86-87	4	358	Conv[c]	No	Yes	Yes	No	Bennetts et al. (1988)
35%	26-44%	86-87	4	317	Conv[c]	No	No	Yes	No	Bennetts et al. (1988)[f]
9%[g]	0-30%	68-83	4,5,6,7	236	Conv[c]	Yes[h]	Yes	No	No	Snyder et al. (1989)
29%[g]	0-100%	68-83	4,5,6,7	256	Conv[c]	Yes[h]	No	Yes	No	Snyder et al. (1989)
23%[g]	0-100%	68-83	4,5,6,7	499	Conv[c]	Yes[h]	Yes	Yes	No	Snyder et al. (1989)
29%	8- 55%	90-93	8	167	Conv[c]	No	No	Yes	No	Toland (1994)
58%	53-63%	94-95	1,2,3,4,5,6,7	233	Conv[c]	No	No	Yes	No	This study

[a] *Locations are: WCA-1 (1), WCA-2A (2), WCA-2B (3), WCA-3A (4), Lake Okeechobee (5), Lake Kissimmee (6), Lake Tohopekaliga (7), and Upper St. Johns Marsh (8).*

[b] *Differs from 183 reported by source author because success was unknown for 8 of the 183 nests.*

[c] *Conventional- Success estimated as (# Successful Nests/Total # Nests)*

[d] *Nests placed in nest baskets were treated as all other nests.*

[e] *Success estimated using maximum likelihood estimator (MLE) described by (Mayfield 1961, 1975, Hensler and Nichols 1981).*

[f] *Was not reported by Bennetts et al. (1988), but data from their study were avalaible to derive estimate.*

[g] *Not reported by source authors, but estimated from annual success in Snyder et al. (1989a, Table 2). Annual success for 1978-1983 was reported seperately for lakes and WCA-3A by source authors, but combined here for estimate of mean annual success. All years were included in estimate regardless of sample size.*

[h] *All nests placed in nest baskets were considered to have failed.*

among individuals (collectively called process variance). For modeling populations, sampling variation is a source of noise and should be removed from the overall variance estimate. Burnham et al. (1987) provided the theoretical framework and formulae for estimating process variance. We used this framework to estimate process variance for nest success based on estimates reported from 1968-1995 using only nests found after the first egg was laid, but before hatching. Based on the data from table 5-3, we estimated $\hat{\sigma}^2=0.08$ and $\hat{\sigma}=0.28$.

INFLUENCES OF NEST SUCCESS

There are a multitude of factors that could potentially influence the outcome of Snail Kite nests. Factors that have been reported to significantly affect nest success include location (i.e., area)(Snyder et al. 1989a), water levels (Sykes 1987b, Bennetts et al. 1988, Snyder et al. 1989a, Toland 1994), date of initiation (Bennetts et al. 1988), nest substrate (Snyder et al. 1989a, Toland 1994), nest height (Bennetts et al. 1988, Toland 1994), distance to land (Sykes 1987c), and interspecific coloniality (Snyder et al. 1989a). We used logistic regression to test for the influence of each of these effects, except interspecific coloniality, on a sample of 854 nests using data from Bennetts et al. (1988), Toland (1994, unpubl. data), and this study. Our preliminary univariate analysis, which had a liberal rejection criterion of $\alpha=0.25$ (see methods) for each effect indicated that all of these effects warranted retention for further analysis (Table 5-4). However, our results indicated that the specific substrate, rather than herbaceous versus woody, was warranted for further consideration. Similarly, our results indicated that a categorical threshold distance to land of less than or greater than 200m (Sykes 1987c) was warranted for further consideration, rather than the actual distance.

Although our preliminary univariate analysis supported the retention of these effects, a multivariate analysis with each of the retained effects (but lacking interaction terms) indicated that only year and date of

Table 5-3. Annual nest success reported during studies from 1968 through 1995. Nest success was based on nests found during the egg stage.

Year	No. Nests	No. Successful	Nest Success $(\hat{S})$	Sampling Var $(\hat{S})$[a]	Source
1968	1	1	1.00	0.0000	Snyder et al. (1989a)
1969	--	--	--	--	--
1970	1	1	1.00	0.0000	Snyder et al. (1989a)
1971	--	--	--	--	--
1972	3	1	0.33	0.0741	Snyder et al. (1989a)
1973	18	4	0.22	0.0096	Snyder et al. (1989a)
1974	13	0	0.00	0.0000	Snyder et al. (1989a)
1975	15	0	0.00	0.0000	Snyder et al. (1989a)
1976	18	0	0.00	0.0000	Snyder et al. (1989a)
1977	13	2	0.15	0.0100	Snyder et al. (1989a)
1978	59[b]	25	0.42	0.0041	Snyder et al. (1989a)
1979	78[b]	42	0.54	0.0032	Snyder et al. (1989a)
1980	2	0	0.00	0.0000	Snyder et al. (1989a)
1981	5[b]	0	0.00	0.0000	Snyder et al. (1989a)
1982	12[b]	1	0.08	0.0064	Snyder et al. (1989a)
1983	18[b]	5	0.28	0.0111	Snyder et al. (1989a)
1984	--	--	--	--	--
1985	--	--	--	--	--
1986	107	28	0.26	0.0018	Bennetts et al. (1988)
1987	210	92	0.44	0.0012	Bennetts et al. (1988)
1988	--	--	--	--	--
1989	--	--	--	--	--
1990	26	2	0.08	0.0027	Toland (1994)
1991	39	8	0.21	0.0042	Toland (1994)
1992	59	33	0.55	0.0042	Toland (1994)
1993	43	14	0.33	0.0051	Toland (1994)
1994	57	36	0.63	0.0041	This study
1995	176	94	0.53	0.0014	This study

[a] *Sampling variance was not reported by the source authors, but was estimated based on a binomial distribution.*

[b] *Annual success for 1978-1983 was reported seperately for lakes and WCA-3A by source authors, but combined here for estimate of annual success.*

initiation were warranted at more restrictive rejection criteria of $\alpha = 0.05$ (Table 5-5).

Our final model indicated an area, but not a year effect, as was indicated by our preliminary analyses (Table 5-6). However, area and year effects were highly confounded in these data because the studies included in this analyses that were conducted during different years were also conducted at different areas. Thus, we do not believe that we can reliably distinguish between these effects. Differences in success among areas and years are not surprising given the many causes of nest failures (Sykes 1987c, Bennetts et al. 1988, Snyder et al. 1989a).

Our data indicated an effect from the date of initiation in all phases of this analysis; although it was not completely clear as to whether this effect was quadratic or linear. Overall nest success (all years combined) was highest during January with a generally decreasing trend over time (Fig. 5-3). However, the overall trend is somewhat misleading because it was heavily influenced by one year (1987) of exceptionally high success in January (Fig. 5-4). Most years had the peak of success in February (3 of 7) or March (2 of 7). In only one year was peak success in January (1987) and one year in April (1993). In only one year did we observe nesting during December (1985), and success was lower than during January, February or March of that year.

These temporal effects of success were undoubtedly confounded with year effects because studies conducted from 1991-1993 by Toland (1994, unpubl. data), which were included in this analysis, were conducted in the northern part of the kite's range where the date of initiation was often several weeks later than in the southern portion of their range. In contrast, most of the data from other years were from the southern

Table 5-4. Summary statistics from individual univariate logistic regression models for the factors effecting nest success.

Source	df	χ^2 [a]	$P > \lvert \chi^2 \rvert$
Year	7	63.18	<0.001
Area[b]	3	45.90	<0.001
Nest Substrate (NSUB)[c]	6	29.50	<0.001
Herbaceous vs Woody Substrate	1	0.01	0.918
Date of Initiation (DOI)[d]	1	35.94	<0.001
DOI * DOI [e]	1	12.83	<0.001
Water Depth at DOI	1	19.98	<0.001
Nest Height (HGT)	1	5.18	0.023
Distance to Nearest Land (LAND)	1	0.31	0.578
Distance > 200 m (D200)[f]	1	2.42	0.120

[a] *Chi Square was based on Wald Statistic (SAS Inc. 1988).*

[b] *Areas were WCA-3A, WCA2B, Upper St, Johns Marsh. Because other areas had insufficent sample sizes to be effectively included, they were grouped into an "other" category.*

[c] *Substrates were Willow, Pond Apple, Meleleuca, Wax Myrtle, Cypress, Cattail, and "other".*

[d] *Estimated Julian date of first egg.*

[e] *A visual inspection indicated the possibility of a quadratic, rather than linear, relationship of DOI.*

[f] *Sykes (1987b) suggested that nests within 200m of land were more prone to failure.*

Table 5-5. Summary statistics from preliminary main-effects multivariate logistic regression model for the factors effecting nest success.

Source	df	χ^2 [a]	$P > \lvert \chi^2 \rvert$
Year	7	17.65	0.007
Area[b]	3	0.38	0.944
Nest Substrate (NSUB)[c]	6	8.66	0.194
Date of Initiation (DOI)[d]	1	7.66	0.006
DOI * DOI [e]	1	3.14	0.076
Water Depth at DOI	1	0.39	0.532
Nest Height (HGT)	1	1.31	0.253
Distance > 200 m (D200)[f]	1	2.49	0.114

[a] *Chi Square was based on likelihood-ratio test of models between the fully saturated main-effects model with and without each main effect (Hosmer and Lemeshow 1989).*

[b] *Areas were WCA-3A, WCA2B, Upper St, Johns Marsh. Because other areas had insufficent sample sizes to be effectively included, they were grouped into an "other" category.*

[c] *Substrates were Willow, Pond Apple, Meleleuca, Wax Myrtle, Cypress, Cattail, and "other".*

[d] *Estimated Julian date of first egg.*

[e] *A visual inspection indicated the possibility of a quadratic, rather than linear, relationship of DOI.*

[f] *Sykes (1987b) suggested that nests within 200m of land were more prone to failure.*

Table 5-6. Summary statistics from the final most parsimonious (based on AIC and LRTs) logistic regression model for the factors effecting nest success.

Source	df	χ^{2a}	$P>\|\chi^2\|$
Year[b]	7	9.80	0.200
Area[c]	3	10.78	0.013
Date of Initiation (DOI)	1	5.34	0.021
DOI * DOI[d]	1	2.66	0.103
YR * DOI	1	16.63	0.020

[a] *Chi square was based on a LRT between models with and without the source term.*

[b] *Although the main effect of year was not significant at $\alpha=0.05$, it was retained in the final model because of its significant interaction with date of initiation (DOI).*

[c] *Multivariate model indicated that this term did not need to be retained in subsequent models; however, the AIC was lower with this term included. Year and area effects also were confounded because some years included a restricted sample of areas (see Table 5-2).*

[d] *A LRT of models with and without this term indicated that this term was not warranted; although the AIC was slightly lower with the term included.*

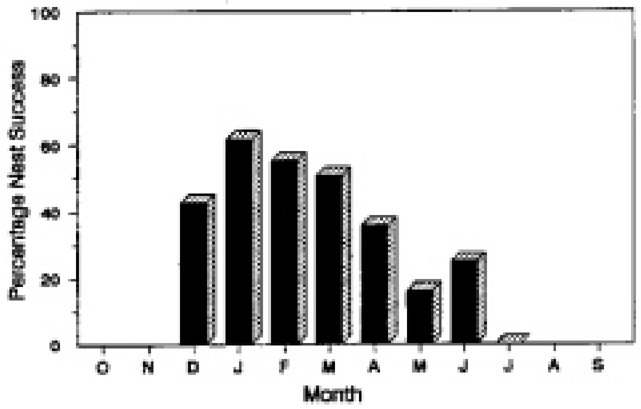


Figure 5-3. The percentage of nests that were successful during each month. Data used in this analysis were from Bennetts et al. (1988)(1986-1987), Toland (1994, unpubl.data)(1990-1993), and this study (1994-1995).

portion of the kite's range. This probably also accounts for the interaction effect of year with date of initiation.

Number of Young per Successful Nest

In contrast to nest success, the number of young per successful nest probably is one of the least variable and has been the least controversial of the reproductive parameters. The relative lack of variability for this parameter is not surprising since it is not unusual for raptors to produce normal numbers of young per successful nest even when other aspects of reproduction (e.g., proportion of population attempting to breed or nest success) are depressed (Brown 1974, Steenhof 1987). For this reason, the number of young per successful nest is not particularly informative in the absence of these other reproductive parameters (Brown 1974).

Several studies have reported estimates for the number of young per successful nest (Table 5-7) and the average from 20 years of reported data is 1.9. Annual estimates reported have ranged from a low of 1.4 (Sykes 1979, 1987b, Bennetts et al. 1988) to a high of 2.5 (Sykes 1979, 1987b)(Table 5-8).

Number of Nesting Attempts Per Year

Snail Kites are capable of raising more than one brood per year and attempts at multiple brooding may be fairly widespread (Snyder et al. 1989a). However, the extent of multiple nesting attempts has been poorly documented. Snyder et al. (1989a) estimated the number of attempts based on a verbal description of the following calculation:

$$\frac{\frac{n_s}{\hat{s}}}{\frac{n_s}{2}} = \frac{\textit{No. Nesting Attempts}}{\textit{No. Pairs}} = \textit{No. Attempts per pair}$$

where n_s = the number of successful nesting attempts found on Lake Okeechobee and WCA-3A in 1978, $\hat{s}$ = the estimate of nest success (estimated as the number

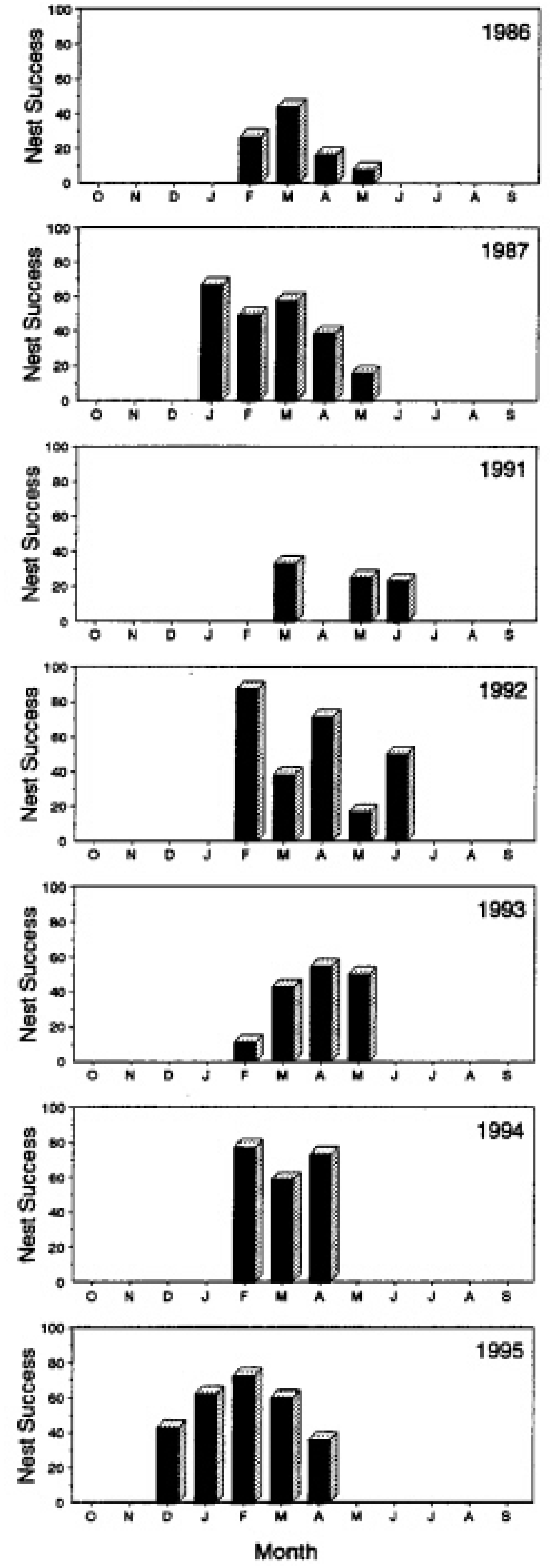


Figure 5-4. The percentage of nests that were successful during each month of each year. Data used in this analysis were from Bennetts et al. (1988)(1986-1987), Toland (1994, unpubl. data)(1991-1993), and this study (1994-1995).

successful nests/ number nests observed) for nests found at the nest building stage at Lake Okeechobee and WCA-3A that were successful, and n_c = the number of Snail Kites counted during the 1977 annual count on Lake Okeechobee and WCA-3A. Using the values reported by Snyder et al. (1989a) produces the following estimate:

$$\frac{\frac{60}{0.29}}{\frac{152}{2}} = \frac{207}{76} = 2.7 \textit{ attempts per pair}$$

We have several concerns about this estimate derived by Snyder et al. (1989a). First, it is important to recognize that this estimate is only applicable to the number of nest building attempts (i.e., courtship attempts by our definition; see discussion of *Semantics* above). It is not an estimate for the number of nesting attempts, if a nesting attempt is defined as having produced at least one egg. If we apply their procedure using nests in which at least one egg was laid and using an estimate of success derived from nests found during incubation (25 successful nests of 59 found during incubation =0.42)(this is less biased than using nests found after hatching; see above) then an analogous estimate for the number of nesting attempts (in which at least one egg was laid) would have been:

$$\frac{\frac{60}{0.42}}{\frac{152}{2}} = \frac{142}{76} = 1.9 \textit{ attempts per pair}$$

Regardless of how a nesting attempt is defined, we believe that the approach used by Snyder et al. (1989a) is inherently biased and produces an unreliable estimate for this parameter. First, there are several assumptions inherent in their calculations for which their estimate is not robust to violation. They correctly pointed out that they assumed (1) the count from 1977 was an accurate census, (2) there was a 1:1 sex ratio, (3) all birds counted during 1977 were potential breeders in 1978, and (4) no birds died between the 1977 count and the end of the 1978 breeding season.

As we discuss in considerable detail in a later chapter (see discussion of the *Annual Count* in Chapter on *Monitoring the Florida Snail Kite Population*), the annual count is **not** a reliable census of the population, as was assumed, and evidence suggests that it is not even a reliable index to the population. Given that it is highly improbable that all birds are counted during the annual count (Rodgers et al. 1988), it is likely that the number

Table 5-7. The annual mean and overall (i.e., all years and locations combined) number young per successful nest from major studies conducted since 1968. A successful nest was considered a nest in which at least one young fledged.

Annual x̄ No. Per Successful Nest[1]	Overall No. Per Successful Nest[2]	Annual Range	Years Included	Location(s)[3]	Total No. Successful Nests	Source
2.0	1.9	1.4 - 2.5	1968-1976	1, 2, 3, 4, 5, 6	84	Sykes (1979)
2.0	2.0	1.4 - 2.5	1968-1978	1, 2, 3, 4, 5, 6	103	Sykes (1987b)
2.0	--[4]	--[4]	1978-1983	4,5,6,7	106	Beissinger (1986)
1.5	1.6	1.4 - 1.7	1986-1987	4	149	Bennetts et al. (1988)
2.0	--[4]	--[4]	1968-1983	4,5,6,7	--[4]	Snyder et al. (1989)
1.9	2.0	1.5 - 2.1	1990-1993	8	57	Toland (1994)
1.8	1.8	1.6 - 1.9	1994-1995	1,2,3,4,5,6,7,8	144	This study

[1] *The annual average number of young per successful nest*

[2] *The total (all years) number of young per total number of successful nests*

[3] *Locations are: WCA-1 (1), WCA-2A (2), WCA-2B (3), WCA-3A (4), Lake Okeechobee (5), Lake Kissimmee (6), Lake Tohopekaliga (7), Upper St. Johns Marsh (8),*

[4] *Not reported and/or insufficient information provided to estimate*

of pairs would have been underestimated, which would have resulted in the number of attempts per pair to have been overestimated. We also have no means of evaluating whether assuming a 1:1 sex ratio was reasonable, but in the absence of such information we agree with Snyder et al. (1989a) that this was a reasonable assumption.

We disagree that all birds counted during the 1977 annual count can be reasonably assumed to be breeders in 1978. Our data, as well as the observations by Snyder et al. (1989a) indicate that juveniles have a lower probability of attempting to breed than do adults. Thus, all birds included in the 1977 count that were juveniles were not potential breeders. This would tend to inflate the denominator (i.e., to reduce the number of pairs in their calculation) and, consequently produce a negative bias; however, there is no reliable way to estimate the extent of the bias, since the proportion of juveniles in the 1977 count was unknown.

We agree with Snyder et al. (1989a) that they had to assume that no birds died between the 1977 annual count and the end of the 1978 breeding season; however, the true assumption was substantially more extensive than they reported. Because their calculation assumed the same population at both time periods (i.e., during the count and during the breeding season) they really assumed that Lake Okeechobee and WCA-3A (the only areas used in their calculation) were a closed population. That is, that there were not only no deaths, but also that there were no births, no immigration, and no emigration. If the time period between the 1977 annual count and the end of the 1978 breeding season were very short, this would be a reasonable assumption. However, the count was conducted in December of 1977 (see the *Annual Count* in Chapter on *Monitoring the Florida Snail Kite Population*) and initiation of the last reported nest of the 1978 breeding season was in August of 1978 (Snyder et al. 1989a). Thus, the interval over which this assumption applied was 8-9 months. We are not especially concerned about the assumption of no births because this assumption can be met by excluding young-of-the-year juveniles from their analysis. Although it is unlikely that no deaths occurred over this period of time, we would also not expected a large bias from this effect due to high adult survival. In contrast to births and deaths, we find the assumption of no immigration or emigration of substantial concern. Our data suggests that the probability of an adult bird moving in any given month is approximately 0.25 (see *Movement*). Thus, over an 8-9 month period it is extremely unlikely that there was no immigration or emigration to or from these areas. Furthermore, our data suggest that at the time the annual count is conducted, there is a greater probability that birds will be in habitats not typically used for nesting. This could result in a substantial overestimate of the number of attempts per pair.

Snyder et al. (1989a) suggested that a bi-modal seasonal distribution of nests that are spaced about 3-4

Table 5-8. The number of successful nests, young fledged, and number of young per successful nest reported for each year from 1968 through 1995.

Year	No. Successful Nests	No. Young Fledged	No. Young per Successful Nest	Source
1968	11	24	2.2	Sykes (1979, 1987b)
1969	8	13	1.6	Sykes (1979, 1987b)
1970	8	12	1.5	Sykes (1979, 1987b)
1971	0	0	--[1]	Sykes (1979, 1987b)
1972	3	7	2.3	Sykes (1979, 1987b)
1973	12	29	2.4	Sykes (1979, 1987b)
1974	6	11	1.8	Sykes (1979, 1987b)
1975	14	35	2.5	Sykes (1979, 1987b)
1976	22	30	1.4	Sykes (1979, 1987b)
1977	8	20	2.5	Sykes (1987b)
1978	11	20	1.8	Sykes (1987b)
1979	54	108[2]	2.0	Beissinger (1986)
1980	--[3]	--[3]	--[3]	--[3]
1981	0	0	--[1]	Beissinger (1986)
1982	2	4[2]	2.0	Beissinger (1986)
1983	10	20[2]	2.0	Beissinger (1986)
1984	--[3]	--[3]	--[3]	--[3]
1985	--[3]	--[3]	--[3]	--[3]
1986	45	65	1.4	Bennetts et al. (1988)
1987	104	172	1.7	Bennetts et al. (1988)
1988	--[3]	--[3]	--[3]	--[3]
1989	--[3]	--[3]	--[3]	--[3]
1990	2	3	1.5	Toland (1994)
1991	8	17	2.1	Toland (1994)
1992	33	68	2.1	Toland (1994)
1993	14	26	1.9	Toland (1994)
1994	50	80	1.6	This study
1995	94	181	1.9	This study

[1] *No successful nests from which to estimate*

[2] *Not reported, but inferred from number of successful nests and number young per successful nest*

[3] *No reported information*

months apart during some years indicated widespread multiple brooding. We agree that a bi-modal distribution of nest initiations may be an indication of multiple brooding during those years. However, a bi-modal distribution may also be attributable in some years to the starting and stopping of nest initiations due to early season temperature changes; although these two explanations are not mutually exclusive. We often observed nest initiations during December or January that coincided with periods of unseasonably warm weather, particularly in the southern habitats. As colder temperatures resumed nest initiations that had not reached the egg laying stage were likely to terminate. Initiations would resume when warm temperatures returned, often a month or two later. This would create a peak of initiations early during the season (usually in

January) followed by a second larger peak one or two months later (usually in February or March) after warm temperatures became prevalent. However, birds that successfully initiated early were also likely to re-nest because completion or failure of their first nest occurred well within the primary breeding season.

Snyder et al. (1989a) correctly limited their inference to 1978. Beissinger (1995) later extended this inference to a general estimate for the number of attempts per year; although he revised the estimate to from 2.7 to 2.2 suggesting that this would be conservative. In order to generalize this estimate to all years, Beissinger (1995) had to assume that 1978 was a "representative" year. Based on the data presented by Snyder et al. (1989a), 1978 was far from representative. Based on both number of nests found and on number of nestlings banded, 1978 was an extremely high year for reproduction (Fig. 5-5). Consequently, application of this estimate to other years would very likely have resulted in an inflated estimate.

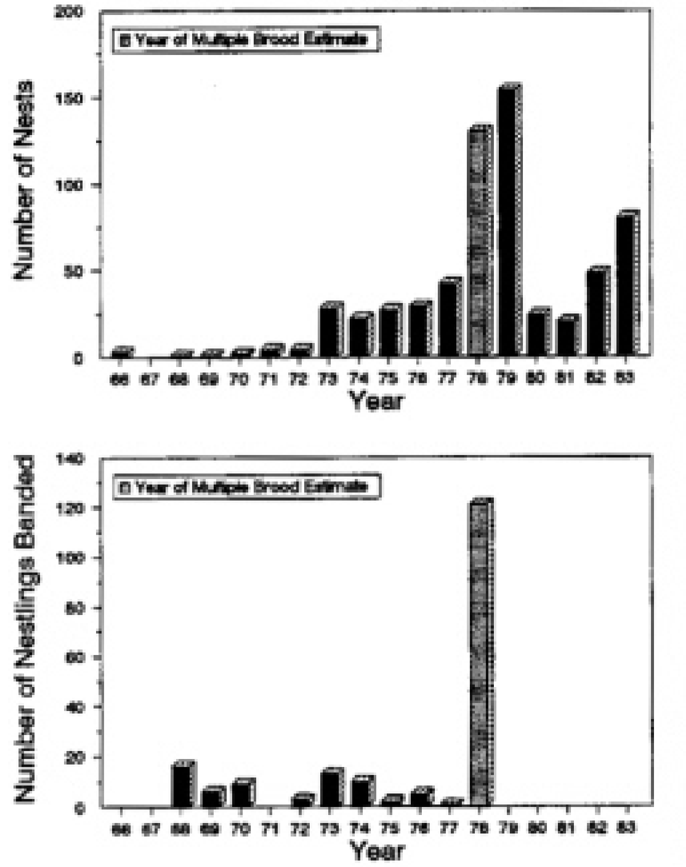


Figure 5-5. The number of nests (top) and number of nestlings banded (bottom) during each year reported by Snyder et al. (1989a). Snyder et al. (1989a) estimated the number of breeding attempts per pair during 1978 and correctly limited their inference of this estimate to 1978. Based on these data, we suggest that estimates from 1978 can not be reliably extended to other years.

In contrast to the approach used by Snyder et al. (1989a), we estimated the extent of multiple broods using radio-transmittered birds. During 1995, we closely monitored 23 radio-transmittered adult Snail Kites for breeding activity in order to assess the number of breeding attempts per year. Of these 23 adults, 14 were females and 9 were males. During the 1995 nesting season, we located each bird on the ground approximately bi-weekly ($\bar{x}$ = 14.1 days ± 8.1 sd) and determined its breeding status (e.g., a nest, courtship, not breeding). Birds in which no breeding activity was detected were generally observed for ≥2 hrs and subsequent visits, usually within 10 days, were required to confirm a non-breeding status and to confirm any nests for birds exhibiting courtship. We found an average of 1.4 (±0.6 sd) nesting attempts per bird (Table 5-9). The interval of our breeding status checks could have resulted in a failure to detect an occasional bird that initiated a nest that failed early during laying or incubation. Consequently, this estimate may be slightly low for 1995. However, most nest failure occurs during the first week after hatching (Bennetts et al. 1988), which would have required nesting activity for at least 4-5 weeks. Consequently, the potential bias from having missed nests over a 14-day period probably was negligible. In addition, 1995 had favorable water conditions throughout the Snail Kite's range in Florida. Consequently, we might also expect our 1995 estimate to be higher than an annual average.

In summary, we agree with Snyder et al. (1989a) that multiple brooding by Snail Kites in Florida is common during some years. However, our data suggest that the estimate of 2.7 attempts per year by Snyder et al (1989a) and even the "more conservative" estimate of 2.2 attempts per year used by Beissinger (1995) were substantial overestimates. A combination of differences in our estimation procedures, difference in our respective definitions of a breeding attempt, and annual variability of this parameter probably account for these discrepancies.

***Conditional Probability of Attempting to Breed*-** An alternative way to look at the number of attempts per year is using conditional probability for the proportion of birds attempting to breed (α_i). That is, α_1 would be the probability that a bird attempted to breed, given that it had not attempted previously during that nesting season. Of 23 birds we monitored for breeding activity during 1995, all 23 attempted to breed at least once. Thus, our estimate of α_1 would be 1.0. Similarly, α_2 would be the probability that a bird attempted to breed, given that it had previously made 1 attempt during that breeding season. Based on our data from 1995, we would

Table 5-9. Number of nesting attempts and number of attempts that were successful for each of 23 adult Snail Kites during the 1995 breeding season.

Frequency	Sex	Number of Attempts	No. Attempts Successful
152.698	F	1	1
152.584	F	1	0
153.496	F	2	0
153.860	F	2	1
152.739	F	3	1
153.931	F	1	1
152.039	F	2	1
153.969	F	2	2
152.494	F	1	1
152.169	F	2	1
153.979	F	2	1
152.777	F	1	1
152.499	F	1	0
152.369	F	1	1
152.869	M	1	1
153.900	M	1	1
152.128	M	1	1
153.390	M	1	1
153.290	M	1	1
152.848	M	1	0
152.858	M	1	1
152.539	M	1	0
152.379	M	2	1

estimate α_2 to be 0.34 (8 of 23). The probability that a bird attempted to breed, given that it had previously made two attempts during that breeding season (α_3) was 0.13 (1 of 8). The variance for these estimates could be derived based on a binomial distribution, although the formula traditionally used for this estimate:

$$Var(\hat{\alpha}_i) = \frac{\hat{\alpha}_i(1 - \hat{\alpha}_i)}{n_i}$$

is intended for large samples (White and Garrott 1990). Hollander and Wolfe (1973) provide alternative procedures that could be used for smaller samples.

Number of Successful Broods per Year- Snyder et al. (1989a) suggested that in some years it was possible for Snail Kites to successfully raise four broods. This was based on the length of the breeding season for certain years (e.g., 1978 and 1979) and the assumption that it would take 10 weeks (70 d) to raise a brood if mate desertion occurred and 16 weeks (112 d) if no mate desertion occurred. Although this is certainly theoretically possible, we believe that the probability of a Snail Kite successfully raising even three broods in a given year is very close to zero. We base our conclusion on several points. First, empirical data do not support Snyder et al.'s (1989a) conclusion. There have been no documented cases of Snail Kites successfully raising > 2 broods in a given year, and the occurrence of successfully raising 2 broods appears quite rare. Out of an 18-year study including 666 nesting attempts, Snyder et al. (1989a) documented only 3 cases of Snail Kites successfully raising 2 broods. Similarly, only 1 of 23 (4%) radio-transmittered birds that we closely monitored for breeding activity during 1995 (a good year), successfully raised two broods. We believe that Snyder et al. (1989a) overlooked some critical aspects of the breeding biology of Snail Kites when making this suggestion. First, although the inclusive dates from the first nest initiated in a given year to the last may span a period of 6-7 months, the initiation of nests is not evenly distributed throughout that period (see *The Breeding Season* above). The majority of nests (82% of the nests reported by Snyder et al. [1989a]) were initiated during a five month period from January through May. This is sufficient time for only two successful broods even when mate desertion occurs. The longest nesting season (time span over which nest initiations were observed) reported by Snyder et al. (1989a) over an 18-year period was only 31.7 weeks. Given that they suggest that it takes 10-16 weeks per successful brood, the longest nesting season they observed did not even have sufficient time to successfully raise four broods (even with mate desertion for all broods), and barely had sufficient time to successfully raise two broods without mate desertion. There also has been no consideration given to energetic costs of raising successive broods. Thus, we believe that a small percentage of birds (e.g., < 10%) may successfully raise two broods during some years; however, there is currently no empirical evidence to support the conclusion that Snail Kites successfully raise > 2 broods per year.

Chapter 6. MOVEMENTS

Natal Dispersal of Juveniles

Natal dispersal is usually defined as the permanent movement of an animal (usually a juvenile) away from an animal's natal site to a new site of actual or potential breeding (e.g., Howard 1960, Greenwood 1980, Greenwood and Harvey 1982). For the purposes of this study, we defined natal dispersal as the initial dispersal of a juvenile from its natal wetland with the understanding that a given individual might, and probably will, return to its natal wetland many times during its lifetime.

The overall cumulative probability of juvenile Snail Kites dispersing from their natal wetland during their first year was 0.81 based on an estimate derived using a Kaplan-Meier estimator (Fig. 6-1). Only 8 of 65 (12%) radio-transmittered birds over a three-year period that survived their entire first year and whose locations were known remained in their natal wetland for their entire first year.

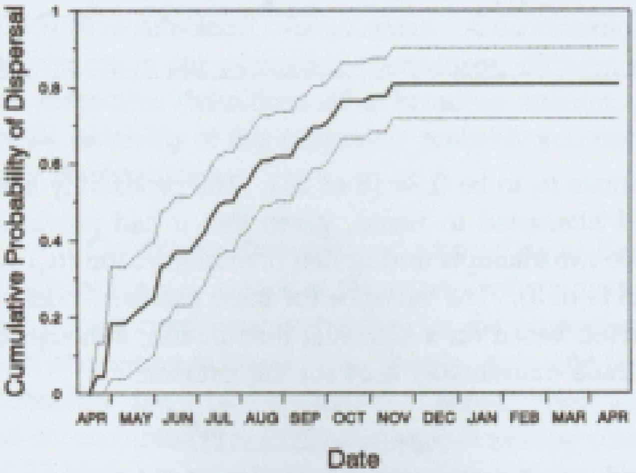


Figure 6-1. Kaplan Meier estimates for the overall cumulative probability of dispersal (solid line). Also shown is a 95% confidence interval (dotted line) for the probability function.

TEMPORAL PATTERNS OF NATAL DISPERSAL

Within-year patterns-- Of the birds that dispersed during their first year (n=57), most (60%) did so within the first 60 days after fledging and all did so within the first 240 days (Fig. 6-2).

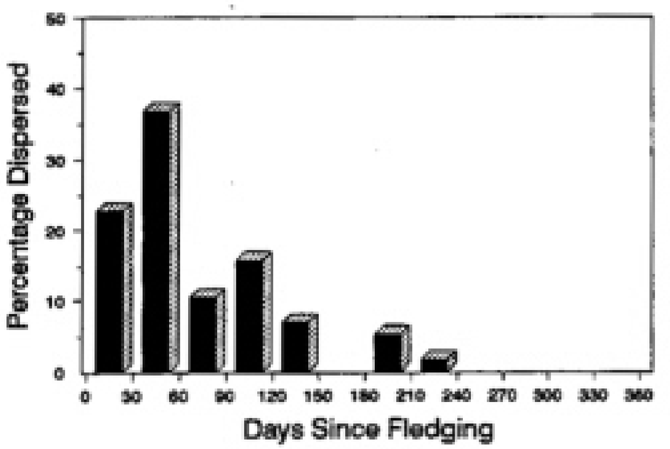


Figure 6-2. The percentage of juvenile Snail Kites that initially dispersed from their natal wetland in each 30-day time period since fledging.

Differences among Years--Dispersal of juveniles from their natal wetland was lowest during 1992 and relatively higher in both 1993 and 1994 (Fig. 6-3). Differences were significant (at $\alpha=0.05$) between 1992 and each of the other years, but not between 1993 and 1994 (Table 6-1)(Appendix 6-1).

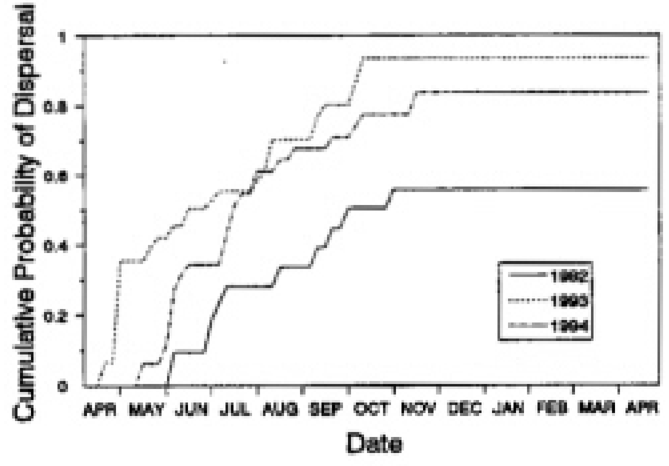


Figure 6-3. Kaplan Meier estimates for the cumulative probability of dispersal in each of the three years. Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 6-1.

Table 6-1. Results of log-rank tests between dispersal functions of juvenile Snail Kites dispersing from their natal wetlands during each study year (SY)(April 15 - April 14).

Comparison	χ^2	df	Prob
1992 vs. 1993	5.246	1	0.022
1992 vs. 1994	4.049	1	0.044
1993 vs. 1994	0.129	1	0.720

DIFFERENCES IN NATAL DISPERSAL BETWEEN NORTHERN AND SOUTHERN REGIONS

We did not have a sufficient sample to compare differences in natal dispersal of juveniles among specific wetlands and/or among specific regions. However, because low waters levels occurred throughout the southern portion of our study area just prior to our study, we were interested in a spatial comparison of natal dispersal. Consequently, we pooled our samples from the southern regions (i.e., Everglades, Loxahatchee Slough, and Lake Okeechobee), which were substantially influenced by the previous drought, and the northern regions (i.e., the Kissimmee Chain-of-Lakes, and Upper St. Johns River Basin), which were relatively unaffected by the previous drought. This analysis indicated that natal dispersal from wetlands in the southern regions (i.e., most affected by the previous drought) was substantially lower than from wetlands in the northern regions during 1992, but not during 1993 or 1994 (Table 6-2)(Fig. 6-4)(Appendix 6-2).

Table 6-2. Results of log-rank tests comparing dispersal functions of juvenile Snail Kites dispersing from the northern regions (i.e., Kissimme Chain of Lakes and Upper St. Johns River Basin) and southern regions (i.e., Everglades, Lake Okeechobee, and Loxahatchee Slough) during each study year (SY)(April 15 - April 14).

Comparison	χ^2	df	Prob
1992	7.530	1	0.006
1993	0.635	1	0.426
1994	<0.001	1	0.994

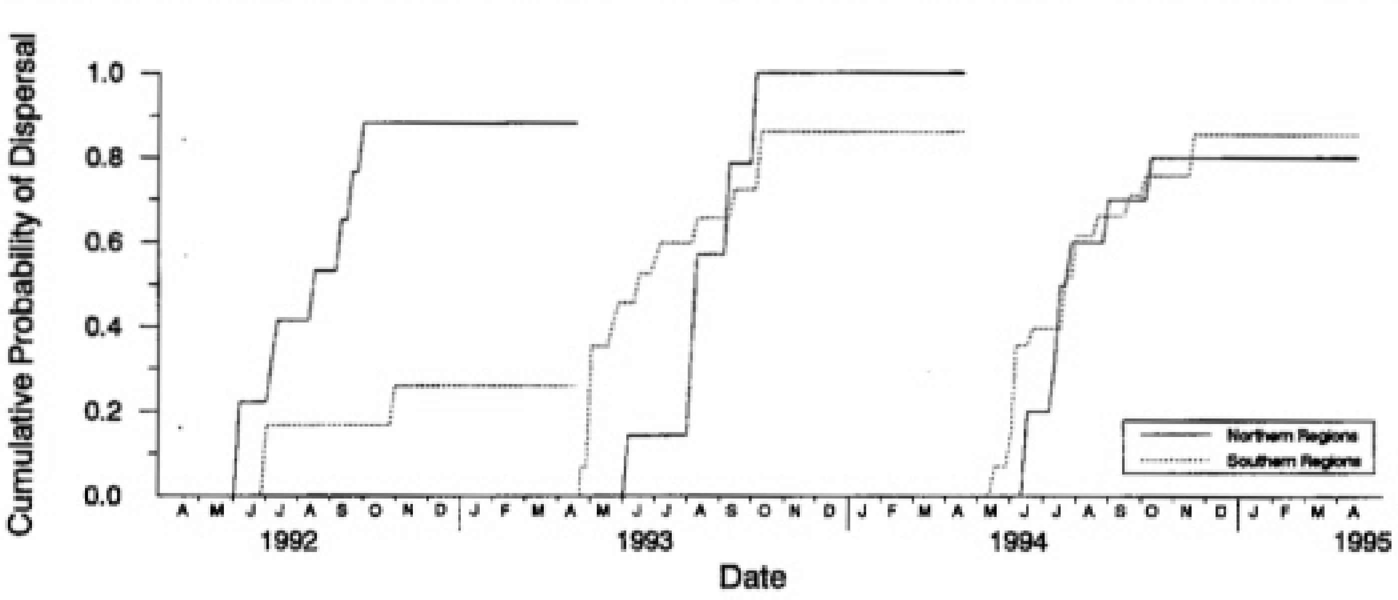


Figure 6-4. Kaplan Meier estimates for the cumulative probability of dispersal from wetlands within northern and southern regions in each of the three study years. Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 6-2.

DIFFERENCES IN NATAL DISPERSAL BETWEEN LAKE AND MARSH HABITATS

Our sample was also insufficient to compare the differences in natal dispersal among each individual habitat; but was sufficiently large to compare between lakes and marshes. We did not observe any differences in dispersal out of lakes compared to marshes for any juvenile cohort at $\alpha = 0.05$; however differences were significant during 1993 at $\alpha = 0.10$ (Table 6-3). Additionally, the number of animals in each sample group (i.e., birds that were alive and whose locations were known for each habitat type during each year) at any given time was relatively low (≤ 15)(Appendix 6-3). Thus, the power to detect even substantial differences in dispersal also was relatively low (see Fig. 3-1 in *Methods* section). There was, however, a consistent pattern for the estimates of the cumulative probability of dispersal out of marshes to be higher than from lakes for each cohort (Fig. 6-5).

Table 6-3. Results of log-rank tests comparing dispersal functions of juvenile Snail Kites dispersing from lake and marsh habitats during each study year (April 15 - April 14).

Comparison	χ^2	df	Prob
1992	0.599	1	0.439
1993	3.071	1	0.080[1]
1994	0.717	1	0.397

[1] Using the altenative tests described by Cox and Oakes (1984)(Appendix 3-3) that are slightly less conservative (i.e., have greater power, but higher risk of Type I error) we estimated $\chi^2=3.801$, $P=0.051$ and $\chi^2=3.653$, $P=0.056$ for alternative tests 1 and 2, respectively.

DISCUSSION OF NATAL DISPERSAL

High rates of natal dispersal are often found for species that exhibit nomadic tendencies or that inhabit fluctuating or unpredictable environments (Baker 1978, Greenwood and Harvey 1982). Thus, the overall high rates of dispersal we found are not surprising.

Two of the more commonly suggested reasons for high rates of natal dispersal are to gain access to resources (e.g., food or mates) in a saturated environment and inbreeding avoidance. The latter will be addressed in a later section (see *Natal Philopatry and Site Fidelity*). Most species studied in which gaining access to resources has been suggested as a reason for dispersal have been territorial species (reviewed by Greenwood and Harvey 1982). In contrast, Snail Kites defend only a few meters around their nest site and only rarely defend feeding areas (Sykes et al. 1995). Thus, access to resources is unlikely to be limited by social behavior (except mate choice), and is more likely due to the overall availability of food or mates.

Given the lack of social exclusion from resources, it might be predicted that if high dispersal were attributable to gaining increased access to

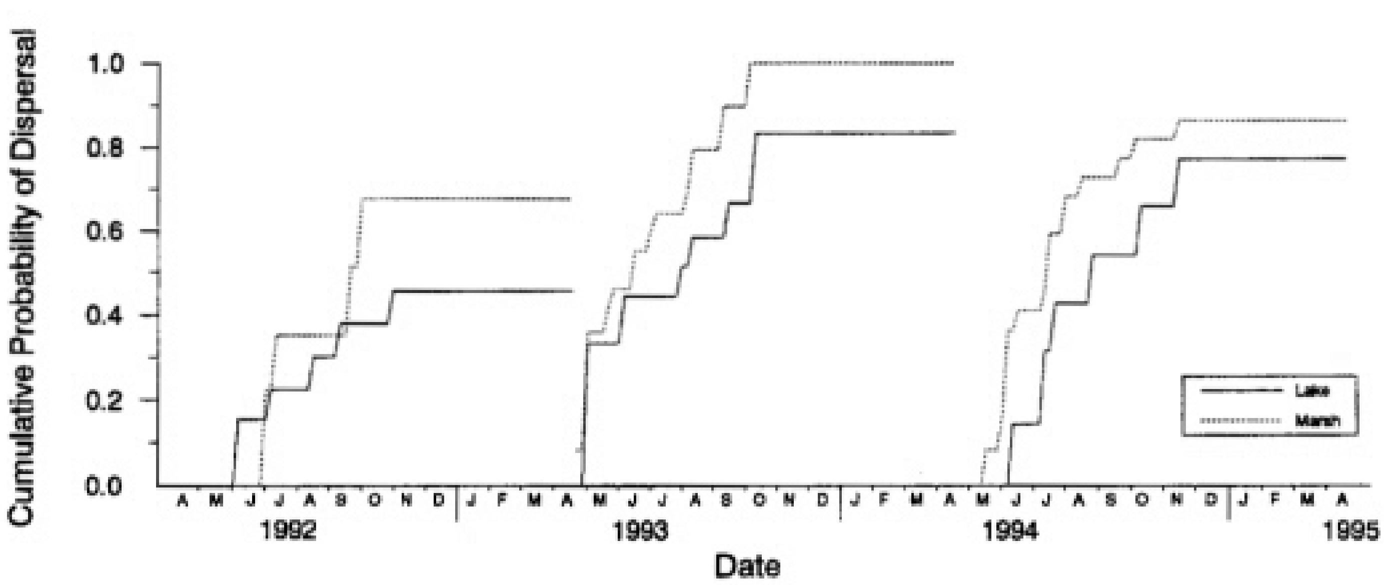


Figure 6-5. Kaplan Meier estimates for the cumulative probability of dispersal from lake and marsh habitats in each of the three study years. Confidence intervals for estimates are not shown to minimize cluttering, but are provided in detail in Appendix 6-3.

resources, then dispersal should be high when local resources are depressed. Our results were not consistent with higher rates of dispersal during periods of low resources availability. Unfortunately, we did not initiate the collection of foraging data until 1993; however, based on hundreds of hours of field observations of birds, its was very apparent that food resources were substantially lower in 1992 (the first year of our study following the previous drought) compared to later years. Our foraging observations (during 1993 and 1994) as well as numerous previous reports (reviewed by Sykes et al. 1995) indicated that the capture of snails often requires < 3 minutes. In contrast, we often observed birds during 1992 that would forage in excess of 30 minutes without capturing a snail. In a few instances during our trapping period, we observed several foraging birds for hours without observing a single snail having been captured. Thus we would have predicted that dispersal would have been highest during 1992. Contrary to our prediction, dispersal was lowest during 1992. Furthermore, during 1992 dispersal was substantially lower in the southern regions where food was more depressed.

Movement Probabilities

In addition to the initial dispersal of juveniles from their natal wetland we also examined general movements of adult and juvenile Snail Kites. Here we treat movement using a conditional logistic regression model based on one month time intervals (see methods). Thus, our model expresses the conditional probability that, given a bird was alive and its location known at time t, that it would be in the same location (or conversely at a different location) at time $t + 1$. We then explored several potential effects on this probability. We based our analysis of general movements on 5,299 locations of radio transmittered birds (3,618 locations of adults and 1,681 of juveniles).

THE EFFECT OF AGE AND SEX ON MOVEMENT PROBABILITIES

A conditional logistic model of movement probability (i.e., the probability of a bird moving between time t and time $t+1$, given that it was alive and its location known at $t+1$) indicated effects of both age (χ^2=5.38, df=1, P=0.020) and sex (χ^2=6.16, df=2, P=0.046) when analyzed separately. However, our model of sex was confounded with age because sex was categorized as male, female, or unknown; where only juveniles were unknown. If these data were constrained to only adults, we found no evidence that sex had an influence on movement probability (χ^2=0.76, df=1, P=0.384). Because the unconstrained model with age (i.e., both age classes included) is a subset of the more general model of sex (with 1 fewer parameter), an alternative approach to test for the effects of sex is a LRT. The LRT between the unconstrained univariate models also indicated that sex does not add significantly to the fit of these data over a model with only age (LRT =0.76, 1 df, P=0.617). A comparison of AIC between these two models adds additional support for this conclusion (the model with age only had a lower AIC)(Table 6-4). Thus, we concluded that age, but not

Table 6-4. Summary statistics for conditional logistic regression model for the factors affecting the probability of movement between times t and t + 1 (at monthly time steps), given that an animal was alive at time t and its location known. Shown are the model description, number of estimable parameters (np), relative deviance (-2ln[$\mathcal{L}$]), and Akaike's Information Criterion (AIC). The model shown in bold would be the one selected from this group based on AIC.

Model	*np*	-2*ln*($\mathcal{L}$)	AIC
Age	**2**	**2502.95**	**2506.95**
Sex	3	2502.19	2508.19

sex, had an influence on movement probabilities. Our estimates indicated that adults had a higher overall probability of movement (excluding any additional factors) than juveniles (Fig. 6-6).

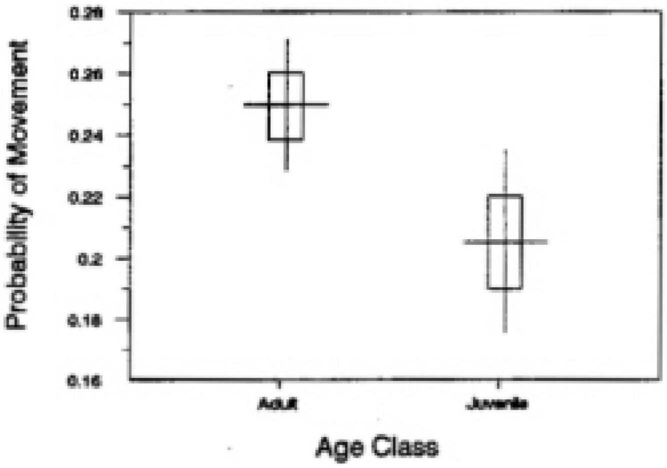


Figure 6-6. Conditional probabilities that adult and juvenile Snail Kites that were alive and their location known at time t, were in the same location (or conversely at a different location) at time t + 1. Also shown are the standard errors (rectangles) and 95% confidence intervals (vertical lines).

TEMPORAL EFFECTS ON MOVEMENT PROBABILITIES

We began testing for an overall time effect using a univariate model based on separate parameter estimates for each month of each year of our study (i.e., 12 months for each of 3 years =36 parameters). This test showed a strong effect of time (χ^2=90.79, df=36, P<0.001)(Fig. 6-7). We then

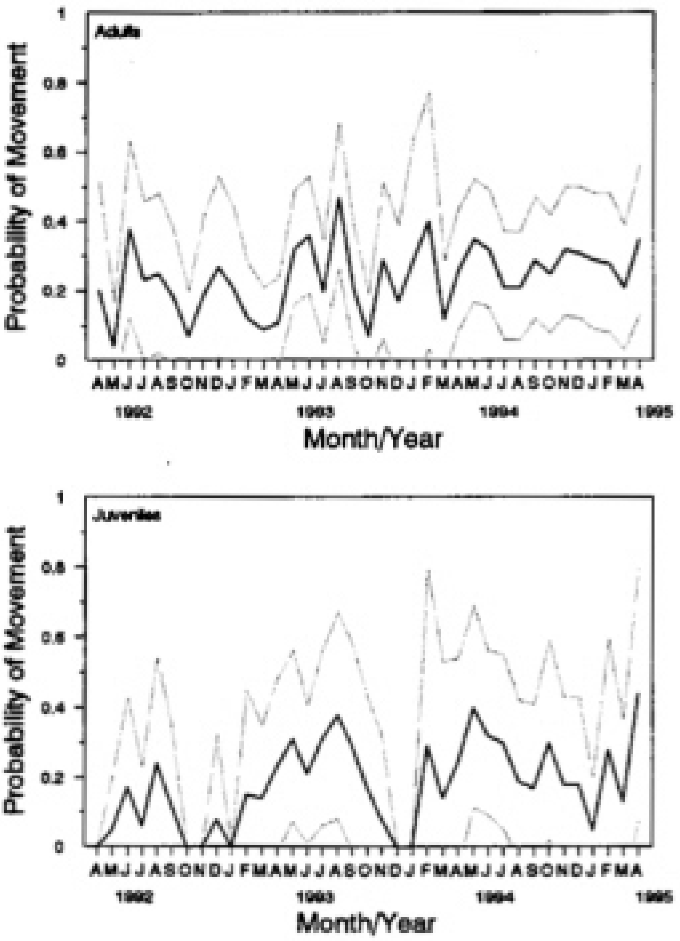


Figure 6-7. Conditional probabilities that adult and juvenile Snail Kites that were alive and their location known at time t, were in the same location (or conversely at a different location) at time t + 1 for each month during this study (solid lines). Also shown are the 95% confidence intervals (dotted lines).

tested whether this effect could be accounted for with a more parsimonious model using separate months, but not for each year (i.e., 1 parameter for each month [12] rather than 36 for the previous model). This model also showed a significant monthly effect (χ^2=32.36, df=11, P<0.001), but a LRT indicated that the more general model (with 36 parameters) was warranted (LRT=73.81, 24 df, P< 0.001). We next explored a series of models in which time was expressed as a seasonal, rather than monthly effect. These models reflected various combinations of 3 and 4 seasons in a sliding window approach (i.e., each iteration shifted the months included by one month) to determine how the months should be divided into seasons. This analysis indicated that one of the 3-season models (of 4 months/per season) was the most parsimonious based on AIC (Table 6-5); however, 2 additional models (the model with a separate parameter for each month and one of the 4-season models) had similarly low AIC values and could not be rejected based solely on AIC criteria. Next, we compared a suite of models including

Table 6-5. Summary statistics for conditional logistic regression models for potential seasonal groupings affecting the probability of movement between times t and t + 1 (at monthly time steps), given that an animal was alive at time t and its location known. Shown are the model description, number of estimable parameters (np), relative deviance (-2ln[ℒ]), and Akaike's Information Criteria (AIC). The model shown in bold would be the one selected from these potential models based on AIC.

Season Model	*np*	$-2ln(\mathcal{L})$	AIC
(JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC)	12	2474.44	2498.44
(JAN FEB MAR APR) (MAY JUN JUL AUG) (SEP OCT NOV DEC)	**3**	**2490.66**	**2496.66**
(FEB MAR APR MAY) (JUN JUL AUG SEP) (OCT NOV DEC JAN)	3	2498.75	2504.75
(MAR APR MAY JUN) (JUL AUG SEP OCT) (NOV DEC JAN FEB)	3	2506.24	2512.24
(APR MAY JUN JUL) (AUG SEP OCT NOV) (DEC JAN FEB MAR)	3	2498.14	2504.14
(JAN FEB MAR) (APR MAY JUN) (JUL AUG SEP) (OCT NOV DEC)	4	2491.16	2499.16
(FEB MAR APR) (MAY JUN JUL) (AUG SEP OCT) (NOV DEC JAN)	4	2497.98	2505.98
(MAR APR MAY) (JUN JUL AUG) (SEP OCT NOV) (DEC JAN FEB)	4	2497.36	2505.36

combinations of the above effects including their interaction terms. This analysis indicated that a model with season (the 3-season model selected from the above analysis), year, and the interaction between season and year was the most parsimonious based on AIC (Table 6-6). As above, two alternative models (individual month model with 36 parameters and the model with season and year without an interaction term) had similarly low AIC values and could not be rejected based solely on AIC. Likelihood ratio tests also indicated that the model with the lowest AIC was preferred ($\chi^2 = 50.72$, df=27, P=0.003 and $\chi^2 = 9.55$, df=4, P=0.049 for each of the alternative models, respectively). Thus, our data support that movement probabilities are influenced by season (Fig. 6-8), year (Fig. 6-9), and an interaction between season and year (Fig. 6-10).

Table 6-6. Summary statistics for conditional logistic regression models for potential temporal effects on the probability of movement between times t and t + 1 (at monthly time steps), given that an animal was alive at time t and its location known. Shown are the model description, number of estimable parameters (np), relative deviance (-2ln[ℒ]), and Akaike's Information Criteria (AIC). The model shown in bold would be the one selected from these potential models based on AIC criteria.

Model	np	$-2ln(\mathcal{L})$	AIC
Time	36	2400.6	2472.6
Month	12	2474.4	2498.4
Season	3	2490.6	2496.6
Year	3	2477.4	2483.6
Month Year	14	2446.6	2474.6
Month Year Month*Year	36	2402.7	2474.7
Season Year	5	2460.9	2470.9
Season Year Season*Year	**9**	**2451.3**	**2469.3**

SPATIAL EFFECTS ON THE PROBABILITY OF MOVEMENT

Here we explored whether the location of a given bird influenced whether or not the bird moved between times *t* and *t* + 1. For this analysis, we were not concerned with the destination of the bird (that will be explored latter in the section on *Spatial Patterns of Movement*); only its location at the time that a movement did or did not occur. We began this analysis with the general null hypothesis that the specific wetland where a bird was located at time *t* did not influence the probability of whether or not it moved to a different location at time *t* + 1. We rejected this null hypothesis based on a conditional logistic regression model ($\chi^2 = 107.38$, 16 df, P <0.001)(Fig. 6-11). We then tested the same hypothesis using the region, rather than the specific wetland, to determine if this might provide a more parsimonious model. This test also rejected the null hypothesis ($\chi^2 = 53.82$, 5 df, P <0.001); however, a comparison of these two models indicated that our data

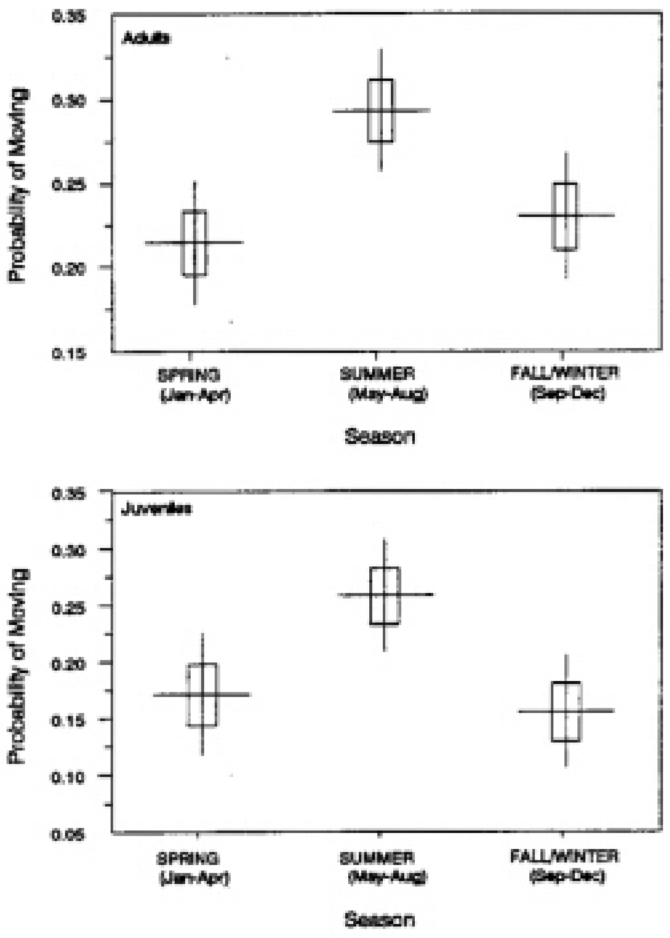


Figure 6-8. Conditional probabilities that adult and juvenile Snail Kites that were alive and their location known at time t, were in the same location (or conversely at a different location) at time t + 1 during each season. Also shown are the standard errors (rectangles) and 95% confidence intervals (vertical lines).

supported use of the more general model (i.e., specific wetlands) based on both a LRT ($\chi^2 = 52.04$, 11 df, $P < 0.001$), and on AIC (Table 6-7).

Table 6-7. Summary statistics for conditional logistic regression models of the probability of movement between times t and t + 1. The model with the lowest AIC (bold) would be selected if based solely on this criterion.

Source	$-2ln(\mathcal{L})$	*np*	AIC
Specific Wetland	**2394.12**	**17**	**2428.12**
Region	2446.16	6	2458.16

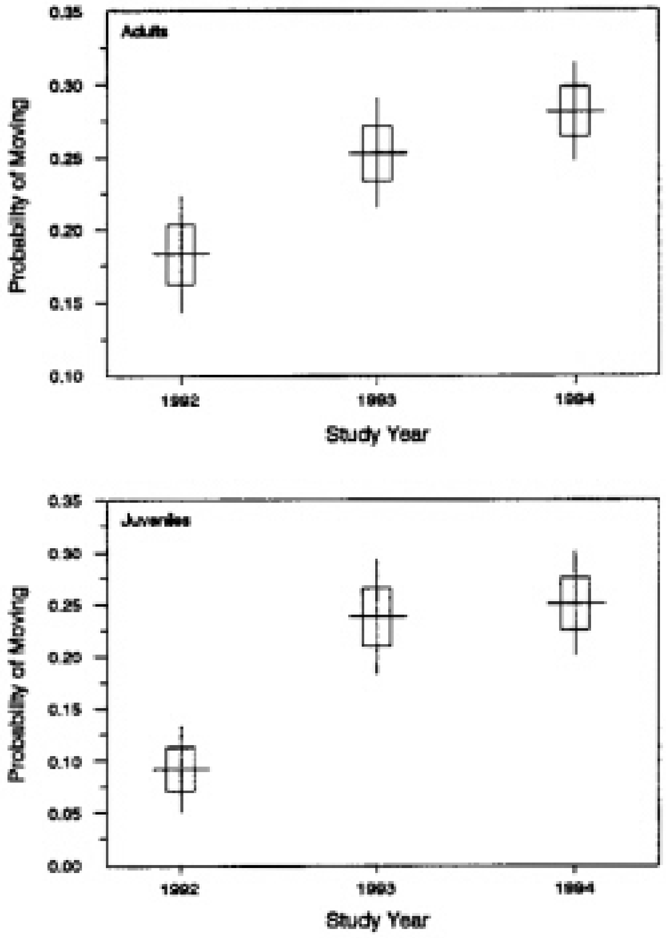


Figure 6-9. Conditional probabilities that adult and juvenile Snail Kites that were alive and their location known at time t, were in the same location (or conversely at a different location) at time t + 1 during each study year. Also shown are the standard errors (rectangles) and 95% confidence intervals (vertical lines).

***Pooling of Locations*–** We next explored whether we could improve our model by some limited selective pooling based on a combination of biological and statistical criteria. Our goal for this exploration was to determine if we could obtain a more parsimonious model by pooling areas in which the overall relative use and seasonal patterns of use were similar enough so as not to warrant separate parameter estimates. We did not attempt to pool some wetlands whose use patterns we felt were biologically different (e.g., wetlands that were used primarily during non-breeding with wetlands used primarily for breeding) even though we could have done so strictly based on statistical criteria. Thus, although a more parsimonious model for the effects of location on movement probability was possible, we preferred to maintain separate parameter estimates for some areas to better ensure the biological integrity of these models.

We began our exploration of potential pooling with areas in the Southern Everglades. The first pooling we considered was Everglades National Park (ENP) and Northeast Shark River Slough (NESRS). Each of these

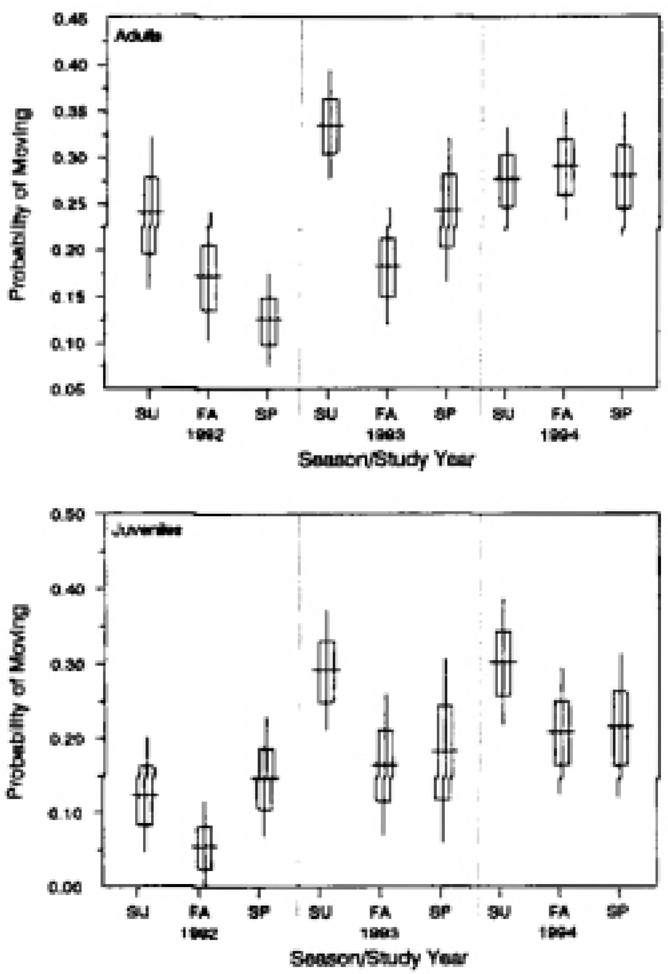


Figure 6-10. Conditional probabilities that adult and juvenile Snail Kites that were alive and their location known at time t, were in the same location (or conversely at a different location) at time t + 1 during each season of each study year. Also shown are the standard errors (rectangles) and 95% confidence intervals (vertical lines).

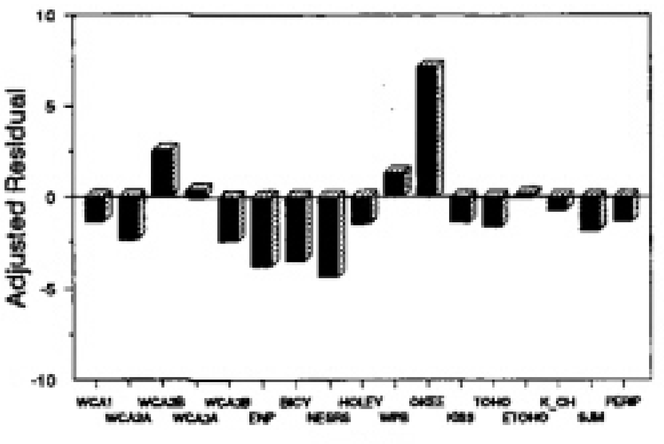


Figure 6-11. Adjusted residuals from a crosstabulation of movement and location at time t. Residuals >0 indicate that birds in this area moved more frequently than expected and residuals <0 indicates that birds in that area moved less frequently than expected.

these areas are administered by the National Park Service, are part of the Shark River Slough (ENP has areas not within the Shark River Slough, but these areas were not used by radio-transmittered kites during our study), receive low to moderate kite use, and are not impounded at their outflow (each have levees at their inflow). A statistical comparison indicated that separate parameter estimates for each of these areas was not warranted based on LRTs and AIC (Table 6-8). Next, we considered including WCA-3B with ENP and NESRS. WCA-3B is also within the Shark River Slough, but is impounded at its outflow and is administered by state agencies. However, its overall relative use and its seasonal patterns of use (each of these areas tended to be used most during early summer) were quite similar to ENP and NESRS. A statistical comparison indicated that separate parameter estimates for each of these areas also was not warranted based on LRTs and AIC (Table 6-8). We considered pooling Big Cypress National Preserve (BICY) with ENP, NESRS, and WCA3B; however, BICY was used more extensively during fall and early winter than these other areas and much of areas used in BICY consisted of cypress prairie habitat which was not generally available in these other areas. Consequently, we did not include BICY with these other areas, even though we probably could have justified doing so on a statistical basis.

Next, we considered pooling the A.R.M. Loxahatchee National Wildlife Refuge (WCA-1), Water Conservation Area 2A (WCA2A), and Holey Land Wildlife Management Area (HOLEY). Each of these areas represents northern Everglades habitats, although their water management histories have differed. Our statistical comparison indicated that separate parameter estimates for each of these areas was not warranted based on LRTs and AIC (Table 6-8).

We next considered areas within the Kissimmee Chain-of-Lakes. First we considered pooling Lakes Tohopekaliga (TOHO) and East Lake Tohopekaliga (ETOHO). Our statistical comparison indicated that separate parameter estimates for each of these areas was not warranted based on LRTs and AIC (Table 6-8). Next we considered including Lake Kissimmee (KISS) with TOHO and ETOHO. Lake Kissimmee received moderately heavy use compared to the other lakes, but all are in close proximity, the seasonal patterns of use were similar, and there was considerable interchange among these lakes. Our statistical comparison indicated that separate parameter estimates for each of these areas again was not warranted based on LRTs and AIC (Table 6-8). In contrast, other lakes within the Kissimmee-Chain-of-Lakes (e.g., Lakes Marion, Tiger, Walk-in-the Water, and Marian) received substantially less use than

Table 6-8. Summary statistics for conditional logistic regression models of the probability of movement between times t and t + 1 to evaluate the pooling of some parameters. A failure to reject a LRT indicates that the additional parameters of the more general (unconstrained) model may not be supported by these data. The model with the lowest AIC (bold) would be selected if based solely on AIC.

Model No.	Constraints (Pooling)	LRT[1] (χ^2)	df	$P > \chi^2$	$-2ln(\mathcal{L})$	*np*	AIC
1	Unconstrained	--	--	--	2394.12	17	2428.12
2	NESRS = ENP	2.78	1	0.10	2396.90	16	2428.90
3	NESRS = ENP=WCA-3B	2.80	2	0.25	2396.93	15	2426.93
4	HOLEY = WCA1	0.07	1	0.79	2394.20	16	2426.20
5	HOLEY = WCA1=WCA2A	0.14	2	0.93	2394.26	15	2424.26
6	TOHO= ETOHO	1.46	1	0.23	2395.59	16	2427.59
7	TOHO= ETOHO=KISS	1.48	2	0.48	2395.61	15	2425.61
8	PERIPHERAL = KISS_CH	0.00	1	0.99	2394.12	16	2426.12
9	Reduced Model (2,4,6,8)	4.31	4	0.36	2398.44	13	2424.44
10	Reduced Model (2,4,7,8)	5.39	6	0.49	2399.52	11	2421.52
11	Reduced Model (2,5,6,8)	4.38	5	0.50	2398.51	12	2422.51
12	Reduced Model (2,5,7,8)	4.40	6	0.62	2398.52	11	2420.52
13	Reduced Model (3,4,6,8)	4.34	5	0.50	2398.46	12	2422.46
14	Reduced Model (3,4,7,8)	4.36	6	0.63	2398.48	11	2420.48
15	Reduced Model (3,5,6,8)	4.41	6	0.62	2398.53	11	2420.53
16	**Reduced Model (3,5,7,8)[2]**	**4.43**	**7**	**0.73**	**2398.55**	**10**	**2418.55**

[1] Based on comparison with unconstrained model
[2] Includes all proposed constraints (pooling)

KISS, TOHO, and ETOHO and the seasonal pattern of use was quite different (i.e., they were used most frequently during non-breeding periods). The seasonal pattern of use of these smaller lakes more closely resembled that of the peripheral habitats. Consequently, we next considered pooling the smaller lakes of the Kissimmee-Chain-of-Lakes with the peripheral habitats. Our statistical comparison indicated that separate parameter estimates for each of these areas were not warranted based on LRTs and AIC (Table 6-8).

Finally, we compared various combinations of pooling to the general unconstrained model and among each other. This analysis indicted that the model containing all of our proposed pooling was a substantial improvement over the unconstrained model (i.e., with no pooling). Additionally, the model with all of our proposed pooling had the lowest AIC; although overall differences among all of the models we compared were relatively small. Consequently, we used the most parsimonious model (Model 16) of this set of models in further analyses of the influence of location on movement probability. This model had 10 parameters compared to the unconstrained model with 17 parameters; but was still a substantial improvement ($\chi^2 = 47.61$, 7 df, $P < 0.001$) over the 6-parameter model using regions, rather than location.

HYDROLOGIC EFFECTS ON THE PROBABILITY OF MOVEMENT

We tested the influence of water levels on the probability of movement for a subset of the data (1787 of 2994 months). We were unable to use the complete data because applicable hydrologic data were not readily available for all areas. Our subset, however, included most of the major wetlands used by kites. Probably the most notable exception was the Upper St. Johns marsh. Data that were applicable to the areas kites used most during this study (i.e., the Blue Cypress Water Management Area and Blue Cypress Marsh Water Conservation Area) were available only from 1991 to present. Because our analysis used long-term averages to assess relative water levels (see below), we did not believe that these data were sufficient for this assessment. Long-term data were available for the adjacent Blue Cypress Lake (which were used for drought assessments; see *Conservation and Management*), but these data did not sufficiently represent the areas most used by kites during the years of our study ($R^2=0.48$ for monthly averages from gauge S-251E [the most applicable gauge for recent kite use] with Blue Cypress Lake), undoubtedly due to changes in water management policies during these most recent years. However, based on our results, exclusion of this area would have been highly unlikely to have influenced our conclusions.

Assessing the effects of water levels on a biological response of Snail Kites (or any other species that can move large distances in short periods of time) can be extremely difficult because of the spatial and temporal variation in both the water levels and the animals. We were unable to use stage (i.e., elevation of the water surface) directly as our measure of water level because the ground elevation differences among areas result in stages among areas being incomparable. At first glance, it seems that local water depth is a suitable alternative to stage; however, we were very concerned about two problems that result from using depth. First, reliable ground elevation data (which are required to determine depth from stage) are sorely lacking for most areas. Although many of the gauges have known ground elevation, there was often considerable distance between the gauges and the areas used by birds such that these known elevations were not reliable indicators of elevations in the areas of interest. Secondly, the lake habitats in particular, often had steep elevation gradients such that a substantial range of water depths may have been used even by a single bird in any given day. The range of depths used by a given bird in a single foraging bout on some lakes (e.g., Lake Kissimmee) often exceeded the range of depths over hundreds of square kilometers in marsh habitats. Consequently, our assignment of elevations and subsequent depths would have been quite arbitrary for many areas. To overcome these problems we wanted a measure that was robust to spatial variation (i.e., "standardized" such that it was comparable among areas) but did not rely on our having to assign an arbitrary elevation to a local site as would have been required by using depth. We also wanted a measure that would adequately reflect the temporal variation of hydrologic conditions. For example, most areas in Florida exhibit seasonal variation in water levels. Consequently, we wanted a measure that enabled us to assess the influence of water levels independently of seasonal variation. Based on these considerations we used the departure from monthly average stages for each area as a measure of relative water levels. Specific gauges used for this analysis are provided in Appendix 6-4. A monthly average over the 26-year period from 1969-1994 (i.e., an overall average of the annual monthly averages) was calculated for each area. The period of record was used for areas that did not have reliable records for all 26 years. The difference (i.e., the residual) between a specific month of a given year and the long term average for that month was used as our measure of relative water levels. The 26-year period of time was sufficiently long to encompass long-term variability and also coincided with the period of time that Snail Kites have been monitored on an annual basis. Because averages were calculated by month, rather than annually, seasonal variation was taken into account. Because this measure is using stage, rather than depth, it also did not require assignment of a local ground elevation. Consequently, we could apply the same measure to birds within, as well as among, wetlands. However, one general caveat that must be included is that this is a measure of relative, rather than absolute, water levels. If birds respond to absolute water conditions (e.g., depth) then this measure may be misleading. There has been considerable effort in recent years to collect reliable data on elevation that can be used to estimate depth. A re-analysis of these data may be warranted in the future as these improvements become more available; however some problems (e.g., steep elevation gradients) will persist even with improved information on depth.

We began our analysis with a univariate approach to logistic regression (Hosmer and Limeshow 1989) using the departure from average stage (described above) as a continuous independent variable. This analysis initially indicated an effect of relative water level ($\chi^2=8.27$, 1 df, $P=0.004$). However, because location (i.e., wetland) and water level are confounded and our previous analyses indicated an effect of location, we next tested a model that included the effects of both location and water level. This test was consistent with our earlier analysis indicating a location effect ($\chi^2=55.88$, 9 df, $P<0.001$); however when included in a model with location, the effect of water level on the probability of movement was no longer apparent ($\chi^2=0.01$, 1 df, $P=0.934$).

Although these results indicated that relative water level was not a major influence on the probability of movement, we must emphasize that the hydrologic conditions under which our study was conducted were generally high water conditions throughout the study area. Consequently, low water conditions that might have triggered movements generally did not occur during this study and inferences regarding the effects of low-water conditions on movement probabilities could not be made. However, previous studies (e.g., Beissinger and Takekawa 1983, Takekawa and Beissinger 1989) have indicated substantial dispersal of Snail Kites during low-water conditions. Given that apple snails may die or become unavailable to kites during dry conditions, these previous reports are certainly reasonable, and may indicate that the lack of an effect of water levels we observed applies only to generally high water conditions.

THE EFFECT OF FOOD RESOURCES ON MOVEMENT

One of the most commonly cited reasons for animals to move is the availability of food (e.g., Krebs et al. 1974, Greenwood and Swingland 1984, Pyke 1984). Animals move if food resources are low or if there is potential for better resources elsewhere (Pyke 1984). Nomadic species are particularly believed to move in response to sporadic food conditions (Andersson 1980). The most commonly suggested reasons suggested for Snail Kites to move are water levels and food (e.g., Beissinger 1988, Bennetts et al. 1994, Sykes et al. 1995) and low water levels are generally implied to represent low food availability.

During 1993 and 1994 we conducted 343 hours of foraging observations (including 814 prey captures) to assess the influence of food resources on movement. To minimize confounding variation, all observations were conducted on adult birds between 2 hours after sunrise and 2 hours before sunset. In addition, we restricted our observations to days that were not unseasonably cold (i.e., during the passage of cold fronts), were not raining, and winds did not exceed 10 mph. For comparisons of food acquisition, we also used only complete observations of foraging bouts. That is, observations in which we observed an individual for the entire length of time it took to capture a snail.

There was also potential confounding attributable to foraging behavior. Course hunting (hunting by low flight over the marsh) is the most commonly used method of prey capture in Florida (Beissinger 1983a, Sykes 1987a) and accounted for 671 of 814 (82%) of the captures we observed. Still (perch) hunting accounted for the remaining 143 (18%) captures and the proportion of use among these 2 behaviors was highly dependent on habitat type ($\chi^2=249.78$, 3 df, $P<0.001$). Perch hunting was primarily observed in cypress prairie habitats (Fig. 6-12). In contrast, we had a more reliable sample of course hunting observations in each habitat type, season, and year. Thus, our comparisons among seasonal and annual food acquisition by kites was limited to course hunting to reduce confounding between these different behaviors.

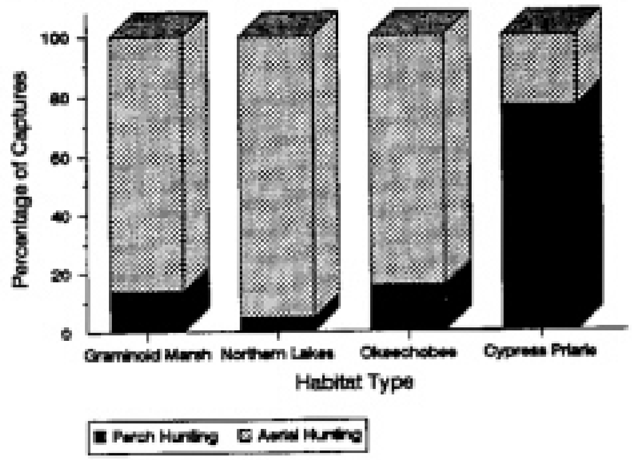


Figure 6-12. The percentage of captures by perch hunting and aerial (course) hunting in each of 4 habitat types.

We compared food acquisition among seasons and years using the foraging time per capture as the dependent variable in an ANOVA model. Our results showed a difference among years, seasons, and an interaction between year and season (Table 6-9). Capture times were lowest during summer, relatively higher during spring, and still higher during autumn of each year (Fig. 6-13). Capture times also tended to be lower during 1994 compared to 1993 for each season. These results suggest that higher movement probabilities corresponded with seasons and years of higher food availability (see *Temporal Effects on Movement Probabilities* above). This is the opposite result of what would be expected if movements were attributable to low food availability.

Table 6-9. Analysis of variance table from model of foraging time per capture as the dependent variable. Mean square (MS) and F values are based on type III partial sums of squares (i.e., they are adjusted for all other terms in the model and are not dependent on the order of entry)(SAS Inc. 1988).

Source	df	MS	F	P
Year	1	386.79	29.65	<0.001
Season	2	374.80	28.73	<0.001
Year x Season	2	166.65	12.78	<0.001
Error	175	13.04		

In addition to comparisons among seasons and years, we also observed 8 movements of 7 radio-transmittered birds (one bird moved twice) for which we had foraging observations prior to a subsequent movement. This enabled obtaining foraging observations immediately after the movement for paired comparisons

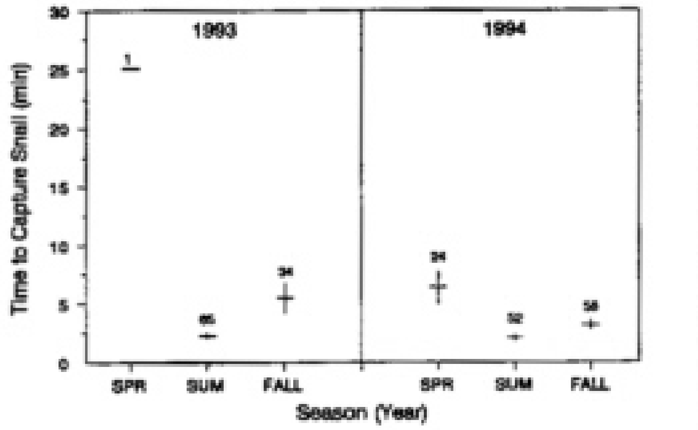


Figure 6-13. The mean (± SE) foraging time to capture snails. Sample sizes (number of complete bouts observed) are also shown.

of food acquisition before and after moving. To reduce confounding, we restricted this analysis to those observations where the movement was within 30 days of obtaining the first foraging observation. This reduced the potential for seasonal differences in food acquisition to be confounded with differences between locations. To further reduce confounding, we matched the time of observations before and after moving. Thus, if the foraging observations before moving were conducted between 1100 and 1300 h, then observations after moving were also conducted between 1100 and 1300 h. We then tested the null hypothesis (H_0) that the difference in mean foraging time per capture before and after moving was zero. These data indicated no difference in food acquisition before and after moving (t=0.60, P=0.57). Furthermore, in 4 of the 8 movements we observed, birds increased the time required to capture snails (Fig. 6-14). In the remaining 4 cases, birds decreased the time required to capture snails. Although these data are limited, they do not support the hypothesis that birds are moving to enhance their foraging opportunities. However, the only case (bird 153.564) where we observed a second movement immediately following a previous movement, was when the time required to capture snails was higher than at all other locations. This suggests that there might be a threshold of food acquisition, below which birds will move if there are more favorable sites elsewhere.

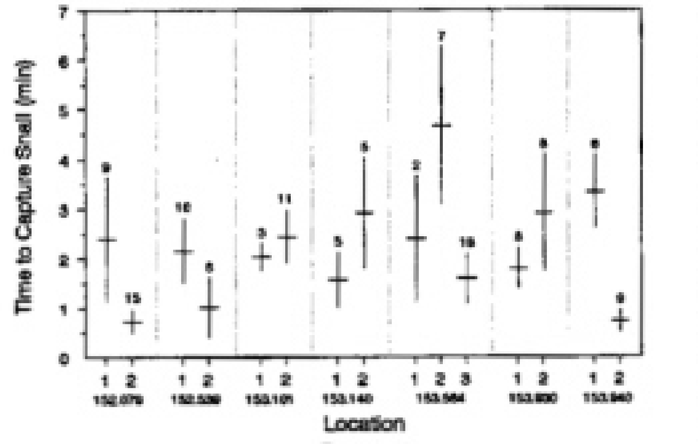


Figure 6-14. The mean (± SE) foraging time to capture snails by radio-transmittered birds before (location 1) and after (location 2) moving. Sample sizes (number of complete bouts observed) are also shown.

MODEL SELECTION AND DISCUSSION OF EFFECTS ON MOVEMENT PROBABILITIES

We began our model selection using the procedure described by Hosmer and Limeshow (1989)(see *Methods*). First we conducted a univariate analysis of each potential term (i.e., age, season, study year, and location). Based on the preliminary analyses above, we used location, rather than region. We also used the 10-parameter model for location rather the full 17-parameter model. Because all terms were significant at the α level (0.25) suggested by Hosmer and Limeshow (1989), we next used each term in a multivariate model of only main terms (i.e., no interactions were included at this point). In both the univariate and multivariate analyses all terms were significant (Table 6-10) and consequently retained for further model selection procedures. Next we began exploring which, if any, interaction terms should be included in the model. A LRT between a fully saturated model (i.e., with all interaction terms) and the multivariate model without any interaction terms indicated that at least some interactions were warranted (Table 6-11, test 23). A comparison of the fully saturated model with a model excluding the 4-way interaction term indicated that the 4-way interaction was not warranted (Table 6-11, test 24). However, comparisons among models with various combinations of 2 and 3-way interactions indicated that some 2-way interaction terms (Table 6-11, tests 2,3,7,8,10,12, and 13) and some 3-way interaction terms (Table 6-11, tests 17,18,19,20,22) were warranted. Our tests did not support retaining an age * location, age * season, or age * year interaction terms (Table 6-11, tests 1, 4, and 5); but did support retaining 2-way interaction terms for season x location and year * location at α= 0.05 (Table 6-11, tests 2 and 3) and a season * year interaction at α=0.10. All further tests using season x location and year * location interaction terms indicated that these terms were warranted (Table 6-11, tests 7,8,10,12 and 13); however, retention of the season * year interaction was not supported when included with these other interactions (Table 6-11, tests 9, 11, and 14). Thus, we retained season*location and year*location interaction

Table 6-10. Maximum likelihood analysis of variance table for univariate models (i.e., each source term represents a separate model) and multivariate models (i.e., each source term is contained within 1 model) of potential sources of variation of the probability of movement between times t and t + 1.

	Univariate			Multivariate		
Source	χ^2 [1]	df	$P < \chi^2$	χ^2 [1]	df	$P < \chi^2$
Age	5.38	1	0.020	9.87	1	0.002
Season	17.85	2	<0.001	22.35	2	<0.001
Year	28.28	2	<0.001	25.48	2	<0.001
Location	103.36	9	<0.001	110.98	9	<0.001

[1] *Based on Wald χ^2 statistic (SAS inc. 1988).*

Table 6-11. Likelihood ratio tests (LRTs) comparing conditional logistic regression models of the probability of movement between times t and t + 1. The null hypothesis (H_o) from a LRT is that the reduced model (i.e., the model with fewer parameters) fits the data equally well as the more general model (i.e., with more parameters). Thus, a rejection of H_o favors the more general model and a failure to reject H_o favors the more reduced model.

No.	General Model[1]	Reduced Model[1]	LRT χ^2	df	$P > \chi^2$
1	A S Y L A*L	A S Y L	13.61	9	0.14
2	A S Y L S*L	A S Y L	45.22	18	<0.01
3	A S Y L Y*L	A S Y L	30.82	18	0.03
4	A S Y L A*S	A S Y L	1.01	2	0.60
5	A S Y L A*Y	A S Y L	2.99	2	0.22
6	A S Y L S*Y	A S Y L	8.12	4	0.09
7	A S Y L S*L Y*L	A S Y L S*L	34.44	18	0.01
8	A S Y L S*L Y*L	A S Y L Y*L	48.84	18	<0.01
9	A S Y L S*L S*Y	A S Y L S*L	4.64	4	0.33
10	A S Y L S*L S*Y	A S Y L S*Y	41.74	4	<0.01
11	A S Y L S*L Y*L S*Y	A S Y L S*L Y*L	2.51	4	0.64
12	A S Y L S*L Y*L S*Y	A S Y L Y*L S*Y	45.12	18	<0.01
13	A S Y L S*L Y*L S*Y	A S Y L S*L S*Y	32.31	18	0.02
14	A S Y L + all 2-way Interactions	A S Y L S*L Y*L	22.23	17	0.18
15	A S Y L S*L Y*L A*S*Y	A S Y L S*L Y*L	5.16	4	0.27
16	A S Y L S*L Y*L A*S*L	A S Y L S*L Y*L	21.06	18	0.27
17	A S Y L S*L Y*L A*Y*L	A S Y L S*L Y*L	32.76	18	0.02
18	A S Y L S*L Y*L S*Y*L	A S Y L S*L Y*L	59.63	36	<0.01
19	A S Y L S*L Y*L S*Y*L A*Y*L	A S Y L S*L Y*L S*Y*L	33.59	18	0.01
20	A S Y L S*L Y*L S*Y*L A*Y*L	A S Y L S*L Y*L A*Y*L	60.77	36	<0.01
21	A S Y L +all 2 & 3-way Interactions	A S Y L S*L Y*L S*Y*L A*Y*L	39.57	39	0.44
22	A S Y L +all 2 & 3-way Interactions	A S Y L + all 2-way Interactions	110.87	76	<0.01
23	Fully Saturated (all interactions)	A S Y L	247.78	16	<0.01
24	Fully Saturated (all interactions)	A S Y L +all 2 & 3-way Interactions	35.02	36	0.52

[1] *Model terms are A=Age, S=Season, Y=Study Year, L=Location (with pooling from Table 6-8)*

terms, but not a season* year term. Using a base model with these 2-way interaction terms we tested whether the data supported the addition of any 3-way interaction terms. Our results indicted that two of the 3-way interaction terms (Age*Year*Location and Season*Year*Location) were supported by the data (Table 6-11, tests 17,18, 19, and 20) and the remaining two were not (Table 6-11, tests 15 and 16). Thus, based on LRTs, our data support a model with all main effects, two 2-way interaction terms (Season*Location and Year*Location) and two 3-way interaction terms (Age*Year*Location and Season*Year*Location).

The results from using AIC were not in complete agreement with LRTs. The model with the lowest AIC (Table 6-12, Model 7) was a model with all main effects and only one 2-way interaction term (Season*Location); however, the AIC of the model with both of the 2-way interaction terms supported by LRTs (Table 6-12, Model 12) was very close. AIC did not support inclusion of the 3-way interaction terms. Differences between models indicated by LRTs and AIC are not uncommon and represent conceptual differences between an approach of hypothesis testing (LRTs) and optimization (AIC). Both approaches were consistent in that they indicated that the effects of age, season, year, and location were all supported by the data and that there is an interaction between time and location. The methods only differ in suggesting to what degree of complexity the interactions are supported by the data.

Our results indicated that considerable

Table 6-12. Summary statistics used for model selection of conditional logistic regression models of the probability of movement between times t and t + 1. The model with the lowest AIC (bold) would be selected if based solely on AIC criterion.

Model No.	Model Description	$-2\ln(\mathcal{L})$	*np*	AIC
1	Age (A)	2502.95	2	2506.95
2	Season (S)	2490.66	3	2496.66
3	Year (Y)	2477.48	3	2483.48
4	Location (L)	2398.55	10	2418.55
5	A S Y L	2339.23	15	2369.23
6	A S Y L A*L	2325.62	24	2373.62
7	**A S Y L S*L**	**2294.01**	**33**	**2360.01**
8	A S Y L Y*L	2308.41	33	2374.41
9	A S Y L A*S	2338.22	17	2372.22
10	A S Y L A*Y	2336.24	17	2370.24
11	A S Y L S*Y	2331.11	19	2369.11
12	A S Y L S*L Y*L	2259.57	51	2361.57
13	A S Y L S*L S*Y	2289.37	37	2363.37
14	A S Y L S*Y Y*L	2302.20	37	2376.20
15	A S Y L S*L Y*L S*Y	2257.06	55	2367.06
16	A S Y L with all 2-way Interactions	2237.34	68	2373.34
17	A S Y L S*L Y*L A*S*Y	2254.41	55	2364.41
18	A S Y L S*L Y*L A*S*L	2238.06	69	2376.06
19	A S Y L S*L Y*L A*Y*L	2226.81	69	2364.81
20	A S Y L S*L Y*L S*Y*L	2199.63	87	2373.63
21	A S Y L S*L Y*L S*Y*L	2166.04	105	2376.04
22	A S Y L with all 2 & 3-way	2126.47	144	2414.47
23	Fully Saturated	2091.45	180	2451.45

movement occurs that is not directly related to water levels. We cautioned, however, that this analysis was conducted entirely during a period of relatively high water. Based on anecdotal evidence we believe that Snail Kites do move in response to low water levels. Thus, we believe that there is a threshold response to water levels. If water levels become low enough to negatively affect food resources, then kites will likely move from that area. However, during most years there is considerable movement that appears to be independent of current water levels. We suggest a hypothesis for this movement pattern below.

Dispersal is also generally thought to be favored when local resources (e.g., food) are low or better conditions exist elsewhere (Horn 1984). In contrast, our results from both within-year and between year comparisons suggest that higher probabilities of movement occur when food resources are high. We also found that natal dispersal of juveniles was lower in areas where food resources were likely to have been depressed. At first it may seem counter-intuitive to leave an area if food resources are high; however, we suggest a hypothesis that this may be a reasonable strategy given the dynamic and unpredictable nature of a kite's environment. A virtual certainty about any specific wetland inhabited by Snail Kites is that it will go dry. What is not certain is which wetlands will go dry in which years. Thus, there is an advantage for kites to have experience regarding the availability of wetlands throughout their range so that when a local drying event does occur past experience reduces the need for "blind" searching for suitable alternative habitats. Thus, in years that food is not limiting, which for kites may be most years, high food resources may **enable** kites to "explore" their potential habitats with little risk of starvation. The resulting experience from many locations may then help kites to locate food resources faster during times when food is limiting.

Spatial Patterns of Movement

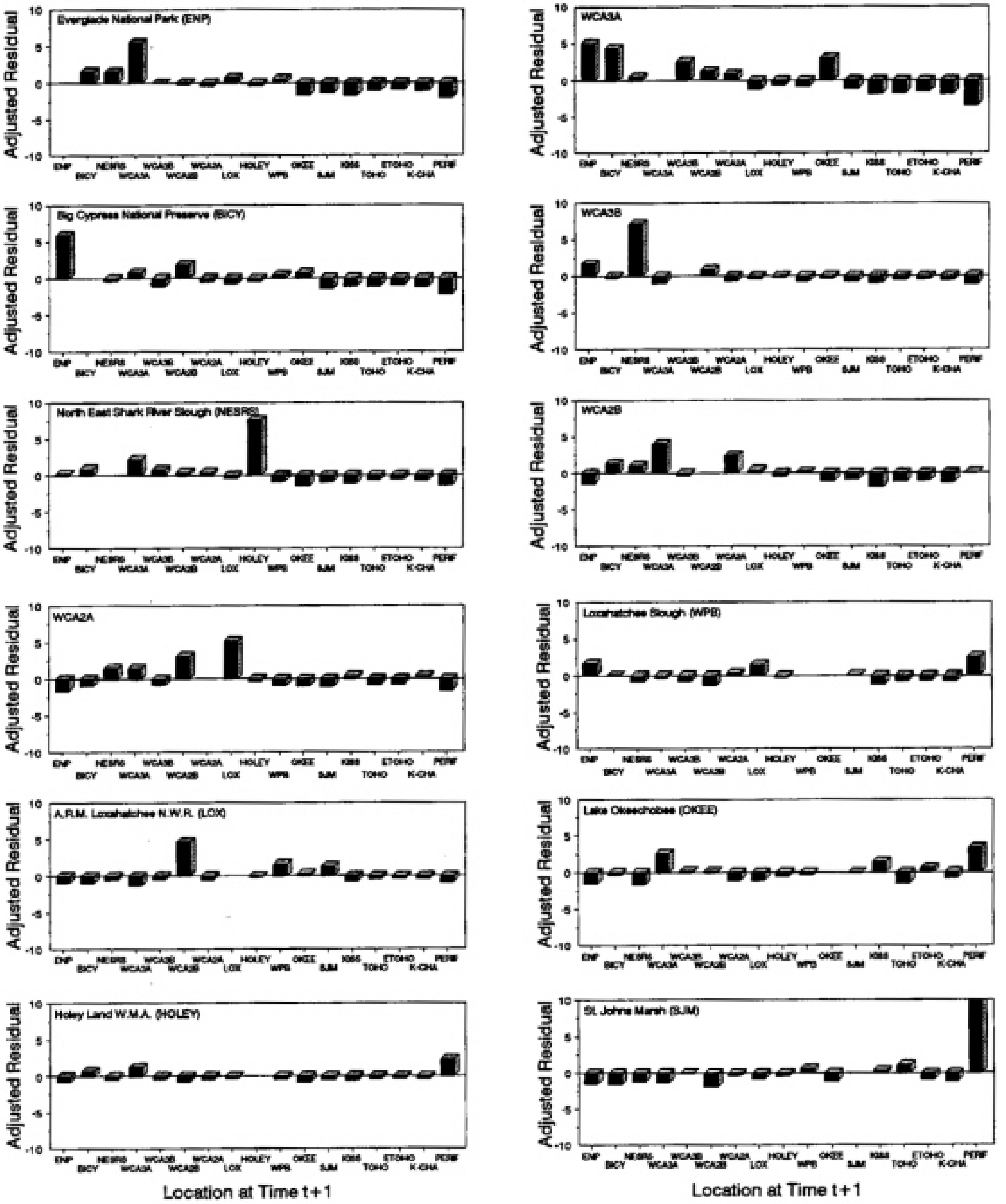
Here we ask the question that given a bird at location r at time t has moved, what is the probability that it will be at location s at time $t + 1$. Thus, our conditional setting is that a bird is alive, its location at times t and $t + 1$ are known, and it has moved from its location at time t.

We approached this problem by first establishing whether the locations at time t and $t + 1$ are independent (i.e., our null hypothesis [H_0] is that the probability of moving to a given location does not depend on the bird's previous location). For our initial exploration we used a fully unconstrained data set with no pooling of locations). This hypothesis (H_0) is strongly rejected ($\chi^2=1014.41$, df=256, $P < 0.001$). Thus, our data suggests that the probability of movement to a given location does depend on the bird's previous location. The residuals from this analysis provide some insight into how these movement patterns departed from what would have been expected if H_0 were true (Fig. 6-15).

EFFECT OF DISTANCE

What becomes apparent from the above residuals is a tendency to move to areas in relative proximity to a bird's current location. For example, birds at WCA-3A had the greatest positive departure from expected when they moved to Everglades National Park and Big Cypress National Preserve, both of which are immediately adjacent to WCA-3A. The greatest negative departures from expected were movements to the lakes within the Kissimmee chain-of-lakes (at the opposite end of the kites' range in Florida. This pattern of higher than expected values for locations in proximity and lower than expected values for distal areas can be seen throughout these data.

We further explored the relationship between distance and the location of movements by ranking each location (wetland) with respect to its relative distance from each other location. Thus, the closest wetland to any given wetland was given a rank of 1 and the furthest was given a rank 15. We excluded the peripheral habitats and the Kissimmee Chain-of-Lakes from this analysis because they were not contiguous and it would have been virtually impossible to perform an analysis for every wetland. When more than one wetland was immediately adjacent to another, we used the areas that were most frequently used by kites within each wetland to determine their relative ranking. We then tested for the effect of distance using the null hypothesis (H_o) that the distance rank is equal for all movements (i.e., the expected values for a goodness-of-fit test among distance classes were equal). We strongly rejected H_o ($\chi^2=320.83$, 13 df, $P < 0.001$) and concluded that distance does have an influence on the locations to which a bird moves. Not surprisingly, the residuals from this analysis indicated that birds exhibited a greater than expected frequency of moving to a new location in proximity to their previous location, and a lower than expected frequency of moving to areas that were most distant from their previous location (Fig. 6-16). This does not imply that birds will not move long distances (our data show that they do); but rather, that long distance movements have a tendency to be made in short increments.


Everglade National Park (ENP)

WCA3A

Big Cypress National Preserve (BICY)

WCA3B

North East Shark River Slough (NESRS)

WCA2B

WCA2A

Loxahatchee Slough (WPB)

A.R.M. Loxahatchee N.W.R. (LOX)

Lake Okeechobee (OKEE)

Holey Land W.M.A. (HOLEY)

St. Johns Marsh (SJM)

Figure 6-15. Adjusted residuals from the crosstabulation of the frequency of movements to each location (at time t + 1) from each location at time t. A residual value of ±1.96 is an approximate indicator of that residual being significant at an α = 0.05 level of significance.

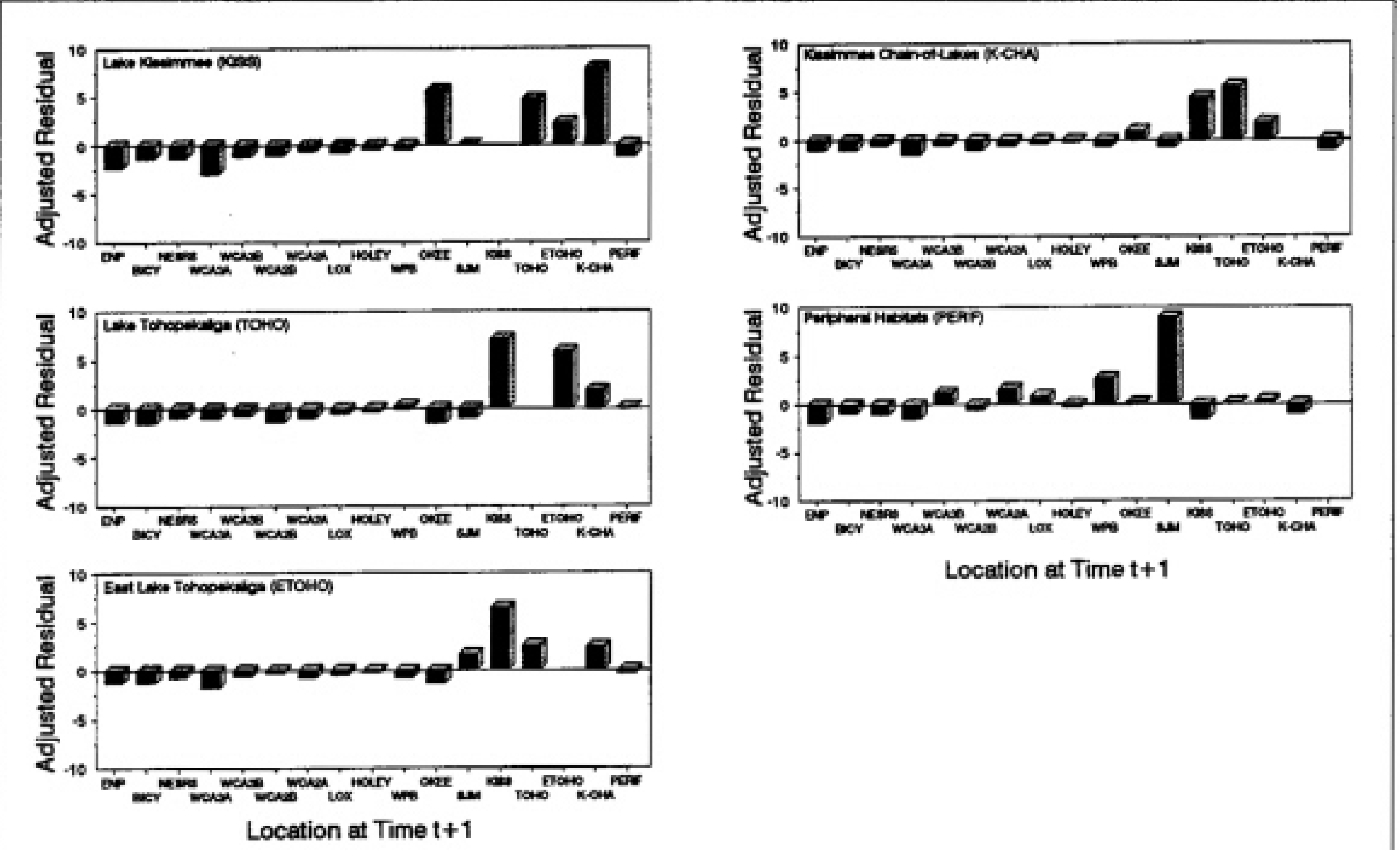


Figure 6-15. Cont.

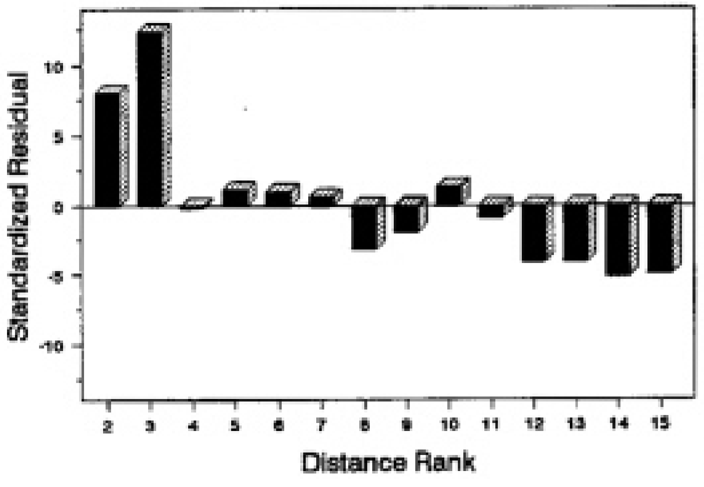


Figure 6-16. Standardized residuals from a contingency table of the frequency of movements to wetlands in each relative distance class. Expected values were derived under a null hypothesis (H_o) of equal probability for each distance class.

THE EFFECT OF AGE, SEX, AND TIME ON MOVEMENTS BETWEEN SPECIFIC LOCATIONS

We tested for the effects of age, sex, and time (i.e., season and year) on the location-specific movement probabilities using a LRT between a log-linear model of specific location effects (using the reduced model from Table 6-10) and models which include the effects of each of these independent variables. We found no effect of age (χ^2=17.7, df=23, P=0.773), sex (χ^2 =27.9, df=47, P=0.988), season (χ^2=39.04, df=44, P=0.684), or year (χ^2=11.72, df=48, P>0.999). This does not imply that there were no effects from these independent variables, but rather that if there were such effects, our data were insufficient to detect them. Given the large number of parameters (>100) in these models this latter result would not be surprising.

SEASONAL SHIFTS IN LATITUDE

It has been previously suggested (e.g., Sykes 1983a, Sykes et al. 1995) that Snail Kites tend to move south during colder winters. Although no data have previously been presented in support of these suggestions, our data are consistent with this conclusion. There was a general tendency for Snail Kite occurrence to shift north during the summer (May-August) and south during Fall/Winter (September-December)(χ^2=27.68, df=4, P<0.001)(Fig. 6-17).

We used a LRT to test whether this relationship was influenced by age, sex, or year by comparing a fully

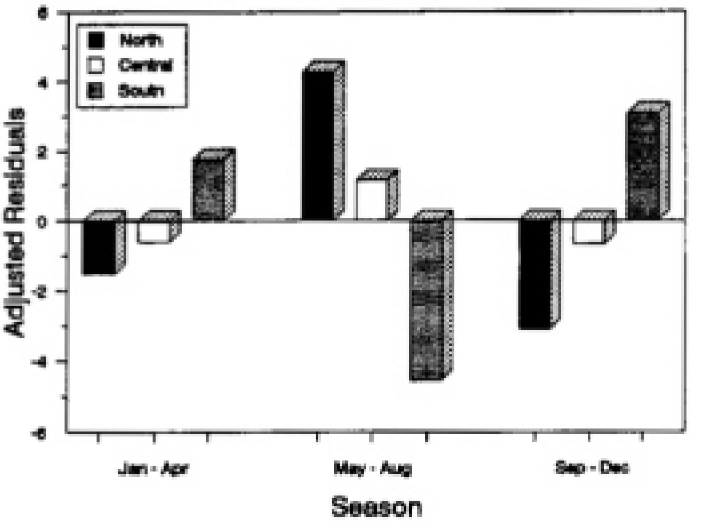


Figure 6-17. Adjusted residuals from a contingency table of the frequency of movements to wetlands in northern, central, and southern regions during each season.

saturated model to one without each of these effects. These tests indicated that these seasonal shifts in latitude were influenced by age (LRT=15.68, df=4, P =0.004), sex (LRT=22.47, df=8, P=0.004), and year (LRT=51.60, df=8, P<0.001).

Although we found evidence to suggest that there were effects of age, sex, and year on these seasonal shifts, the AIC was substantially lower for a reduced model without these effects (9,837 compared to 12,651 for the closest model). Although this result appears contradictory, it is not uncommon, and reflects the difference between hypothesis testing where a specific effect is being tested and model selection, which views model selection as more of an optimization problem (Spendelow et al. 1995). In other words, there may be real influences of age, sex, and year, but our data are insufficient to effectively incorporate separate parameter estimates for each of these influences.

SHIFTS IN REGIONAL USE

Factors such as resource abundance and disturbance that influence patterns of distribution at one scale may be expressed quite differently at a different scale (Wiens 1989). Consequently, we looked at broad-scale movement patterns over the duration of the study in addition to patterns occuring within monthly time steps. We accomplished this by examining how the proportion of birds in different regions shifted throughout the study.

Because our capture protocol used the proportion of birds in different areas as a biasis for our sampling, we believe that our initial conditions were a reasonable representation of the distribution of birds at the start of this study. We then looked at the proportion of locations each month in each region to examine how these proportions changed over time. It was quite apparent from these data that shifts in regional use had occurred over the duration of the study. We tested for a linear trend over the 37 month period from April 1992 through April 1995 using linear regression on the proportion (after an arc-sin transformation) of locations in each region. We tested the null hypothesis (H_0) that the observed slope over this period was zero using a t test (SAS Inc. 1988).

The proportion of birds using the Everglades Region decreased over this interval (t=6.27, P<0.001)(Fig. 6-18). The proption of birds using the Okeechobee and Upper St. Johns Regions decreased over the interval (t= -5.77, P<0.001 for the Okeechobee Region and t=-3.94, P <0.001 for the Upper St. Johns Region). The proportion of birds did not exhibit a linear trend for the Kissimmee Region (t=-0.028, P=0.916), the Loxahatchee Slough Region (t=-1.415, P=0.166), or the Peripheral Region (t=-1.088, P=0.284); although the seasonal shifts in some regions (e.g., the Peripheral Region) may have been better represented by a higher order polynomial regression.

Effect of Hydrology-- Our analysis of regional shifts is strictly correlative and can not reliably be used to infer cause and effect. However, it is quite possible that, at least some of the shifts in regional use, were attributable to hydrologic changes. For example, the Everglades Region experienced a relatively severe drought just prior to our study. It is quite likely that the low proportion of birds in this region at the beginning of our study was attributable to this drought. Our anecdotal observations of foraging birds in this region during 1992 clearly indicated that food resources were diminshed. We often observed birds foraging for long periods (sometimes > 1-2 hours) without capturing a snail; whereas, under good conditions, foraging birds capture snails in just a few minutes (see *Effect of Food Resources on Movement*).

The relatively high proportion of birds in the Okeechobee and Upper St. Johns Regions at the beginning of this study may well have been birds displaced from the Everglades Region. The Okeechobee Region also had experienced the drought preceding our study; however, virtually all of the birds we observed in this region at the beginning of our study were confined to the outer marsh of Lake Okeechobee which had not dried during the drought. Over the duration of our study the proportion of birds decreased at Lake Okeechobee and those birds present in this region shifted from the outer marsh to more interior marshes, that had been dry

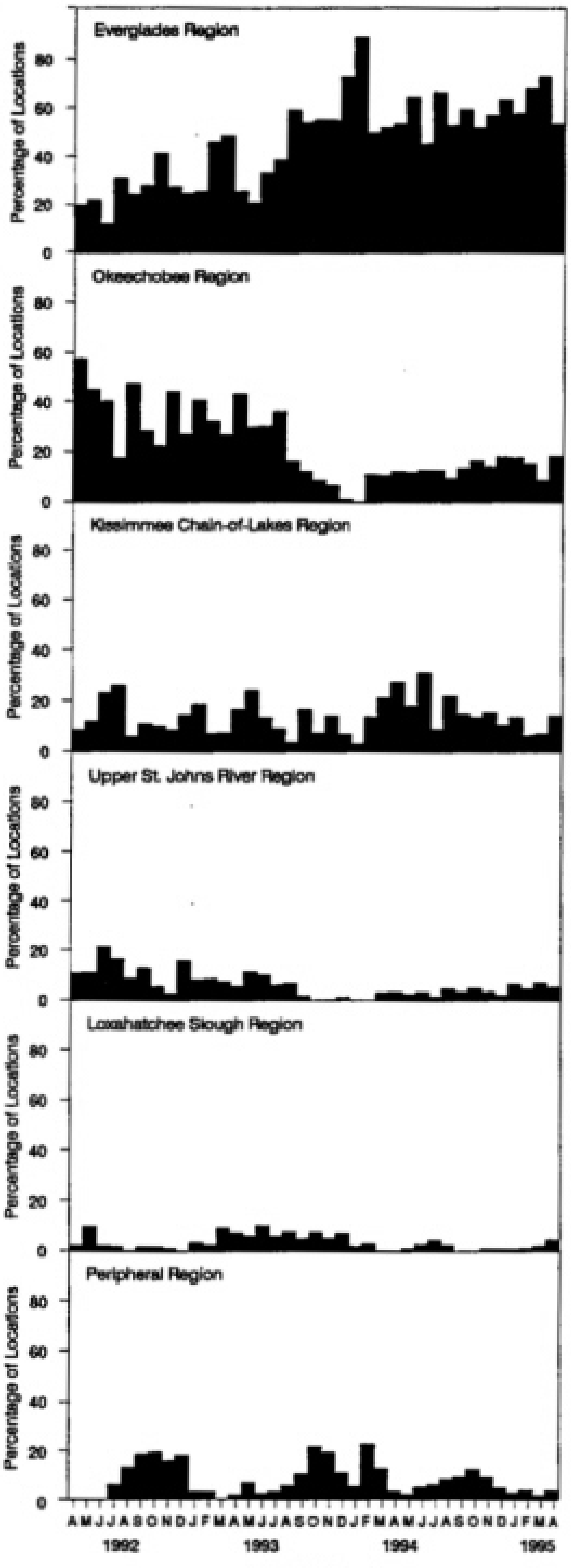


Figure 6-18. The percentage of Snail Kite locations in each region during each month from April 1992 through April 1995.

during the preceding drought. The Upper St. Johns Region had not experienced a drought just prior to our study. The Northern Lakes Region also had not experienced the recent drought and a higher proportion of birds in this region might also have been expected. However, the Northern Lakes Region had extremely high numbers of birds in 1991 (J. Rodgers Jr, J. Buntz, GFC, Pers. Comm.). Thus a high proportion of birds probably had been using this region, but had already dispersed by the start of our study.

SEASONAL SHIFTS IN HABITAT USE

During this study it became apparent that there were substantial seasonal shifts in the use of different habitats by Snail Kites. Consequently, we conducted a "post hoc" evaluation of these habitat shifts. Because this study was not designed to evaluate habitat relationships and because there is high variability in micro-habitat, our analysis was limited to five broad habitat categories (described in *Study Area*). We assigned each location to one of these five habitat classes. We then examined how the proportion of use of each habitat for each month shifted over the duration of the study.

Our results indicated that Snail Kites exhibit strong seasonal patterns in their relative use of some habitats (Fig. 6-19). Relative use of Lake Okeechobee fluctuated greatly, but was not as predictable seasonally as other habitats. Use of Lake Okeechobee was relatively high for the first year of our study then dropped to very low use during the winter of 1993-1994, and increased again to moderate use (discussed above in *Shifts in Regional Use*).

The use of other habitats exhibited more seasonal fluctuation. Peak use of graminoid marshes and northern lakes coincided with the periods of major breeding activity; whereas, cypress prairies and peripheral habitats were used more extensively outside of the primary breeding season. One potential explanation for the use of graminoid marshes and lake habitats during breeding is the relative predictability of hydrologic conditions in these habitats compared to cypress prairies or peripheral habitats. Cypress prairies tend to have shorter hydroperiods than are typically used by breeding birds. Given that a breeding attempt requires 10-16 weeks per clutch (Snyder et al. 1989a), the probability of an area drying out in cypress prairie during a breeding attempt is greater in this habitat compared to those typically used by nesting kites. Thus, the probability of a nesting attempt failing probably is also greater. Similarly, peripheral habitats were usually more ephimeral wetlands or were used for agricultural purposes and were subject to extreme fluctuations for

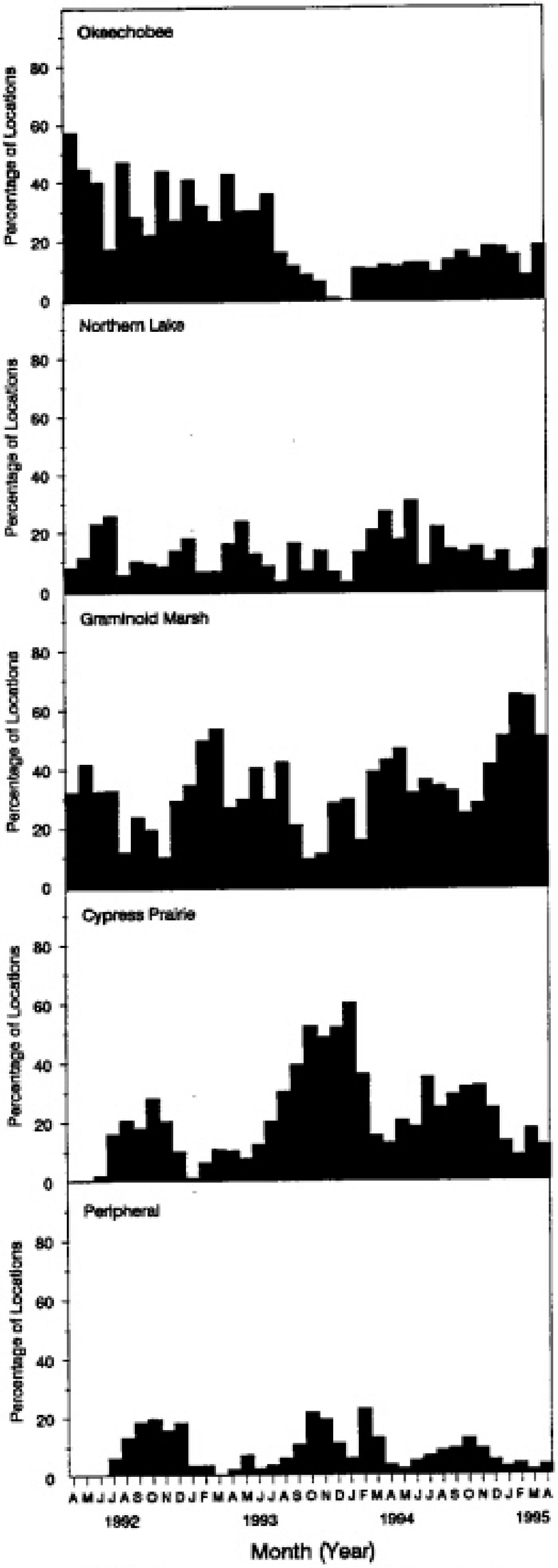


Figure 6-19. The percentage of Snail Kite locations in each habitat during each month from April 1992 through April 1995.

agricultural use. Thus, the probability of this habitat remaining in suitable hydrologic condition for the extent of a breeding attempt also was likely diminished.

Although hydrologic predictability may provide an explanation for why graminoid marshes and lake habitats were more likely used during breeding seasons, it does not explain why cypress prairies and peripheral habitats were used during non-breeding periods. We can offer some potential hypotheses, all of which remain to be tested. First, birds in cypress habitats tend to hunt from perches, rather than by flight (see *The Effect of Food Resources on Movement*). This could offer an energetic advantage since perching requires less energetic expenditure than flight. Secondly, using alternative habitats to the primary breeding habitats could allow snail populations to be repelinished prior to the next breeding season. The summer months when birds shift to cypress and peripheral habitats also coincides with peak breeding activity of apple snails. Lastly, exploring alternative habitats when food resources are not limiting may better enable kites to locate food during periods of localized drought. This latter hypothesis was previously discussed in more detail in the section on *Model Selection and Discussion of Effects on Movement Probabilities*.

The detectability of Snail Kites is probably very low in both cypress prairies and peripheral habitats compared to graminoid marshes, the northern lakes, or the Lake Okeechobee habitat types. Many of the peripheral habitats were either on private land (e.g., agricultural areas) or on public land in which access was limited (e.g., water control districts). Much of the cypress habitat also had very limited access (e.g., some management units of Big Cypress National Preserve do not allow airboat access) and even large numbers of birds in this habitat type were very easy to overlook because of the dense vegetation. On several occasions we had reports of a few birds in cypress habitats only to discover with more intensive searching that the "few" birds turned out to be a large number of birds (50-400).

This seasonal use of habitats with low detectability can have important implications regarding population monitoring of Snail Kites in Florida. For example, the annual count conducted each year (see *Monitoring of Snail Kite Populations in Florida*) in Florida coincides with the period of relatively high use (July-January) of the peripheral and cypress prairie habitats. Consequently, the number of birds detected during these surveys may be greatly influenced the number of birds in these habitats. This can cause a substantial undercounting of birds and may influence the variability among counts depending on what proportion of the population is in these habitats in any given year.

These problems are discussed in detail in the chapter on *Monitoring of Snail Kite Populations in Florida*.

Beissinger et al. (1983) reported that Snail Kites in Florida have long been known to "disappear" from their usual haunts in summer and subsequently "reappear" during mid-October. This observation led to the speculation that Snail Kites in Florida may move to Cuba (Beissinger et al. 1983). No birds that had been banded in Florida were found during an expedition to search for such birds in Cuba (Beissinger et al. 1983). Although movement to Cuba is certainly possible, our data suggest that a more simple explanation for the disappearance of kites during summer may be the shifts in habitat use. The time of disappearance of birds reported by Beissinger et al. (1983) coincides with the time that we observed increased use of peripheral and cypress habitats (where they are less likely to be observed). The reappearance in mid-October also coincides with the time that birds begin shifting back to the graminoid and lake habitats.

Natal Philopatry and Site Fidelity

Philopatry is usually defined as the tendency for an animal to remain at (or very near) its natal site (e.g., Mayr 1963, Shields 1984). However, Snail Kites by their nature do not typically remain anywhere, but may have an affinity to return to their natal site. Consequently, for our analyses, we have relaxed the definition of philopatry to the tendency for a bird to occur in its natal wetland even though birds may, and probably do, regularly also occur elsewhere. We also emphasize from the outset that our analyses of natal philopatry and site fidelity were intended only as a "post hoc" cursory exploration. Our study was not designed to answer questions regarding these topics, and we urge caution in interpretation of our results beyond preliminary exploration. However, because almost no information exists on natal philopatry or fidelity for this species (Sykes et al. 1995), we believed that this preliminary exploration was warranted.

NATAL PHILOPATRY

Our primary data for assessing natal philopatry were the resightings of 414 banded Snail Kites, whose natal wetlands were known. Of these sightings 157 (40%) were of birds that were sighted in their natal wetland. The proportion of birds observed in their natal wetland was not dependent on the breeding status (i.e., actively nesting or not nesting) (χ^2=0.45, 1 df, P=0.50) based on a subsample of 255 birds whose breeding status was known (Fig. 6-20). The proportion of birds observed in their natal wetland was, however, influenced by the bird's sex (χ^2=6.02, 1 df, P=0.014)(Fig. 6-21), natal wetland (χ^2=39.75, 7 df, P<0.001)(Fig. 6-22), and the year (χ^2=10.12, 3 df, P=0.018)(Fig. 6-23).

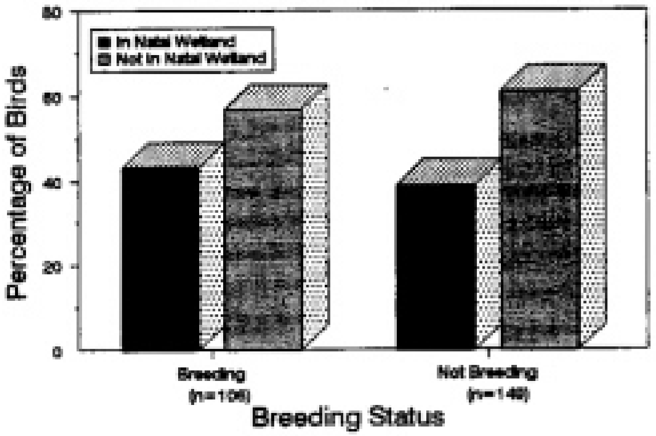


Figure 6-20. The percentage of banded birds that were observed to be actively breeding (including courtship) or not breeding that were or were not resighted in their natal wetland. Only birds whose breeding status was known were included in our sample.

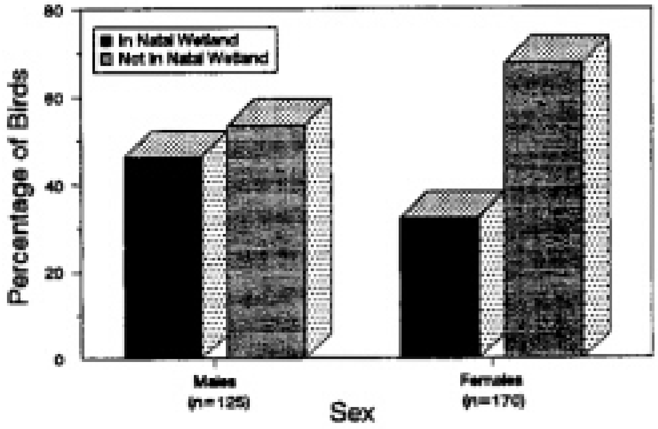


Figure 6-21. The percentage of male and female banded birds that were or were not resighted in their natal wetland.

Differences in natal philopatry between males and females are not uncommon among bird species and the avoidance of inbreeding is a frequently suggested reason for these sexual differences (e.g., Bengtsson 1978, Greenwood et al. 1978); even though there are few examples of the harmful effects of inbreeding in birds (Greenwood and Harvey 1982). Differences among sexes in natal philopatry usually are reported for philopatric species and not generally known to occur in nomadic species (Greenwood and Harvey 1982). Snail Kites in Florida, however, probably have a more

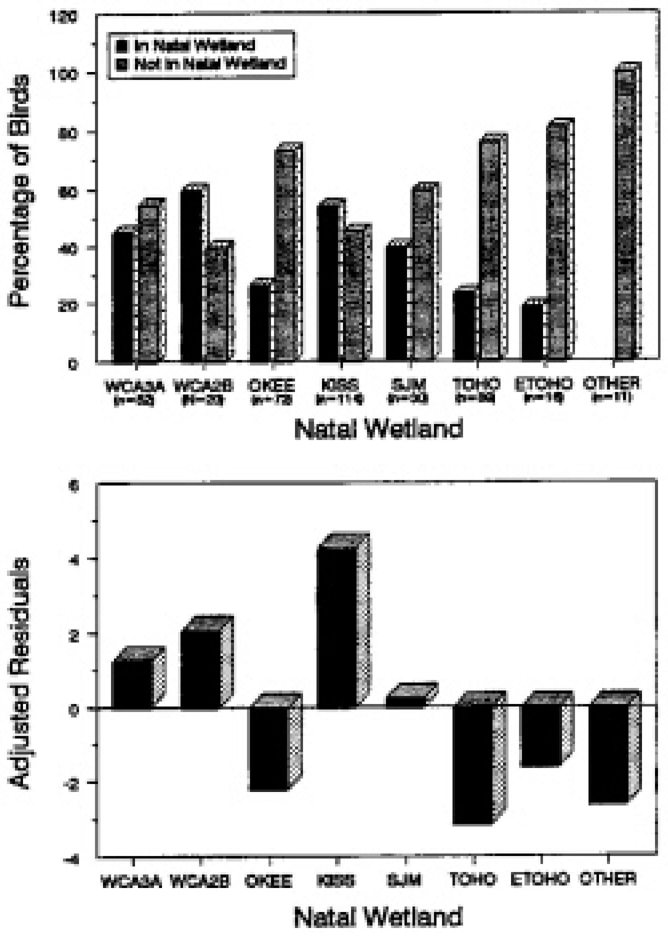


Figure 6-22. The percentage of banded birds from each (natal) wetland that were or were not resighted in their natal wetland. Only birds whose whose natal origins were known (n=414) were included. Also shown are the adjusted residuals from a crosstabulation of natal wetland and whether or not they were resighted in their natal wetland. For visual clarity, only the residuals from birds that were resighted in their natal wetland are shown; however the residuals from birds that were not resighted in their natal wetland are an approximate mirror image of those shown.

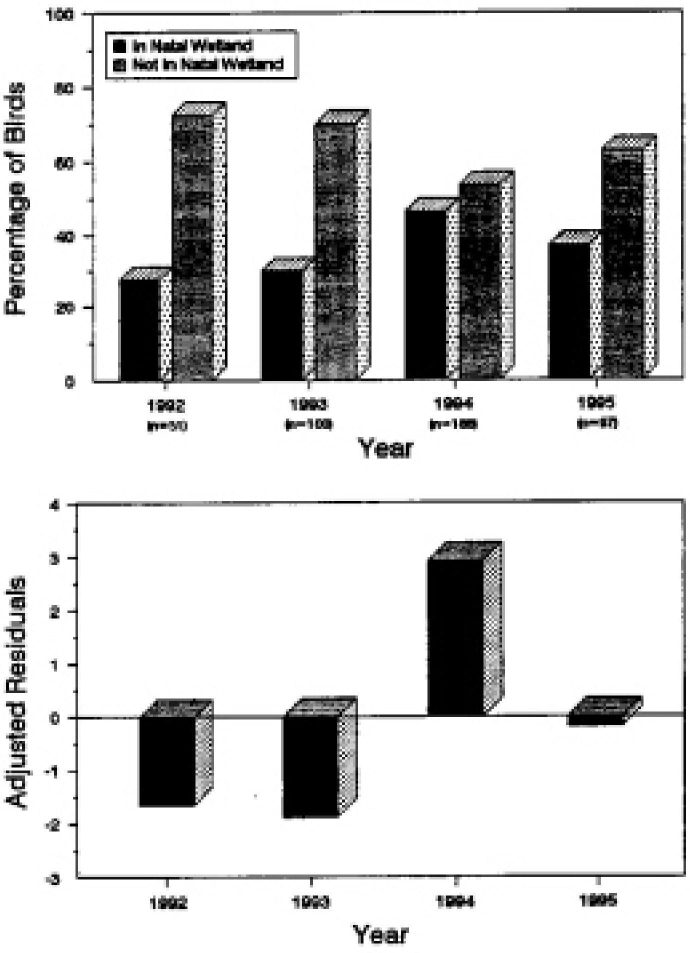


Figure 6-23. The percentage of banded birds during each calendar year that were or were not resighted in their natal wetland. Also shown are the adjusted residuals from a crosstabulation of natal wetland and whether or not they were resighted in their natal wetland. For visual clarity, only the residuals from birds that were resighted in their natal wetland are shown; however the residuals from birds that were not resighted in their natal wetland are an approximate mirror image of those shown.

restricted range than most nomadic species and consequently, similarly to philopatric species, may have a greater probability of inbreeding. Thus, our results are not necessarily inconsistent with the inbreeding avoidance hypothesis; nor do we have any data to support this potential explanation for the differences in philopatry between male and female Snail Kites.

The differences among years and specific wetlands are even less clear. Our data were insufficient to explore the details of interactions among these sources of variation; however, interaction effects would be likely. For example, if one part of the Snail Kites' range had an ongoing drought then it would be unlikely for birds that had fledged from that part of their range to be in their natal wetland until conditions improved. Consequently, our results should be viewed in light of current conditions and probably should not be extrapolated beyond the environmental conditions we encountered. The extent of fidelity to a given birds natal wetland is undoubtedly influenced by the current condition of that natal wetland and other wetlands throughout the state.

SITE FIDELITY

In the previous section we addressed the tendency for Snail Kites to return to their natal wetland. Using radio telemetry, we also examined whether individual birds have a tendency to return to the same wetlands from year to year, irrespective of their natal area and breeding status. To test fidelity, White and Garrott (1990) suggest using a chi-square test of independence for situations in which locations of animals can be assigned to discrete areas (e.g., our designations of wetlands). For our initial exploration, we used this procedure, without any pooling, for all individuals for which we had sufficient data. Because we have already shown that there are strong seasonal effects in locations used by Snail Kites, we conducted analyses independently for each season (using the season designation previously supported by our data). We did not include any individuals in this analysis for which we had fewer than five radio locations in each season of each year of comparison. Although five locations was an arbitrary criterion, we believed that fewer locations would likely have produced spurious results because we would have likely had representation from only a small portion of the season. Based on our sampling interval (≈ 14 d), five locations were likely to have represented locations from over half of the season of interest (the expected number of locations during any one season, if the radio were operational for the entire season, was ≈ 8). Additionally, chi-square tests have been known to perform poorly when the expected values of cells are less than five (Cochran 1954). Our criterion was intended to reduce these problems.

A departure from fidelity was common for Snail Kites in each season. During the late-winter/spring (January through April) season 5 of 7 (71%) of the individuals, for which we had sufficient data to test fidelity, showed a departure from fidelity at $\alpha=0.05$ level of significance (Table 6-13). Similarly, 16 of 24 (67%) individuals showed a departure from fidelity during the summer season (May through August)(Table 6-14), and 4 of 8 (50%) showed a departure from fidelity during the autumn/early-winter season (September through December)(Table 6-15).

Because each test was an individual analysis from an individual bird, we did not attempt any detailed model selection for additional effects (e.g., sex or year). We also did not believe that the data warranted any extensive meta-analysis for these effects. On a purely descriptive note, however, we found no obvious patterns with respect to sex or year. There was a slight tendency for a greater departure from fidelity during the non-breeding seasons (summer-early winter) early during the study, but given the small sample sizes, we are not convinced that this is anything more than random variation.

We emphasized at the beginning of this section, that this was a "post hoc" exploratory analysis. In particular, there are two problems which need to be identified. First, except for the summer season, in which we had 24 individuals meeting our criteria, these tests were conducted using a very small number of individuals. These small sample sizes were likely a result of the battery life of our radios. The expected life of our radios was 12 months and this may have been an optimistic expectation from some of the manufacturers. Thus, our analyses were only possible for individuals whose radios exceeded their expected life (or were replaced) and whose locations were generally known. Because most radios were attached during spring, the summer season was the first full season following attachment and the most likely to have had individuals for which we had > 1 year of data. This is probably why our sample was so much higher for summer. The specifications of the mortality switches of our radios precluded some radio designs that would have

Table 6-13. Test results from χ^2 tests of independence for the number of locations of individual radio-transmittered Snail Kites during the late-winter/spring season (January - April) at each location between years.

Freq	Sex	Year 1	Year 2	N 1[1]	N 2[2]	χ^2	df[3]	P
152.104	M	93	94	5	5	6.67	1	0.010
152.630	M	93	94	7	6	4.55	2	0.103
152.362	F	93	95	17	7	24.00	4	<0.001
152.030	F	94	95	5	7	2.86	1	0.091
152.480	F	94	95	8	7	4.77	1	0.029
152.499	F	94	95	6	8	14.00	3	0.003
152.584	F	94	95	7	6	13.00	2	0.002

[1] *Total number of locations for individual during this season for year 1.*

[2] *Total number of locations for individual during this season for year 2.*

[3] *Because df = rows-1 * columns-1 and all individuals had locations in only 2 years (rows) for this season, the total number of locations we observed for the individual equals df+1.*

Table 6-14. Test results from χ^2 tests of independence for the number of locations of individual radio-transmittered Snail Kites during the summer season (May - August) at each location between years.

Freq	Sex	Year 1	Year 2	Year 3	N 1[1]	N 2[2]	N 3[3]	χ^2	df	P
152.120	M	92	93	--	6	8	--	4.20	2	0.122
152.200	F	92	93	--	8	8	--	8.50	3	0.037
152.230	F	92	93	--	7	5	--	8.40	1	0.004
152.312	F	92	93	--	5	7	--	5.60	2	0.061
152.350	F	92	93	94	15	9	9	39.23	6	<0.001
152.362	F	92	93	94	10	18	16	52.49	10	<0.001
152.480	F	92	93	94	7	6	9	23.76	4	<0.001
152.490	M	92	93	--	7	7	--	11.00	4	0.027
152.620	M	92	93	--	5	5	--	10.00	2	0.007
152.860	M	92	93	--	8	8	--	7.27	2	0.026
152.880	M	92	93	--	8	8	--	2.29	1	0.131
152.900	M	92	93	--	6	7	--	13.00	1	<0.001
153.100	F	92	93	--	9	5	--	10.73	2	0.005
152.020	F	93	94	--	9	9	--	18.00	2	<0.001
152.104	M	93	94	--	8	5	--	13.00	3	0.005
152.254	F	93	94	--	5	7	--	1.71	1	0.190
152.463	F	93	94	--	8	6	--	14.00	1	<0.001
152.494	F	93	94	--	7	9	--	0.04	1	0.838
152.584	F	93	94	--	7	8	--	6.56	2	0.038
152.630	M	93	94	--	9	7	--	4.28	3	0.232
152.646	F	93	94	--	6	9	--	1.81	2	0.405
153.125	F	93	94	--	5	8	--	13.00	2	0.002
153.564	M	93	94	--	6	9	--	1.54	1	0.215
153.770	M	93	94	--	9	5	--	14	2	0.001

[1] *Total number of locations for individual during this season for year 1.*

[2] *Total number of locations for individual during this season for year 2.*

[3] *Total number of locations for individual during this season for year 3.*

Table 6-15. Results from χ^2 tests of independence for the number of locations of individual radio-transmittered Snail Kites during the autumn/early-winter season (September - December) at each location between years.

Freq	Sex	Year 1	Year 2	N 1[1]	N 2[2]	χ^2	df[3]	P
152.200	F	92	93	8	5	13.00	2	0.002
153.100	F	92	93	11	7	4.41	1	0.036
152.362	F	92	94	7	7	14.00	1	<0.001
152.020	F	93	94	8	7	4.77	3	0.189
152.480	F	93	94	9	5	2.39	2	0.303
152.584	F	93	94	8	7	1.22	1	0.268
152.630	M	93	94	10	6	6.58	3	0.087
152.646	F	93	94	6	7	6.74	1	0.009

[1] *Total number of locations for individual during this season for year 1.*

[2] *Total number of locations for individual during this season for year 2.*

[3] *Because df = rows-1 * columns-1 and all individuals had locations in only 2 years (rows) for this season, the total number of locations we observed for the individual equals df+1.*

had greater battery life (e.g., solar radios). Had the focus of our study been on fidelity, rather than survival, alternative radio designs would have likely have been used.

A second concern of our analysis is that even with our criterion for five locations from each season, most cells had expected values <5. Although some statisticians believe that a general criteria for expected values <5 may be too restrictive (e.g., Lewontin and Felsenstein 1965, Roscoe and Byars 1971), it is at least reason for some concern. Consequently, we conducted an additional set of analyses on these same data where we pooled each comparison into a 2 x 2 table in which we tested a more restrictive hypothesis that the proportions of locations observed at the most frequently used area (based on marginal totals) was the same among years. For these analyses we used Fisher's exact test, which is more robust to small sample sizes because it uses the exact probability distribution of the observed frequencies, rather than a chi-square approximation (Everitt 1992).

The results from these analyses were similar in that there was a substantial departure from fidelity in all seasons. Based on these analyses 6 of 7 (86%) of the individuals, for which we had sufficient data, showed a departure from fidelity at $\alpha = 0.05$ level of significance for the late-winter/spring season (Table 6-16). Similarly, 20 of 30 (67%) of the tests indicated a departure from fidelity during summer (Table 6-17);

Table 6-16. Test results from Fisher's exact tests for the number of locations of individual radio-transmittered Snail Kites during the late-winter/spring season (January - April) in the location of most frequent use (as determined by marginal [column] totals) compared to all other locations pooled.

Freq	Sex	Year 1	Year 2	N 1[1]	N 2[2]	P[3]
152.104	M	93	94	5	5	0.004
152.630	M	93	94	7	6	0.007
152.362	F	93	95	17	7	<0.001
152.030	F	94	95	5	7	0.205
152.480	F	94	95	8	7	0.008
152.499	F	94	95	6	8	<0.001
152.584	F	94	95	7	6	<0.001

[1] Total number of locations for individual during this season for year 1.

[2] Total number of locations for individual during this season for year 2.

[3] Based on two-tailed Fisher's exact test.

Table 6-17. Test results from Fisher's exact tests for the number of locations of individual radio-transmittered Snail Kites during the summer season (May - August) in the location of most frequent use (as determined by marginal [column] totals) compared to all other locations pooled.

Freq	Sex	Year 1	Year 2	N 1[1]	N 2[2]	P[3]
152.120	M	92	93	6	8	0.733
152.200	F	92	93	8	8	0.317
152.230	F	92	93	7	5	0.004
152.312	F	92	93	5	7	0.018
152.350[4]	F	92	93	15	9	0.039
152.350[4]	F	93	94	9	9	0.001
152.350[4]	F	92	94	15	9	0.074
152.362[4]	F	92	93	10	18	0.018
152.362[4]	F	93	94	18	14	<0.001
152.362[4]	F	92	94	10	14	<0.001
152.480[4]	F	92	93	7	6	0.308
152.480[4]	F	93	94	9	6	<0.001
152.480[4]	F	92	94	7	9	<0.001
152.490	M	92	93	7	7	0.018
152.620	M	92	93	5	5	0.002
152.860	M	92	93	8	8	0.007
152.880	M	92	93	8	8	0.131
152.900	M	92	93	6	7	<0.001
153.100	F	92	93	9	5	0.001
152.020	F	93	94	9	9	<0.001
152.104	M	93	94	8	5	0.008
152.254	F	93	94	5	7	0.190
152.463	F	93	94	8	6	<0.001
152.494	F	93	94	7	9	0.838
152.584	F	93	94	7	8	0.010
152.630	M	93	94	9	7	0.515
152.646	F	93	94	6	9	0.264
153.125	F	93	94	5	8	<0.001
153.564	M	93	94	6	9	0.215
153.770	M	93	94	9	5	0.001

[1] Total number of locations for individual during this season for year 1.

[2] Total number of locations for individual during this season for year 2.

[3] Based on two-tailed Fisher's exact test.

[4] We had data for the same individual for >2 years and Fisher's exact test is intended for a 2x2 table. Consequently, we conducted this test separately for each comparison.

however, three individuals had more than two years of data and contributed to 9 nine of the 30 tests. It is interesting to note that one of these individuals (152.480) showed fidelity to wetlands during the summers of 1992 and 1993, but departed substantially during 1994 from these first two years. During the autumn/early-winter season 5 of 8 (63%) of the individuals showed a departure from fidelity (Table 6-18). Thus, the conclusion from these tests is similar to the tests of independence in that they indicate that a lack of fidelity to seasonal use of particular wetlands is common among Snail Kites, but some individuals do show fidelity during some years.

Table 6-18. Test results from Fisher's exact tests for the number of locations of individual radio-transmittered Snail Kites during the autumn/early-winter season (September - December) in the location of most frequent use (as determined by marginal [column] totals) compared to all other locations pooled.

Freq	Sex	Year 1	Year 2	N 1[1]	N 2[2]	P[3]
152.200	F	92	93	8	5	0.002
153.100	F	92	93	11	7	0.036
152.362	F	92	94	7	7	<0.001
152.020	F	93	94	8	7	0.185
152.480	F	93	94	9	5	0.649
152.584	F	93	94	8	7	0.268
152.630	M	93	94	10	6	0.039
152.646	F	93	94	6	7	0.009

[1] *Total number of locations for individual during this season for year 1.*

[2] *Total number of locations for individual during this season for year 2.*

[3] *Based on two-tailed Fisher's exact test.*

In addition to the above data, we had 72 cases of radio-transmittered birds in which we knew the location of consecutive nesting attempts. Of these, 34 (47%) were at the same location as the previous attempt. This contrasts with the 29% (71% departure from fidelity) that was suggested by our tests of independence of fidelity during the spring (breeding) season and 14% (86% departure from fidelity) from our test of fidelity for the most frequently used area during this same season. Thus, our data indicate that there may be a greater fidelity to the actual breeding location than is indicated from merely looking at seasons. However, even these data indicated that most (53%) nesting attempts by Snail Kites were not at the same location (i.e., wetland) as their previous attempt.

We further explored the relationship of breeding-site fidelity by examining the influence of nesting success on the probability of the next attempt occurring at the same or a different location. Of the 72 cases above, we knew the fate (success) of 39 of the first attempts. The percentage of attempts at the same location was higher for birds whose previous attempts were successful (67%) compared to those whose previous attempts were unsuccessful (42%); however, differences were not significant at an $\alpha=0.05$ level of significance ($\chi^2=2.15$, 1 df, $P=0.143$; or Fisher's exact test [two-tailed] $P=0.174$). Thus, although our data are suggestive that nesting success influences the probability of nesting at the same or a different location, data were insufficient to provide convincing evidence of this effect.

Most species of birds studied tend to retain the same nesting area from year to year and most reported exceptions to this pattern are of species whose food resources exhibit considerable spatial and temporal variation (Andersson 1980). Andersson (1980) also predicts that nomadism is favored when variation in food resources are cyclic, rather than random. Given the cyclic patterns of droughts in Florida (Beissinger 1986, Duever et al. 1994) and the spatial variation of these hydrologic patterns (Duever et al. 1994), Snail Kites might be expected to exhibit nomadic tendencies. Our results indicate that Snail Kites exhibit high rates of movement and frequently use different wetlands from one year to the next. These results do not imply that some individuals do not show fidelity...they do. We commonly observed individuals that would use the same wetland, and even the same sites within these wetlands, from one year to the next. However, our results indicate that a departure from this pattern is also common, and may even be more common.

Assumptions, Bias, and Sources of Error

EFFECTS OF RADIO TRANSMITTERS ON MOVEMENT OF SNAIL KITES

We found no difference in survival between birds with and without radio transmitters. In contrast to survival, banding data were insufficient to test movement probabilities for samples of birds with and without radios. Banding data do allow for the evaluation of movement probabilities (Brownie et al. 1993, Nichols et al. 1993), but these probabilities would be annual transition probabilities; a time scale that we believe would be highly inappropriate given the high monthly rates of movement we observed using radio telemetry. However, for the probability of movement, we believed that any effect would likely have been from the disturbance resulting from actual capture, rather than any chronic effect from carrying a radio transmitter and we were able to test for this effect.

We tested for the effects of capture and handling on the conditional probability of moving between time t and $t + 1$ (conditional on a given bird being alive and its location known at both times), using conditional logistic regression with monthly time steps (see *Methods*). We limited this test to adults because we attached the radios on juveniles right at the time of fledging and therefore would expect a higher movement probability regardless of any radio effect. Additionally, we did not have a sample of juveniles that had not been captured in which to compare because birds captured as juveniles the previous year were no longer juveniles. Juveniles also were capture by merely collecting them at the nest; whereas adults captured with a net gun would have experienced a substantially more traumatic method of capture. We also limited this analysis to the movement probabilities only during the months of March, April, May, and June. This limitation was imposed because over 90% of the captures occurred during those months and it would not be reasonable to compare the effects of capture and handling on movement rates during months where few or no captures occurred. For each bird, we assigned a value for each month as to whether or not the bird had been captured during that month. Because previous analyses had indicated both age and time effects on movement probability, we included these effects in our analysis. Effects of time, however, were limited to monthly and yearly effects. Previous analysis indicated that within-year effects were most parsimoniously modeled using a seasonal, rather than monthly, effect. Because this analysis was limited to four months we were unable to test for a seasonal effect.

We began the analysis with a univariate examination of each potential effect. Only an effect of month was indicated from this analysis (Table 6-19). Because potential effects can sometimes be masked in this initial univariate analysis we followed the recommendations of Hosmer and Limeshow (1989) by using a liberal rejection criteria ($\alpha = 0.25$) for elimination of potential effects at this stage of the analysis. Only year was eliminated from further analysis based on this criterion. Next, we constructed and compared models including month and capture effects (including and not including an interaction term). Based on both AIC and LRT, our analysis indicated an effect of month but not capture on the probability of moving between time t and $t + 1$ (Table 6-20). The univariate model with only month effects had the lowest AIC. The model including month and capture effect also had relatively low AIC, although not as low as the model without capture effects. However, a LRT confirmed that inclusion of capture effects was not warranted (LRT=0.017, 1 df, P=0.89).

Table 6-19. Maximum likelihood Analysis of Variance table for the univariate conditional logistic regression analysis for the effects of month, year, and capture on the conditional probability of moving between time t and $t + 1$, given that a bird was alive at time t.

Source	DF	χ^2	P
Month	3	20.07	<0.001
Year	2	1.58	0.453
Capture (y,n)	1	1.77	0.183

Table 6-20. Summary statistics for conditional logistic regression model for the factors affecting the conditional probability of movement between times t and $t + 1$ (at monthly time steps), given that an animal was alive at time t. Shown are the model description, number of estimable parameters (np), relative deviance ($-2\ln[\mathcal{L}]$), and Akiake's Information Criteriion (AIC).

Model[1]	*np*	$-2\ln(\mathcal{L})$	AIC
MON	4	**588.71**	**596.71**
YR	3	610.46	616.46
CAP[2]	2	610.22	614.22
MON CAP[3]	5	588.69	598.69
MON CAP MON*CAP	8	587.93	603.93

[1] Terms are month (MON), year (YR),and capture (CAP)

[2] Dummy variable for capture assigned a 1 if given bird was captured during that month and 0 otherwise.

[3] A Likelihood ratio test (LRT) between this model and the model with the lowest AIC (Month), further indicated inclusion of a capture effect was not warranted (LRT=0.017, df=1, P =0.89).

We tested the power of our above assessment by simulating a capture effect on the probability of movement (see *Methods*). The results from this analysis indicated relatively low power for very minor differences in capture effect (e.g., delta=0.95) and moderately high power for a strong capture effect (e.g., delta=0.50)(Fig. 6-24). Consequently, although we might not have detected some weak effect of capture and handling on the probability of movement, we would have had a reasonable probability of detecting any substantial effect. Additionally, any effect of capture and handling on movement probability, certainly was minor compared to the background temporal variation. For example, the differences in movement probability between March and June (the months included in this analysis) would have been equivalent to delta=0.29 (greater than any effect we simulated).

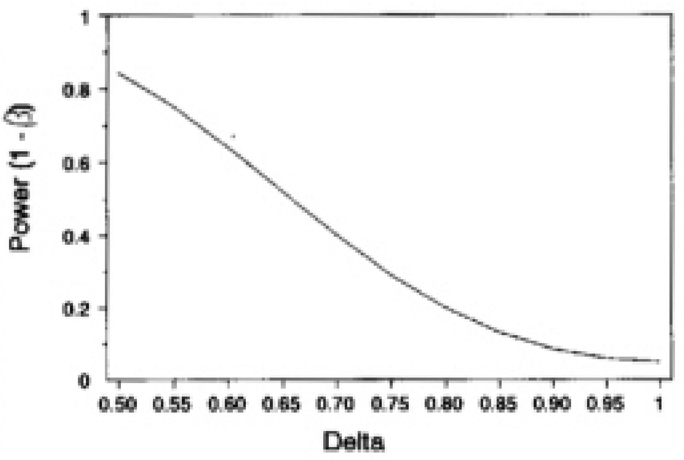


Figure 6-24. The estimated power to detect simulated differences (Delta) in the probability of movement for birds that were and were not captured during a given month. Differences in movement probability were simulated by changing the base probability (from the actual data) for birds captured by a fixed percentage of change (Delta).

CONDITIONAL INDEPENDENCE

For our analysis we have essentially treated movement as a Markovian process such that each month an individual has a probability of moving from a given location regardless of whether or not that individual moved in the previous month. Thus, we have made an assumption of conditional independence between times t and t - 1 (McCullagh and Nelder 1989). We can only speculate at this point as to the influence of violating this assumption. We are currently exploring ways of testing both the validity of this assumption and for incorporating our findings into our analysis.

MONTHLY TIME STEPS

Many of our analyses were conducted using monthly time steps. The logic and tradeoffs of this approach were previously discussed (see *Methods*). Two conditions are readily apparent that may have affected our results. First, a given individual may have moved more than once during any given month. Thus, actual movements may have been more frequent than indicated by the time steps we used. This is not only a function of our analytical time steps, but also our sampling intervals (i.e., = 14 days). In addition, an individual also could have moved to a new location and subsequently returned to its previous location within a given month. Thus, we would have recorded that animal as not having moved, even though it had actually made two (or more) movements. Consequently, we believe that our parameter estimates for the probability of movement are slightly conservative. However, we do not believe that there were a sufficient number of undetected movements to have had a substantial influence on our overall results. We likely would have missed some of the increments of longer moves and some exploratory excursions. It would have been very unlikely, however, for a few undetected movements to have influenced our model selection or conclusions. Consequently, we do not believe that the increased sampling effort that would have been required to detect more movements was warranted.

Chapter 7. MONITORING THE FLORIDA SNAIL KITE POPULATION

Snail kites in the United States occur only within southern and central Florida. Over half of the wetlands within the kites' range have been lost during the past century and those that remain have been highly fragmented and severely degraded (Weaver and Brown 1993). This loss and degradation have prompted planning for the most ambitious and largest scale ecosystem restoration effort ever undertaken (e.g., The 1993 Interagency Agreement on South Florida Ecosystem Restoration). Given the restricted range of the Snail Kite within the United States and the magnitude of past and present changes, and the potential for future changes in this ecosystem, the Snail Kite has been, and probably will be, a high priority for monitoring as these changes occur. Consequently, one of the goals of this project was to provide an assessment of the protocol for monitoring Snail Kites in Florida. Here we examine methods that have been attempted or suggested, explore their assumptions and/or sources of variation, and discuss these techniques in the context of assessing specific parameters or measures of the Florida Snail Kite population.

The Annual Survey

Prior to 1969 the Snail Kite population was monitored only through sporadic and haphazard surveys (reviewed by Sykes 1984). Numbers of Snail Kites in Florida since 1969 have been monitored via a quasi-systematic annual survey (Sykes 1979, 1982, Rodgers et al. 1988, Bennetts et al. 1994). Details of the methodology have been previously reported (Sykes 1982, Rodgers et al. 1988); however, the survey consisted of a combination of airboat transects and evening roost counts. Since these surveys began there have been numerous biological interpretations, often with little or no regard for the inherent sources of variation in these data that could influence the validity of subsequent interpretations. Here we examine several sources of variation inherent in the annual survey and discuss how this variation could influence the validity of interpretations of these data.

SOURCES OF VARIATION

One obvious source of variation in the annual survey is that the actual population size of the Snail Kite in Florida has changed. The variability associated with birth and death rates are a primary focus of this report and is consequently addressed in other chapters. Here we focus on sources of variation in the annual survey which might confound our interpretation of actual demographic change. A common thread of these confounding factors that will quickly emerge is that they all relate to the ability of observers to detect birds that are alive in the population.

Observer effects-- There are two primary observer effects of concern. First, there are inherent differences among observers in their ability to detect birds. For detecting Snail Kites during the annual survey, these differences can be a result of such things as an observer's visual acuity or the ability to focus on the count while driving an airboat (unless a second observer is present). Secondly, differences may exist among observers relating to their experience. These differences can result from such things as familiarity with the terrain or behavior of the birds. Observer differences have long been known to have a major influence on bird surveys (e.g., numerous papers in Ralph and Scott 1981, Verner 1985, Sauer et al. 1994). Unfortunately, we currently have no assessment of the inherent observer differences. This is usually accomplished by comparisons of different observers conducting the same survey. Beissinger (1982) re-surveyed kites twice during early 1982 following the 1981 drought and found differences of 62% (177) in a January count and 104% (222) in a March count compared to the regular survey of 109 conducted by a different observer (J. Rodgers Jr.) during late November and early December. He attributed much of these differences to observer effects in ability to locate roosts (he suggested a lack of experience) and amount of effort. Unfortunately, the temporal differences among these surveys (i.e., surveys were conducted ≈ 1 and 3 months after the regular survey for the January and March surveys, respectively) confound the use of these data for a reliable assessment of inherent observer effects (see *temporal variation* below). Partitioning the annual survey by observers gives a general indication of differences among observers (Fig. 7-1); however, the surveys conducted by Bennetts et al. were confounded by having had radio transmitters on 282 birds; which undoubtedly improved their ability to locate pockets of birds that might have otherwise been overlooked (Sykes et al. 1995). Both the differences in surveys reported by Beissinger (1982) and the possible differences in the slopes of counts by different observers raise concerns that inherent observer differences do exist and should be accounted for in any analysis resulting from the annual survey.

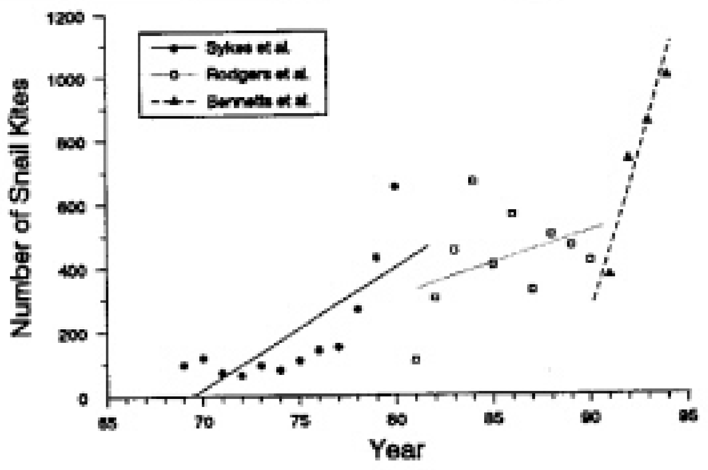


Figure 7-1. Numbers of Snail Kites counted during the annual surveys conducted by P.W. Sykes et al., J.A. Rodgers Jr. et al., and R.E. Bennetts et al. Also shown are least squares regression lines for each observer.

An indication of the effect of experience can be seen by looking at first counts conducted by each of the three observers who have conducted the annual survey. The first surveys of both Rodgers et al. and Bennetts et al. also were their lowest counts (Fig. 7-2). Similarly, the first survey (1967) originally reported by Sykes (1983a) also was his lowest; however, the 1967 and 1968 surveys he reported were not considered as having been complete counts because he was still learning the potential range of kites in Florida and several areas were not included in these early attempts (P. Sykes, pers. comm.). For this reason, most reports (e.g., Sykes 1979, 1983b, Sykes et al. 1995) show 1969 as having been the first year of the annual survey. Although, not including the 1967 and 1968 surveys in his reporting is an appropriate step for maintaining consistency among the surveys, it also illustrates our point that an observer's first survey often is a learning experience and this source of variation should be taken into consideration (Sykes accounted for it by not including these surveys).

Effort-- It has been recognized for decades that the amount of effort expended on surveys of birds (or any organism) has a dramatic influence on the number of individuals (or groups) counted (e.g., Chapman 1951,

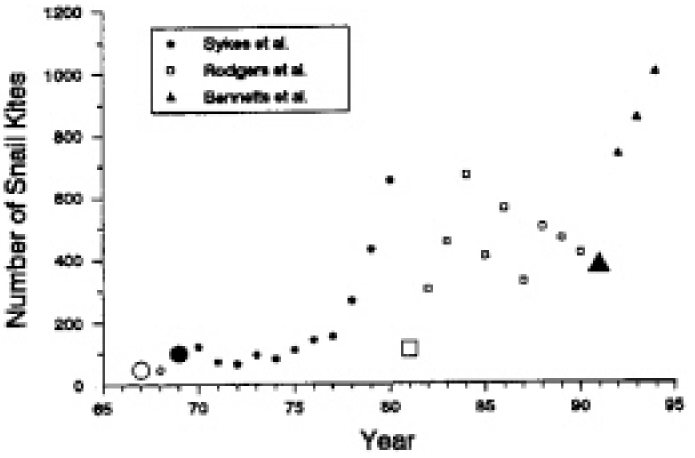


Figure 7-2. Numbers of Snail Kites counted during the annual surveys conducted by P.W. Sykes et al., J.A. Rodgers Jr. et al., and R.E. Bennetts et al. Enlarged symbols represent the first count conducted by each observer. The surveys of 1967 and 1968 (open circles) were preliminary counts conducted by P.W. Sykes and originally reported in Sykes (1983a). These surveys were not reported in later papers (e.g., Sykes 1979, Sykes et al. 1995) because they were conducted at a time when the observer was just learning the areas and all areas were not included. We show them here because it illustrates our point that first surveys are often "learning experiences".

Kenaga 1965, Brown 1973, Davis 1974, Raynor 1975). Numerous attempts have been made to account for this influence for other species by "normalizing" counts such that they are reported as number counted per unit effort (e.g., Kenaga 1965, Brown 1973, Davis 1974, Raynor 1975, Bock and Root 1981). Surprisingly, to our knowledge, no attempt has previously been made to account for effort in the annual Snail Kite survey. We explored this effect on the annual Snail Kite survey by examining the relationship between the number of birds counted on each survey and the number of observer days (i.e., each observer for each day they participated in the survey was counted as one observer day) for that survey (Sykes, Unpubl. data, Rodgers et al., unpubl. data, Bennetts et al., Unpubl. data). Not surprisingly, we found a significant relationship between the total number of observer days for a given survey and the number of kites counted ($R^2=0.69$, $P<0.001$, $n=26$ [1967 and 1968 were not included, see *observer effects* above])(Fig. 7-3). Butcher and McCulloch (1990) concluded that analysts should determine if an empirical relationship exists between surveys and effort to determine if surveys need to be adjusted for effort.

Sampling Error-- Counts of birds are rarely, if ever, made without error; and the amount of stochastic variability introduced by sampling error can be quite large (Barker and Sauer 1992, Lancia et al. 1994).

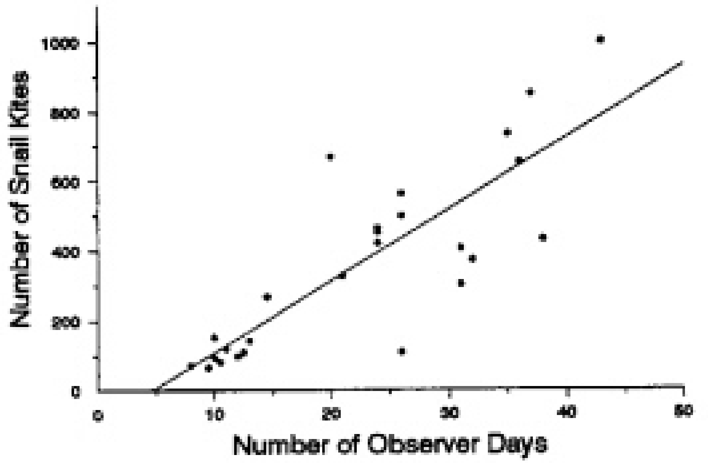


Figure 7-3. Relationship between the number of Snail Kites counted each year during the annual survey and the number of observer days (i.e., each observer counts as 1 observer day for each day they participated in the count).

There are a multitude of potential sources of sampling error for the annual survey of Snail Kites. Here, we present just a few examples to illustrate to magnitude of the potential error. First, for many areas systematic transects are infeasible and the survey relies heavily on roost counts (Rodgers et al. 1988, Bennetts et al. Unpubl. data). Additionally, roost counts often exceed transect surveys because of the difficulty of counting every bird via transect surveys (Rodgers et al. 1988). This can present a substantial source of error if not all roosts are located (Beissinger 1988). Unfortunately, Snail Kites often form several roosts in a given area and may be widely distributed in roosts consisting of single birds or small groups (Sykes 1985, Darby et al. 1996a). In a recent study Darby et al. (1996a) found 9 roost sites being used simultaneously (although it required several days to locate them) in just one subregion of WCA-3A. Similarly, they found 5 roost sites at Lake Kissimmee. Because their results were based on following only a sample of birds during a limited time, they probably did not even find all of the roosts at these locations. Additionally, 57% of the birds they followed roosted either alone (20%) or in small groups of less than 10 (37%)(Darby et al. 1996a). Based on these results, and the amount of effort expended on any given annual survey, it is unlikely that even a majority of the roost sites are found on any given survey.

An additional example of the magnitude of error resulting from not locating all roosts was obtained using radio telemetry. During the 1994 annual survey Bennetts et al, unpubl. data) counted birds in WCA-2B using the traditional procedures of the survey (Sykes 1982, Rodgers et al. 1988). They found what they thought was "the"communal roost and counted 51 birds for the area. After the survey was completed for that area (i.e., the same night that the roost was counted), they checked to verify that all of the radio-transmittered birds known to have been in that area were in the roost that they had just counted. They were not, and a second roost was located, using radio telemetry, that had been overlooked. The next evening an additional 91 birds were counted in the second roost. Thus, 64% of the birds ultimately counted would have been overlooked as a result of not finding the second roost. This does not even include any additional roosts that still may have been overlooked. While it might be easy to just pass off this example by suggesting that we were careless in finding all of the roosts, the fact remains that it would require an enormously impractical amount of effort to locate all roosts in Florida. We have no doubt that there are many other cases of overlooking roosts embedded within reported surveys.

A second general source of sampling error results from differential detectability of birds among habitats or geographic regions. The latter we tested explicitly with our banding data using multi-state mark-resighting models (see section on regional effects in *Estimation of Survival from Banding Data*). Both our model selection procedures and a likelihood ratio test (LRT) between models with and without regional differences in resighting probability (p_i) indicated significant differences (χ^2=25.389, 10 df, P=0.005, Table 4-25) in resighting probability among regions. Although this test applies specifically to our ability to detect marked individuals, we have no reason to suspect that our ability to detect unmarked individuals would not likewise differ among regions. This result is not surprising given the considerable variability among habitat types. Differences in detectability of birds among habitat types also has been previously well documented (e.g., Best 1981, Oelke 1981, Howe et al. 1995); but, unfortunately, this source of error has been previously ignored in the annual survey of Snail Kites.

An additional example of this effect also comes from the use of radio telemetry. During the 1992 annual survey, 216 Snail Kites were counted on Lake Okeechobee (Bennetts et al. 1992). During that year we had been monitoring birds via radio telemetry extensively on Lake Okeechobee and knew that birds were predominately foraging in dense willows (a habitat not generally known to be a major foraging habitat). Consequently, when we conducted the survey on Lake Okeechobee that year, we paid particular attention to this habitat. Of course, we have no way to estimate what proportion of these birds we would have detected without this ancillary knowledge from the radio telemetry. However, most of the birds counted on Lake Okeechobee during 1992 were found in thick willow (a habitat not normally searched during surveys, except for evening roost counts)(Bennetts et al. 1992), and the resulting count was the highest ever recorded for that area during an annual survey.

An additional source of sampling error results from the distribution of birds relative to areas that are included in the survey. There are a multitude of wetlands in Florida that are used by kites that are too small, isolated, ephemeral, used sporadically, inaccessible (physically or because of ownership), or even unknown, to be feasibly included in the survey. Beissinger and Takekawa (1983) and Takekawa and Beissinger (1989) refer to many of these wetlands as "drought related habitats". We often refer to them as "peripheral"habitats because our data indicate that many are used in years other than drought years. Regardless of what they are called, they exist, and the proportion of kites in these habitats in any given year is unknown. This problem is likely amplified during drought years when massive dispersal of kites to these habitats has been reported (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989). This problem was identified by Rodgers et al. (1988) and later by Bennetts et al (1994) and Sykes et al. (1995); however, no accounting for dispersal into peripheral habitats during drought years (or any year) has yet been made. Consequently, comparisons of drought years with non-drought years using the annual survey are particularly suspect.

Spatial Variation-- The areas included in the annual survey have not been consistent from year to year. This probably is due to a combination of shifts in the distribution of kites over time and an increased awareness of locations used by kites. We examined the magnitude of this effect for the Snail Kite data by comparing the total surveys that include all areas with the totals only from areas included in all years. The overall trends appear not to be greatly influenced by the inclusion or omission of some areas (Fig. 7-4); however specific yearly totals may be greatly influenced (Fig. 7-5). For example, in 1990 a substantial portion of the total survey was from Lake Tohopekaliga, which was not even included in the survey until 1981 (the 13th year of the survey). During that year 233 of 422 birds (55%) were counted in areas that have not been included in all years. A similar concern has been previously expressed for widespread bird surveys (e.g., the breeding bird survey [BBS]) in which not all survey routes have been conducted each year. Methods have been proposed to address this concern (e.g., Geissler and Noon 1981, Geissler and Sauer 1990), but to our knowledge, no attempt has been made for the annual Snail Kite survey to account for variation due to

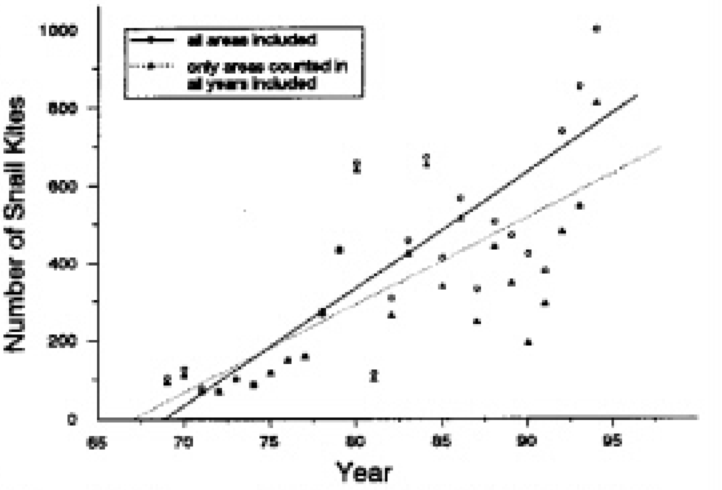


Figure 7-4. Linear relationships of number of Snail Kites counted each year of the annual count when all areas are included and using a restricted data set using only areas that have been included every year of the count.

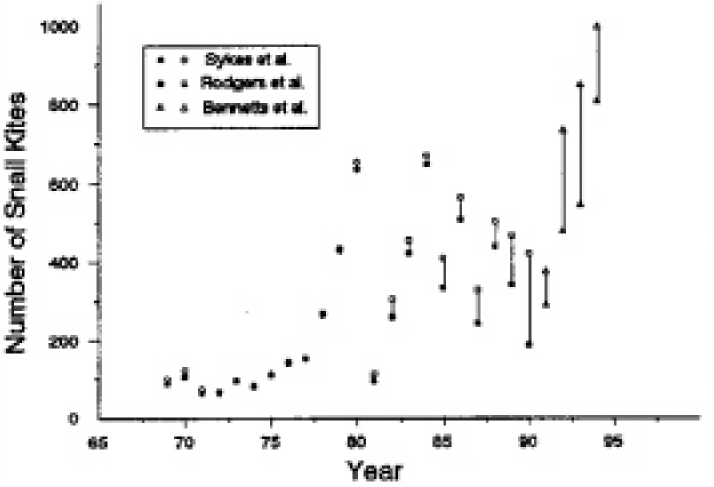


Figure 7-5. Number of Snail Kites counted each year of the annual count when all areas are included (open symbols) and using a restricted data set using only areas that have been included every year of the count (solid symbols). Vertical lines illustrate the difference between these two data sets.

differences in areas surveyed from year to year.

Temporal Variation--The annual surveys have maintained a general temporal consistency in the time of year that surveys have been conducted (i.e., primarily November and December); however, variability within those months does exist (Fig. 7-6). James A. Rodgers Jr. (unpubl. data) paid particular attention to maintaining the temporal consistency during the period (1981-1990) he conducted the surveys. An exception to this consistency is a supplementary survey conducted by an independent observer in March 1982 that was intended to repeat the November/December 1981 survey (Beissinger 1982, 1984, U.S. Fish & Wildlife Service 1986). Beissinger (1982) counted 222 in his March survey compared to 109 counted during the regular survey. This March survey has been frequently substituted for the regular survey (revised to ≈ 250) in later reportings (e.g., Beissinger 1986, 1988, 1995, Takekawa and Beissinger 1989). Our data from radio telemetry has indicated that there is a substantial shift of habitat use by birds between November (when the survey is normally conducted) and March (when the latter supplementary survey was conducted). This shift includes a shift from areas not likely to have been included in the survey (i.e., agricultural areas and cypress regions within the Big Cypress Basin Watershed) to areas more likely to have been included in the survey (Fig. 7-7). Additionally, we have observed a substantial shift from areas where it is relatively difficult to survey birds because of dense vegetation (e.g., cypress regions along the L-28 levee) to areas of more open habitats. Beissinger (1982) also reported that more birds were found in the areas he was surveying (i.e., WCA-3A, WCA-3B, Lake Kissimmee, and Lake Tohopekaliga) in March compared to an additional supplementary survey he conducted in January and that this accounted for the higher number of birds counted in March. This is consistent with the shifts in distribution that we have observed with our radio transmittered birds; however, Beissinger (1982), suggested that the birds in WCA-3A were likely to have been present when the regular survey was conducted, and that their roost sites were simply overlooked.

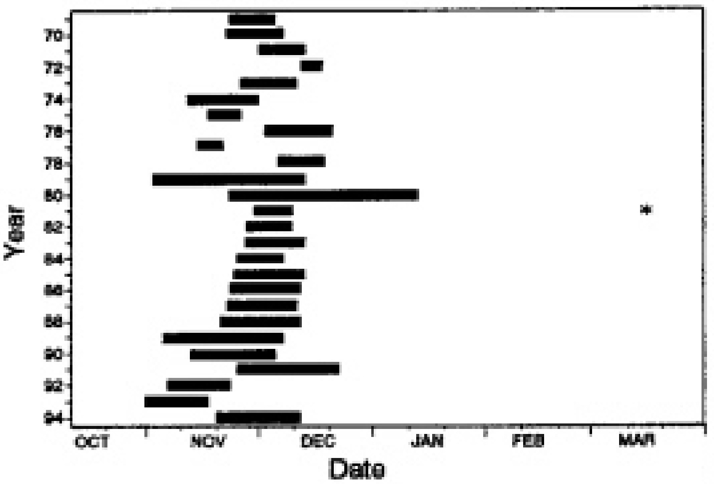


Figure 7-6. Temporal variation in the annual count as indicated by the range of dates within which the annual count was conducted each year. Counts were not necessarily conducted every day within each range. A supplementary count (*) conducted by Beissinger (1982) in 1982 (intended as an alternative to the November/December 1981 count) was reported as occurring in March, but the actual range of dates was not provided.

The shifts in habitat use we have observed would undoubtedly influence the resulting surveys. The time of year that surveys have been conducted (i.e. November - December) also is a time when considerable habitat shifts by kites may occur. Based on our data using radio

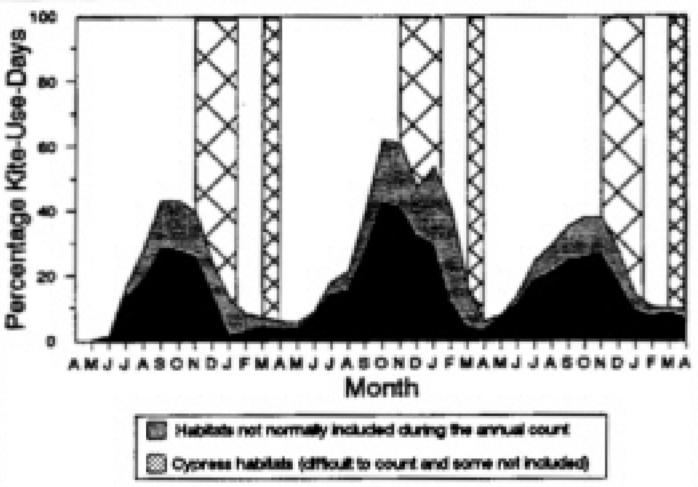


Figure 7-7. Percentage of kite-use-days (see section on Habitat Use in chapter on Movements) by radio-tagged Snail Kites for each month from April, 1992 to April 1995 in peripheral habitats not likely to have been included in the annual count (e.g., agricultural areas, see description in Study Area) and cypress habitats (see description in Study Area), some of which (e.g., Western WCA-3A) are included in the count, but are difficult to count because of vegetation density. Also shown are the range of dates that the annual count has been conducted (large crosshatch) and the potential range of dates (i.e., March, small crosshatch) that a supplementary count by Beissinger (1982) was conducted.

telemetry, the time from 1 September through 31 October would be more consistent with respect to habitat use (i.e., there are fewer shifts). The period between 1 March and 30 April also would be more consistent with respect to habitat use and has a greater proportion of the birds occurring in habitats normally included in the survey. The disadvantage of this latter time period is that birds are likely nesting and the potential for roost counts would be very limited. Regardless of when the surveys are conducted, we suggest that, if they are continued, they be constrained to a narrow time window to minimize the variation due to differential distribution among habitat types or areas. We also suggest that comparisons of surveys conducted at different times of the year (i.e., between March and November/December) would have little validity because of these habitat shifts.

Some Alternative Field Methods to the Annual Survey

As we suggested earlier, the common thread among the sources of variability in the annual survey is that there is no measure of what proportion of the population is being counted on any given survey. Consequently, unless that proportion is constant among years (i.e., there is a correlation between the survey and actual population size), and our data suggest that it is not (see *population indices* below), then few valid inferences can be derived except where enough years are included to "average out" the detectability differences, or preferably, if the sources of variation are incorporated, and accounted for, in the resulting analyses. This problem of measuring an unknown fraction of the population is inherent in count data of this type (Burnham 1981, Nichols 1992, Barker and Sauer 1995, Johnson 1995) and one which will inevitably continue to haunt those who attempt to extract broad inferences from these data. Consequently, in this section we have intentionally omitted potential alternatives to the annual survey (e.g., point counts) that suffer from all of the weaknesses described for the annual survey above. We have focused below on some general field methods which have the potential to account for detectability. In this section we also focus primarily on the feasibility for using each of these techniques. Their applicability for monitoring populations and/or to assess specific parameters is addressed in the subsequent section on *Recommendations for Monitoring Snail Kite Populations in Florida.* Radio telemetry and banding (mark-resighting) have both been used extensively in this study, and their inherent properties have been directly evaluated for use with the Florida Snail Kite population. Although not used extensively on this study, distance sampling was attempted during the fall of 1991, and we believe we are also in a position to evaluate its potential for this population.

RADIO TELEMETRY

Radio telemetry has emerged in recent decades as one of the most extensively used methods for monitoring wildlife populations. Several important properties of radio telemetry make this technique particularly well suited for some questions. First, although telemetry is discrete at the interval of obtaining radio locations (e.g., hourly, daily, weekly, etc.), it is a relatively continuous measure compared to most alternative techniques, that derive inferences from "snapshot" surveys (e.g., distance sampling or the annual survey) or from an extended interval between sampling periods (e.g., capture-recapture models [banding]). Consequently, it enables information to be gathered about such things as habitat use and the cause of death (for studies of survival). Secondly, radio telemetry data are usually at least three dimensional, with x and y coordinates denoting location (space) and t denoting time (White and Garrott 1990). Thus, the movement of an animal through time and space are monitored simultaneously. This lends itself particularly well to studies of movement patterns. Other variables (e.g., habitat or activity at the time of location) may also be incorporated as explanatory variables of the time and space vectors (White and Garrott 1990). Thirdly, radio telemetry enables the monitoring of animals remotely. Thus, the observer need not be present at the location of the animal to monitor many aspects of its activity. Radios can usually be equipped with activity switches to determine whether a bird is flying or perched, or mortality sensors to determine if an animal is alive. This is particularly useful for studies in which the animal's response to the observer will confound the results (although the presence of the radio itself may confound the results, see discussion on *Assumptions, Bias, and Sources of Error for Survival Estimators*).

Like all techniques, radio telemetry has its limitations and disadvantages, many of which we have discussed in detail in the previous section on *Assumptions, Bias, and Sources of Error for Survival Estimators* and a detailed discussion will not be repeated here. However, one assumption of particular concern is that the radio transmitter itself does not influence the animal (White and Garrott 1990, Anderson et al. 1993). Our data suggest that it does not influence survival (See *Assumptions, Bias, and Sources of Error for Survival Estimators*); however, this assumption should be carefully considered when deciding on a monitoring technique(s). An additional disadvantage is cost. Radio telemetry is expensive and for many questions, there are cheaper alternatives. Depending on the brand and quantity ordered, radio transmitters are likely to cost from $150 to $250 each (satellite transmitters would be considerably more expensive). The specific design and specifications of the radios depend much on the purposes for which they would be used and many sources of information on this subject are available (e.g., Kenward 1987, White and Garrott 1990). Additionally, the most efficient means of monitoring radio-transmittered birds is via aircraft, which is also relatively expensive.

For some applications (e.g., Kaplan Meier estimates of survival), it is assumed that the probability of detecting an animal at each sampling period is 1 (Pollock et al. 1995); however, even when this assumption is violated unbiased estimates of survival are possible by censoring animals from the data, provided that an alternative assumption (see the "*Censoring is Random*" assumption in section on *Assumptions, Bias, and Sources of Error for Survival Estimators*) is met. Additionally, unlike the annual survey, the probability of detecting a given individual is not a complete unknown (although the fate of an undetected animal may be unknown) and an estimator has recently been developed that provides estimates for the probability of detecting a radio-tagged animal for any given sampling occasion (Pollock et al. 1995).

We will discuss specific applications of radio telemetry below in section on *Recommendations for Monitoring Snail Kite Populations in Florida*.

CAPTURE RECAPTURE (MARK-RESIGHTING) DATA FROM BANDING

In earlier chapters we have discussed mark-resighting methods in some detail. Based on our preliminary assessments, we believe it to be a feasible and practical means of monitoring survival. An investigation of its applicability to estimating population size is also currently underway (Dreitz et al., unpubl. data). There has been a wealth of recent developments on the general subject of deriving inference from marked animals (extensive overviews have been provided by White et al.1982, Burnham et al. 1987, Pollock et al. 1990, and Lebreton et al.1992; see also numerous papers in Lebreton and North 1993 and the Journal of Applied Statistics Volume 22, nos. 5 & 6 [special issues devoted completely to this subject]).

DISTANCE SAMPLING

Distance sampling is another area in which there has been considerable advancement in recent years. Distance sampling represents a unification of its precursors in transect sampling (Hayne 1949, Eberhardt 1968, Gates et al. 1968, Burnham and Anderson 1976, Burnham et al. 1979) and variable circular plot sampling (e.g., Ramsey and Scott 1979), and has been summarized in considerable detail by Burnham et al. (1979) and Buckland et al. (1993). It is generally used to estimate density of animals within a specified area, rather than population size over a broader area; although inferences can be made regarding the latter. The principal concept behind distance sampling is that the density of objects (e.g., Snail Kites) can be estimated using a detection function $g(y)$ to represent the probability of detecting an individual, given that it is at some distance y from the transect line or point (Burnham et al. 1980, Buckland et al. 1993). Distance is measured as either continuous or categorical, and as perpendicular distance from a transect or radial distance from a point. The detection function is generally a decreasing function with increasing distance from the transect or point (i.e., the farther animals are away the less likely they are to be detected).

We illustrate the conceptual framework for distance sampling using hypothetical data that represent the number of animals occurring randomly in each of 10 distance categories (Fig. 7-8). Each distance category

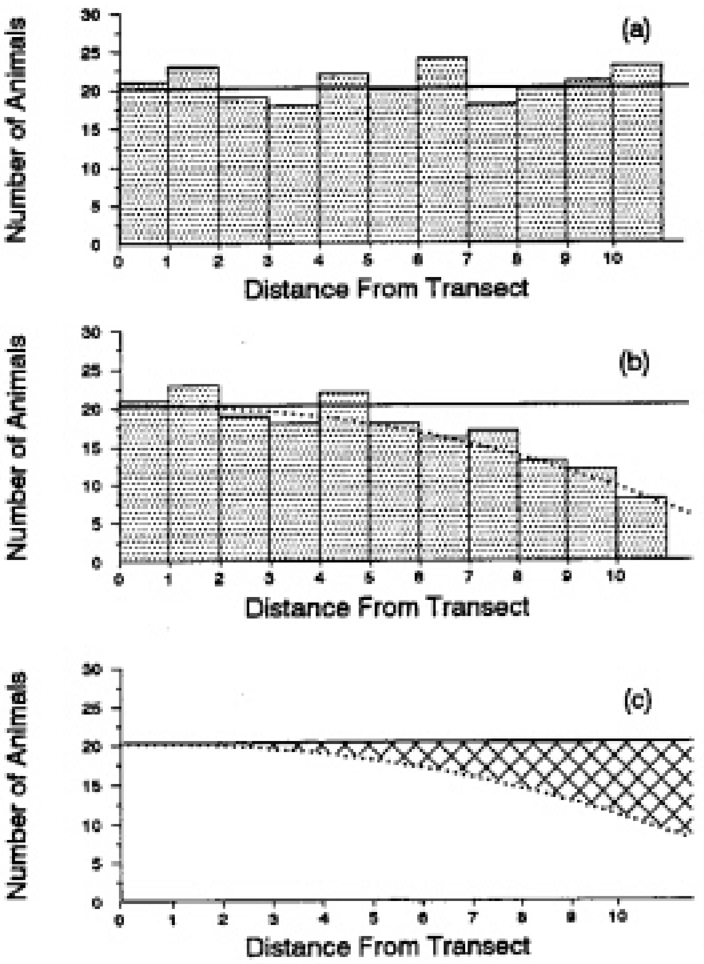


Figure 7-8. Hypothetical data representing the number of animals occurring randomly in each of 10 distance categories (a). A horizontal line shows the expected value for each category. In this case the expected value equals the mean of all distance categories. The number of animals actually detected (observed) in each category (b) would likely decrease with increasing distance from the transect. A detection function can be derived using a variety of curve fitting techniques (dotted line). The difference between the observed and expected values © (crosshatched area) is a measure of the undetected proportion of animals that can be used to estimate the proportion of animals that were detected and ultimately to "correct" the estimate of density for the area sampled. Adapted from Buckland et al. (1993).

represents a strip of width w away from a transect line of length l *(note: for a real transect there would likely be a strip on each side of the transect line, such that width would actually be* 2w). Thus, the area of the ith strip is simply:

$$a_i = l_i \times w_i,$$

and the density of animals (d_i) for each strip is:

$$d_i = \frac{n_i}{a_i}$$

where n_i is the number of animals present on strip i. The first case we consider for these data is one in which all animals are detected. For this case, the expected number of animals for each strip could be estimated as the mean of the strips (Fig. 7-8a). In real life, however, the probability of detecting animals farther away from the transect line would likely decrease with increasing distance. We could represent this decreasing detection function based on the number of animals detected (observed) in each distance category (Fig. 7-8b). The departure between the observed and expected number of animals can then be used to estimate the proportion of animals that were not detected on a given survey (Fig. 7-8c); of which the complement is the proportion of animals that were detected. This then provides a basis for "correcting" the survey to account for animals that were not detected and to provide an estimate of density. For purposes of illustration, we have present an extremely simple example. The current state-of-the-art for this type of sampling includes an extensive array of statistical tools for determining how to select and evaluate the detection functions and resulting density estimates.

Assumptions of Distance Sampling**--** There are several assumptions of distance sampling required to ensure a valid estimate of density (Buckland et al. 1993). The primary assumptions are:

1.) All animals on the transect line (i.e., distance = 0) are detected (i.e. the probability of detection = 1.0). In practice, this assumption can be violated such that objects near the line are almost certainly detected; however, substantial violations of this assumption will lead to biased estimates.

2.) Animals are detected at their initial location (i.e., animals are not moving before detection). Again, in practice, if animal movements are random then no serious bias exists; however, if animals tend to move away from the transect line (as might be expected) then the estimate would likely be biased.

3.) Distance measurements are recorded without error. Violations of this assumption can often be rectified by grouping data into distance classes.

4.) The distribution of animals is such that they may be sampled by random transects or points . That is not to say that the animals must be randomly distributed; rather that they are distributed in areas such that they could be sampled by a random distribution of lines and/or points.

Of course, all additional concerns about study designs and field procedures apply.

Assumption one is the most critical for obtaining reliable estimates for density (Buckland et al. 1993). Based on our preliminary field trial during 1991, it is also extremely likely to be violated when sampling Snail Kites. The only logistically feasible method for conducting transects in Snail Kite habitat is by airboat. Our experience using fixed-wing airplanes indicated that only a small proportion (< 10%) of the birds present are observed without repeated passes over the same area. Helicopters, although slightly better, suffer similar problems and are extremely expensive for large-scale surveys. Although many kites remain perched upon the approach of an airboat or aircraft, many do not. Given the density of vegetation in some areas, it is extremely likely that some birds will flush (and may or may not be detected depending on the habitat) upon approach. This response to airboats or aircraft results in severe violation of both the first and second assumptions of distance sampling. After conducting approximately 3 transects by airboat during fall of 1991 and numerous flights by both fixed-wing airplanes and helicopters for other aspects of the study (e.g., radio telemetry), we concluded that the violations of these assumptions were too severe to warrant continuation. In addition to violating assumptions, we also were unable to navigate straight-line transects by airboat through vegetation. In principle, a transect line does not need to be straight so long as it is random with respect to encountering animals. Our preliminary efforts suggest that the routes we followed were very much nonrandom with respect to encountering animals. Following paths of navigable water through vegetation has a strong influence on our detection of animals. While it is certainly possible to develop a sampling scheme in which areas are stratified by vegetation type, it would consist of numerous very short transects that would be logistically laborious and many vegetation types would likely be poorly sampled or overlooked completely. Consequently, we believe that the conditions under which Snail Kites precludes using distance sampling as a general approach for monitoring Snail Kites in Florida. This approach may, however, be useful for some situations (e.g., comparisons of density over time) for some habitats (e.g., relatively open habitats) in which the above assumptions can be reasonably met.

Discussion and Recommendations

How the Florida Snail Kite population is best monitored depends greatly on the goals of monitoring. Consequently, we have provided a brief discussion below of several parameters or measures that might be of interest in a monitoring program. We discuss how various monitoring techniques might, or might not, be applicable to these measures.

POPULATION SIZE

Population size (N) is one of the most frequently assessed parameters in wildlife studies and is frequently used for management decisions. For example, the interim recovery goal (i.e., to be considered for re-classification) for the Snail Kite is an annual population average of 650 birds with annual population declines not to exceed 10% of the average (U.S. Fish & Wildlife Service 1986). A logical assumption of this goal is that we know the population size and how much it varies annually.

Contrary to numerous reports (e.g., Sykes et al. 1983b, 1979, Snyder et al. 1989, Beissinger 1995), the annual survey of Snail Kites in Florida is not a census (see also Rodgers et al. 1988). A census is a complete count of a population (Lancia et al. 1994). Without an enormous effort it is virtually impossible to survey every marsh in central and southern Florida each year. Nor is it even remotely likely that every bird is counted in the thousands of square kilometers that are surveyed each year during the annual survey. It is generally believed that counting of birds at communal roosts helps to eliminate much of the problems associated with detectability in large areas or in habitats non conducive to visual detection during quasi-systematic transects (citations). However, recent work by Darby et al. (1996a) showed that kites in a given area may use several communal (or even non-communal) roosts simultaneously. Thus, unless all roosts are located (again requiring an impractical amount of effort) entire groups of birds using undetected roosts may be overlooked. Thus, it is not reasonable to expect that the annual survey represents a complete census of all birds in the population. Problems with using the annual survey as a census also have been recognized by all researchers who have conducted the survey (e.g., Rodgers 1988, Bennetts et al. 1994, Sykes et al. 1995).

An inherent problem with count data is that they represent an unknown fraction of the population of interest (Nichols 1992). Without having an estimate of what proportion of the population is being detected, the use of count data for estimating population size is scientifically unsound and unreliable (Burnham 1981, Nichols 1992, Barker and Sauer 1995). In contrast to the annual survey, an implicit component of both mark-resighting and distance-based methodologies is the estimation of detectability. For mark-resighting models, the probability of detection (p_i) is one of the parameters being estimated directly. For distance-based models, detectability is modeled as a function of distance from the transect line or point. Based on preliminary evaluations, we believe that mark-resighting methods are the most promising for estimating population size of Snail Kites in Florida. Although the violation of assumptions is a concern for any estimator, our preliminary assessments indicated that the assumptions more likely to be violated using distance-based methods (e.g., the probability of detection on the line is 1.0) are ones to which the estimator is quite sensitive. In contrast, the assumptions more likely to be violated by capture-recapture models (e.g., occasional misreading of bands) are ones to which the estimator is more robust.

Based on our mark-resighting results for survival estimation (i.e., CJS models), we believe that mark-resighting is a feasible approach for estimating population size. A pilot study to determine the feasibility of using mark-resighting methods for estimating population size is currently underway (Victoria Dreitz et al., pers. comm.).

POPULATION INDICES

Given that the annual survey is not a complete census, the question arises as to its usefulness as an index (i.e., is it correlated with population size?). Without having some independent estimate of population size, it cannot be known to what extent the annual survey is correlated with population size. However, a critical assumption to using an index to assess year to year changes is that the relationship between the index and population size also remain constant over the interval being assessed (Lancia et al. 1994). Results from our banding data indicate that the probability of detecting marked individuals is not constant among years or among regions. Consequently, the critical assumption above is unlikely to be met. Rodgers et al. (1988) also correctly point out that we do not know the extent to which changes in the annual survey are influenced by dispersal of kites out of the surveyed wetlands. We do know that kites tend to disperse to peripheral habitats (i.e., that are not usually surveyed) during drought years (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989). Thus, we would also expect a decrease in detectability to occur in those years as a result of birds dispersing to areas that are not included in the survey. Rodgers et al. (1988) also suggested that the annual survey is more appropriately considered as an index among surveyed wetlands than as a census. However, given the failure of the survey to meet the critical assumption of equal detectability, we believe that the annual survey is not even a reliable index among wetlands.

POPULATION CHANGE AND VIABILITY

Trajectories or Trends – Most methods for assessing trends in long-term count data use some form of parametric or non-parametric regression analysis (e.g., numerous papers in Sauer and Droege (1990). Linear regression has been used in several studies to assess the trends of the Snail Kite populations in Florida using the annual survey data (e.g., Sykes 1979, 1983b, Bennetts et al. 1994). Regression-based approaches to monitoring trends have received considerable review as a tool for long term population trends for birds (e.g., the Breeding Bird Survey [BBS] and Christmas bird count [CBC]). Criticisms of linear regression approaches have focused on accounting for many of the sources of variation we have identified for the annual survey of Snail Kites (e.g., observer differences, effort, and spatial variation)(e.g., Butcher et al. 1990, Droege 1990). Several analyses have been proposed to help account for some of these sources of variation (e.g., route regression, Geissler and Noon 1981, Geissler 1984 Geissler and Sauer 1990, and locally weighted regression, Cleveland 1979, Taub 1990, James et al. 1990). Despite numerous suggestions that a reliable evaluation of trends requires accounting for sources of variation and the emergence of statistical tools to accomplish this, there have been no attempts of which we are aware to apply these advances to the analysis of trends for the Florida Snail Kite population. We recognize that controversy remains regarding the specific applications of many of these statistical tools; however, we also recognize that a failure to account for variation in the annual survey leads to spurious conclusions.

Link and Sauer (1997) recently reported a new approach for modeling population trajectories using count data that looks quite promising. The goal of their approach is to estimate trajectories (a smoothed and scaled summary of population change) or trends (the geometric mean trajectory over some specified time interval). Their approach uses quasi-likelihood procedures for estimating parameters and provides a mechanism for incorporating external variability (e.g., observer effects) into the models. This approach enables straightforward model selection using AIC, and hypothesis testing based on likelihood ratio procedures (see methods for discussion of AIC and Likelihood ration tests). Thus, trajectories can be estimated while accounting for external sources of variability. We are currently exploring use of this approach for Snail Kites and our results should be forthcoming within the next year.

Regardless of what approach is used, we suggest that evaluations of population trends of Snail Kites must begin to account for the sources of variation in the annual survey. Assuming that the annual survey mirrors population size is not scientifically reliable without accounting for the variability of detection.

Viability-- In recent years there has been an exponential increase in the use of population viability analyses (PVA)(Soule 1987a). Some concerns over the use of PVA were recently summarized in a status review of the Northern Spotted Owl *(Strix occidentalis caurina)*(Anderson et al. 1990) to evaluate whether or not federal listing was warranted under the Endangered Species Act. For example, PVA models often lack empirical estimates for critical parameters and assumptions are substituted for reliable estimates (Anderson et al. 1990). Incorporating a different set of assumptions will likely lead to different biological conclusions (Ewans et al. 1987, Anderson et al. 1990). In some cases the assumption of an effect can even be incorporated into a model and concluded to be important based on the assumed values (i.e., circularity) (Anderson et al. 1990). For example, Beissinger (1995) recently reported a PVA for Snail Kites in which the most sensitive parameter in his model was drought-related survival. Because no reliable estimates of this parameter were available, Beissinger used values that were based on differences in the annual survey for a subset of the drought years that had occurred. This use of the annual survey is highly questionable (see *Sources of Variation*) and would likely inflate this parameter estimate because there is also a negative detectability bias associated with droughts (see *Sources of Variation*). Beissinger concludes that drought frequencies < 3.3 years will result in population declines; however, this conclusion is highly dependent on the assumed estimate of drought related mortality. Thus, an assumed value of mortality rates associated with droughts leads to a conclusion of the importance of droughts (i.e., a circular argument). We agree with Beissinger that droughts are an important influence on the Florida Snail Kite population. However, until reliable estimates of drought-related survival are available we have little confidence in the reliability of specific predictions.

A second concern is that mathematical representations of biological phenomena are often restricted in their ability to reflect biological reality by limitations of mathematical theory (Ewans et al. 1987). The implications of this concern, however, depend greatly on the expectations of the model. It is often not the intent of the modeler to mirror biological reality so much as to evaluate the potential effects of particular sources of variation in an "all else being equal" scenario or in the context of evaluating the relative sensitivities of the input parameters. In these types of situations, hypotheses about populations can often be tested in an environment that need not be an accurate portrayal of biological reality.

A third concern of PVA is that there may be a tendency to expect too much predictive power from these types of models (Ehrlich 1989). PVA models are often interpreted as if they are accurate predictors of population viability over relatively long time scales (e.g. >100 years). This, of course, assumes that either we have reliable knowledge about the environmental changes that will occur over the predicted time period (e.g. 100 or 1000 years), or that environmental conditions will not change over that time period. These assumptions are obviously absurd. This does not imply that PVA models are not useful. They can be excellent tools to explore such things as the relative magnitude of different sources of variability on long term population trends. However, the limitations of applicability of these models should be carefully considered. Although we recognize that PVAs can be useful tools, we agree with the conclusion of Soule (1987b) that these "mathematical models serve as useful vehicles for thought, but it would be foolish to hitch a bandwagon to any particular one".

The predictive capability of models will likely improve as we are better able to estimate critical parameters and their relationship with environmental conditions. However, in the interim, we suggest that the most prudent approach for management decisions is to rely on direct estimates of the parameters of interest.

Finite Rate of Population Change-- Analyses of trends, trajectories, and/or population viability all assess population change over a number of years. It is also possible to evaluate population change in shorter time scales (i.e., a more "snapshot" approach) using actual estimates of demographic parameters. We currently have the capability to estimate the finite rate of population change (λ, Lambda) directly using mark-resighting methods for estimating survival in conjunction with direct nest monitoring for estimating reproduction. Matrix approaches to such assessments (e.g., Leslie 1945, 1948, Lefkovitch 1965) are currently available.

Beissinger (1995) incorporated a matrix approach to his PVA; however, he used unreliable values for critical parameters to extend the scope of his analysis beyond that for which we have reliable data. We suggest that if a matrix approach is intended as a biologically realistic estimate of λ, that it be restricted to post hoc estimates for years in which reliable data are available for critical parameters. Substituting assumed or unreliable values for critical parameters only leads to predicting the very assumptions that were introduced into the model by those values (Anderson et al. 1990).

ESTIMATES OF DEMOGRAPHIC PARAMETERS

Survival– Differences in the annual survey from one year to the next has been frequently used as an estimate of survival, particularly during drought years (e.g., Beissinger 1986, 1988, 1995, Takekawa and Beissinger 1989). For example, the difference between the 1980 and 1981 surveys has been widely cited as an estimate of mortality during a widespread drought in 1981 (e.g., Beissinger 1986, 1988; Takekawa and Beissinger 1989). Unfortunately, the surveys in 1980 and 1981 were conducted by different observers, and the observer in 1980 was substantially more experienced. The 1980 and 1981 counts involved different effort (36 and 26 observer days for 1980 and 1981, respectively). Additionally, when reporting the annual survey results for 1981, some authors (e.g., Beissinger 1986, 1988; Snyder et al. 1989) also substituted a survey conducted in March of 1982, by still a different observer, in lieu of the official survey conducted in December 1981 (U.S.F.W.S. 1986, Snyder et al. 1989). Use of the survey for estimating survival is further confounded by an inability to distinguish changes in recruitment from survival (Rodgers et al. 1988). Changes in the number of birds counted can result from either changes in the detectability of birds or as a result of changes in population size. Count data, without an estimate of the proportion of birds in the population being counted, can not distinguish among these effects (Burnham 1981, Nichols 1992, Johnson 1995). For example, during droughts, Snail Kites often disperse to numerous peripheral habitats that are not included in the survey (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989). Investigators can not distinguish a failure to detect birds that have temporarily moved to drought refugia from an actual population decline using the annual survey. Based on these inherent problems, we believe that using the annual survey for estimating survival, particularly during droughts, has little scientific validity and we suggest that use of the annual survey for this purpose be avoided.

Radio telemetry offers one alternative to the annual survey for estimating survival. Radio telemetry avoids most of the pitfalls of using the annual survey since known individual birds are monitored over time. A critical assumption of radio telemetry for estimating survival is that the radio itself does not influence survival. The assumption has been shown to be violated for several species of birds (e.g., Marks and Marks 1987, Patton et al. 1991). We explicitly tested this assumption using banding data from birds with and without radio transmitters and found no evidence that this assumption is violated for Snail Kites for our study. We emphasize, however, that this does not imply that transmitters of a different design, weight, or method of attachment might not have an effect. Our data are only applicable for the conditions under which we tested. Thus, we would encourage any future users of radio telemetry for Snail Kites to exercise caution in extrapolating our conclusions to different circumstances.

A second consideration for the use of radio telemetry for estimating survival is cost. Radio telemetry is quite expensive and cheaper alternatives (e.g., mark-resighting) exist for estimating survival. Thus, we suggest that radio telemetry is not the preferred method for estimating survival; unless the goals of the monitoring include other parameters that are more suited to radio telemetry (e.g., movements).

Another alternative approach for estimating survival is mark-resighting. In contrast to the annual survey, mark-resighting methods have a long and solid statistical foundation (e.g., Cormack 1964, Jolly 1965 Seber 1965, Brownie et al. 1978, White 1983, Pollock et al. 1990, Lebreton et al. 1992; Nichols 1992; see also numerous papers in Lebreton and North 1993 and the Journal of Applied Statistics Volume 22, nos. 5 & 6 [special issues devoted completely to this subject])). In contrast to radio telemetry, mark-resighitng is considerably less expensive and bands are less likely to influence the birds (radio-tagged birds have bands in addition to the radio). We previously describe the conceptual basis for a mark-resighting approach (see *Methods*); however, the underlying structure to this approach uses the Cormack-Jolly-Seber (CJS) model, which allows for explicit estimation of survival and its associated standard error, and enables testing of hypotheses relating to differences attributable to age, sex, and environmental conditions (Lebreton et al. 1992). The CJS model also explicitly estimates both resighting probability and survival, parameters which are confounded in the annual survey.

The assumptions and sources of error for this approach also have been previously discussed (see *Assumptions, Bias, and Sources of Error for Survival Estimators*); however, our preliminary assessment does not indicate any substantial violation of these assumptions, and the CJS models are relatively robust to the minor violations that are likely to have occurred for Snail Kites. Additionally, there are tests available to explore the violation of most assumptions of these models (e.g., Burnham et al. 1987, Lebreton et al.

1992). Thus, we suggest that mark-resighting methods offer reliable estimation of survival, at a cost considerably less than that required for radio telemetry. However, mark-resighting models require a reasonable level of resighting to obtain a reasonable level of precision. Nichols et al (1980) suggested that a mark-resighting approach to estimating survival would be desirable; however, they suggested that suitable resighting probabilities would be difficult to obtain. Our data have shown that it is feasible to obtain resighting probabilities sufficient for reasonable estimates of survival; however, it requires a substantial and well planned effort.

Reproduction– Several parameters are required to effectively measure reproduction: (1) the proportion of the population attempting to breed, (2) the proportion of nesting attempts that are successful, (3) the number of young produced per successful nest, and (4) the number of nesting attempts per year (Brown 1974). Of these parameters, numbers 2 and 3 have been well studied for Snail Kites. Not surprisingly, they are also the easiest to measure. Reliable estimates for numbers 1 and 4 have been lacking (see discussion in chapter on *Reproduction*).

The proportion of birds attempting to breed can be a difficult parameter to measure and previous estimates have been heavily dependent on unrealistic assumptions (see *Proportion of Birds Attempting to Breed* in chapter on *Reproduction*). We suggest two approaches to estimating this parameter are radio telemetry and/or mark-resighting. We used radio telemetry to estimate this parameter during the 1995 breeding season. Although we were able to successfully estimate this parameter, it was very labor intensive and very expensive. We suggest that radio telemetry only be the method of choice if other needs for telemetry warrant its use. A potentially cheaper alternative to radio telemetry is multi-state models from mark-resighting data (Brownie et al. 1993, Nichols et al. 1993). Using multi-state models, the investigator would record the breeding state (i.e., nesting or not nesting) for each individual banded bird resighted. The resulting models would then include a parameter for the probability that an individual bird was breeding, given that it was alive in the population. A potential problem with this approach is that the breeding season for Snail Kites can be lengthy, and a single sighting may not provide a realistic estimate for this parameter. There are some potential solutions to this problem that involve developing models that incorporate multiple sightings of individuals within a given year to account for the probability of detecting a breeding attempt in a given year. A pilot investigation is currently being conducted to evaluate the potential for this approach (Dreitz et al., pers. comm.).

The proportion of nests that are successful is relatively easy to measure; however, there have been disagreements among researchers regarding how to measure this parameter. These disagreements have been discussed in detail a previous section of this report (see *Nesting Success* in chapter on *Reproduction*) and will not be repeated here. However, we suggest that if the primary focus of monitoring nesting success is its use as a demographic parameter, then the Mayfield estimator (Mayfield 1961, 1975, Miller and Johnson 1978, Steenhof and Kochert 1982, Hensler and Nichols 1981, Hensler 1985) probably provides a less biased estimate than does apparent success (i.e., number of successful nests divided by the total number of nests found). For this analysis, we recommend that a nesting attempt be defined by having a nest containing at least one egg (Steenhof 1987). If, however, the emphasis of monitoring is to evaluate the environmental or behavioral (e.g., mate choice) conditions that result in a breeding attempt, then including the courtship phase (i.e., prior to egg laying) might be warranted. However, we caution that our data suggest that many attempts at courtship are very short-lived (e.g., ≤ 1 day) and attempting to interpret these data as a demographic process are likely to yield spurious or ambiguous results (see discussion of *Nesting Success* in chapter on *Reproduction*). We also caution that regardless of what analysis is used, there is considerable spatial variability in nesting success and sampling at a local scale does not provide reliable inference for the statewide population. Lastly, we caution that investigators should be fully aware of their potential influence on estimates of nesting success and take precautions to minimize their impact.

The number of young per successful nest is relatively easy to measure and there has been no controversy, of which we are aware, regarding the measurement of this parameter for Snail Kites. We do however, repeat the cautions above that there is considerable spatial variability and a sampling scheme should take into consideration its geographic scope and the influence of the investigator.

Reliable estimates of the number of breeding attempts per year also have been lacking and are difficult to obtain. Snyder et al. (1989a) made a crude attempt at estimating this parameter; however, we believe that the assumptions required for their estimate were grossly violated and this estimate is not reliable (see discussion on *Number of Breeding Attempts Per Year* in chapter on *Reproduction*). Additionally, our data using radio telemetry also suggest that their estimate was biased high. We suggest that radio telemetry is the most feasible method for estimating this parameter. Radio telemetry, however, is extremely expensive and its use for only this purpose may not be justified. It is possible to estimate this parameter using mark-resighting methods; however, this would require a more extensive "within year" effort that may not be feasible or practical. An exploration of this approach is currently being conducted (Dreitz et al., pers. comm.); however, based on our efforts using mark-resighting, we are not overly optimistic that sufficient data can be obtained for reliable estimates. Consequently, we suggest that until reliable data are available, demographic evaluations treat this parameter as an unknown, and evaluate the resulting models based on a range of reasonable values.

EXTERNAL INFLUENCES ON THE POPULATION

Hydrology has long been believed to be a major influence on Snail Kite populations (Sykes 1983b, 1979, Beissinger 1986, 1988, Rodgers et al. 1988, Snyder et al. 1989, Bennetts et al. 1994). Consequently it is not surprising that a number of attempts have been made to relate the annual Snail Kite survey to hydrologic conditions. There have been several approaches to assessing this relationship, from anecdotal accounts relating observed decreases in birds seen with low water levels (citations) to various ways of quantifying a correlation between water levels and the annual survey (e.g., Sykes 1983b, Bennetts et al. 1994, Beissinger 1995). In some cases (e.g., Sykes 1983b, Beissinger 1995) the total statewide survey has been correlated to the water levels at one or more "key" habitats. In contrast, the analysis by Bennetts et al (1994) used the surveys for specific wetlands and the corresponding water levels for that same wetland. Regardless of the approach, correlation approaches to time series data tend to provide questionable results due to a lack of experimental design (Walters 1985) and confounding variables (Draper and Smith 1981). In particular here, all of these methods based on the annual survey still cannot distinguish whether any relationship found (or not found) is due to an actual numeric population response (i.e., that the population size actually decreased or increased in relation to water levels) or to a behavioral response (e.g., movement out of the surveyed habitats) of the birds. It is quite probable that it is a combination of these responses (Rodgers et al. 1988) along with the various errors associated with measuring these responses.

CONCLUSIONS

Based on our data and on logic of valid scientific inference, we suggest that the annual survey is not a valid estimator of population size; nor should year to year variation in the survey be used to estimate demographic parameters (i.e., survival or recruitment). We do, however, believe that the annual survey has some value for examining long term population trends or trajectories provided that the sources of variation identified above be incorporated into any analysis. Link and Sauer (1997) provide one potential statistical framework for such an analysis. Their approach uses quasi-likelihood estimation of trajectory parameters combined with a maximum likelihood based (e.g., AIC, see methods) approach to model selection. Additionally, some sources of variation (e.g., temporal variation and effort) can be minimized by standardization of the survey. For example, the survey should be conducted at the same time each year and, if possible, using the same observers. Finally, any interpretations from this survey should be made cautiously with full awareness of its limitations.

Inferences made from the annual survey regarding the environmental influences on the Florida Snail Kite population can certainly be made; however we urge caution and careful consideration of the potential pitfalls and sources of error. We also strongly agree with the suggestion of Temple and Wiens (1989) that, whenever possible, primary demographic parameters (i.e., estimates of survival and fecundity) be used as the dependent variable for analyses of factors influencing populations. Our results show that these data are obtainable for Snail Kites and their use for such analyses encouraged.

An additional consideration for any monitoring program is its geographic scope. Our data indicate that the Florida population of Snail Kites is one population that exhibits considerable mobility. Consequently, to monitor kites at a few "key" areas will likely be extremely misleading. Snail Kites in Florida can shift in distribution frequently and it is also not unusual for individuals to nest at different locations from year to year. Thus, monitoring at only a local level would likely yield spurious results with respect to demographic processes. Monitoring at only a local level would likely result in confounding of survival and movement estimates (as currently exists with the annual survey), and would likely lead to false conclusions about annual productivity. Thus, we suggest that any monitoring effort be targeted for the whole population and include samples from at least the major habitats.

Chapter 8. MANAGEMENT AND CONSERVATION

Water Management and Snail Kites

DROUGHT SEMANTICS

There has been considerable discussion in the literature about the influence of drought on Snail Kite populations (e.g., Sykes 1979, 1983a, Beissinger 1986, 1995, Snyder et al. 1989a). Given the potential importance for this influence, it is surprising that these authors have not defined a drought sufficiently to enable an independent observer to designate a given year as a "drought year" based on objective criteria. Drought can be measured in several ways and be based on either water levels or rainfall (Duever et al. 1994). Snyder et al. (1989a) and Beissinger (1995) designated each year over their period of study as a either a drought year, lag year (the first year post drought), or high water year (i.e., non drought) based on water levels. However, the water levels that were used to assign a given year as a drought year were not defined by these authors, nor was there consistency between these authors as to which years were drought years. Of the years that drought status was reported by both studies (1969-1983), Snyder et al. (1989a) determined that 1971, 1974, 1981, and 1982 were drought years; whereas, Beissinger (1995) determined that 1971, 1973, 1974, and 1981 were drought years. It seems a logical starting point that before any serious evaluation of the influence of drought on Snail Kite populations can be made, that at least it be clear as to what constitutes a drought. We believe that an absence of clear definitions has led to considerable misunderstanding among researchers and managers. For example, Beissinger (1995) suggested that Snail Kite populations would decline if the interval between droughts was less than 3.3 years. We have some serious concerns about the parameter estimates he used to derive this conclusion; however, we do not necessarily disagree with his conclusion; **provided** he is referring to widespread multi-regional droughts (see *Spatial Extent* below). We would strongly disagree, however, if he is suggesting that **local** drying events at intervals less than 3.3 years would result in population declines. In fact, much of the habitat used by kites during our study (and over the past decade) has dried out (on average) more frequently than every 3.3 years and all evidence (i.e., our data and/or the annual count) suggest that the overall population has been stable or increasing. Thus, we believe that this may, or may not, be a valid recommendation depending on how it is interpreted. There are three essential characteristics of droughts that should at least be considered and operationally defined for effective evaluation of droughts (Lin et al. 1984) and their influence on Snail Kite populations. They are the intensity, spatial extent, and temporal extent (e.g., duration and/or number of consecutive drought years) of the droughts being considered.

Intensity-- We consider the intensity of a drought as being a measure of "how dry it was". This is probably best measured from the "well" type of gauges, which are capable of recording water stage even below ground level at the recording station. One approach to measuring intensity is to assess water levels at a given location in relation to a reference elevation. (e.g., ground elevation at that location). We have shown as an example the annual minimum stages for WCA-3A as recorded at the 3-28 gauge, (the gauge reportedly used by Beissinger [1995] because of its proximity to areas used by kites)(Fig. 8-1). We have also shown some reference elevations that might be used to designate a given year as having been a drought year. To illustrate ambiguities that can result from not defining criteria used to designate a given year as a drought, we have also shown which years were determined to be drought years by Snyder et al. (1989a) and Beissinger (1995). It quickly becomes apparent that Beissinger (1995) could have defined a drought year (for WCA-3A) as a year in which the minimum annual water stage was < 2 m. A similar criteria based on this gauge was not apparent for the assignment of drought years by Snyder et al. (1989); however, it is quite possible that they may have based their designation on a different location or using different criteria. Since WCA-3A and Lake Okeechobee were the two primary areas in each of these studies, we conducted a similar assessment of the stages of Lake Okeechobee using a standard 10-gauge average (provided by the U.S.Army Corps. of Engineers) to account for spatial variation among gauges (Fig. 8-2). The designation of drought years by Snyder et al. (1989) is a little more apparent based on data from Lake Okeechobee (all years they assigned as drought years had stages less than 3.57 m). However, it is not clear why 1968 was considered as a drought year, but not 1975 and 1976, which had very similar minimum water levels. The designation of drought years by Beissinger (1995) also becomes less clear using data from Lake Okeechobee. For example, Beissinger (1995) determined 1973 to be a drought year but not 1975, 1976, and 1982, all of which had lower stages at Lake Okeechobee. Our point is not to agree or disagree with which years these authors determined to be drought years; but rather, to point out that without defining the criteria, the designation of drought years becomes subjective.

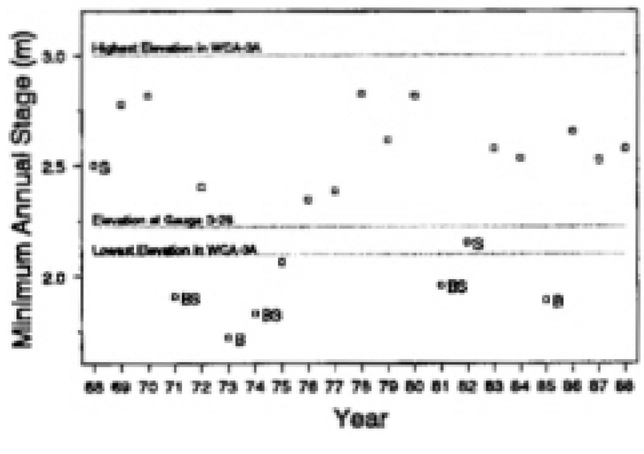


Figure 8-1. The minimum annual water stage for gauge 3-28 in Water Conservation Area 3A (WCA-3A) for the period of 1968-1988. Shown for reference are the minimum and maximum ground elevation in WCA-3A, and ground elevation at the 3-28 gauge. Points mark with an "S" were years identified by Snyder et al. (1989a) as drought years and those mark with a "B" were identified by Beissinger (1995) as drought years.

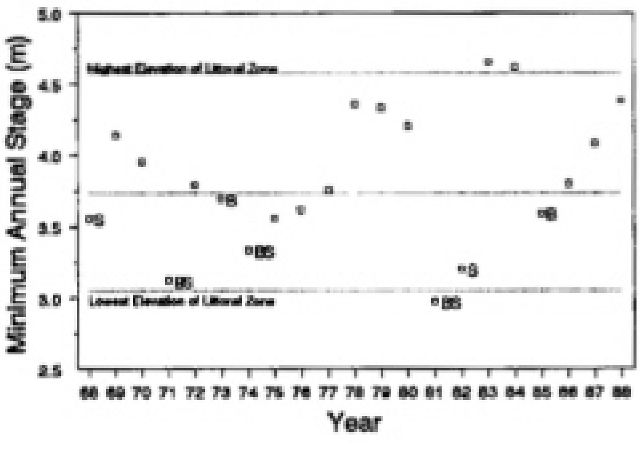


Figure 8-2. The minimum annual water stage for a 10-gauge average at Lake Okeechobee for the period of 1968-1988. Shown for reference are the minimum and maximum ground elevation for the littoral zone at Lake Okeechobee (based on Pesnell and Brown [1977]). Points marked with an "S" were years identified by Snyder et al. (1989a) as drought years and those mark with a "B" were identified by Beissinger (1995) as drought years.

If the intensity of a drought is used to measure the behavioral or demographic response of the population, then it is also not always the case that drying to ground elevation should be used as the measure. For example, anecdotal evidence suggests that Snail Kites move from a drying area well before it reaches ground level. In some cases it may be more meaningful to distinguish a **functional dry down** (i.e., the water level at which the response occurs) from a **physical dry down** (i.e., water level ≤ ground elevation). But again, we suggest that the criteria for such a designation be defined.

An alternative approach, and one that we prefer, for assessing the intensity of a given drought is to use a statistical measure of the variability (e.g., the standard deviation) of the actual water data. For example, we determined the minimum annual water level for gauge 3-28 for each year from 1969 through 1995. We then calculated the mean and standard deviation for these minimum annual water levels. If we use this approach and define a drought year as any year in which water levels were lower than 1 standard deviation below the mean minimum water level, then we would have selected exactly the same years as Beissinger (1995) for the period that he used in his analysis (Fig. 8-3). Although, as above, this approach would not necessarily have indicated that wetlands other than WCA-3A were experiencing a drought in those years. A separate analysis would have to have been performed for each area of interest (see *Spatial Extent* below). The advantage of this approach compared to assigning a reference elevation is that the same criteria (e.g., > 1 standard deviation below the mean) can be used for any area. This eliminates the subjectivity imposed by assigning a different reference elevation for each area and all areas determined to be drought years have an equal relative intensity.

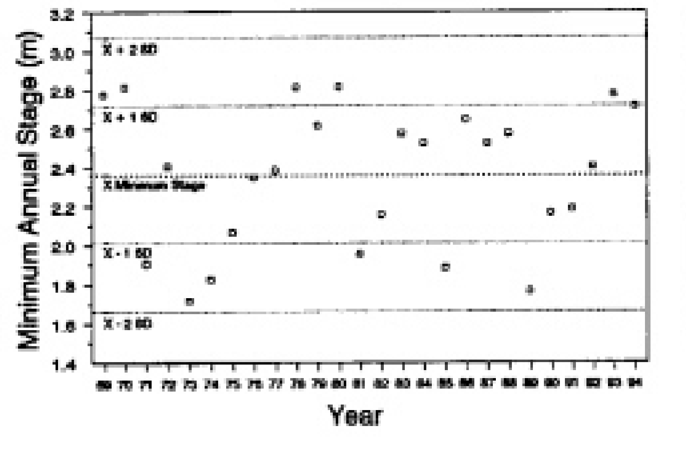


Figure 8-3. The minunum annual water stage for gauge 3-28 in Water Conservation Area 3A (WCA-3A) for the period of 1969-1994. Shown for reference are the average annual minimum stage, ± 1 standard deviation, and ± 2 standard deviations.

Spatial Extent-- In virtually every year, the water level in some portion of the habitat reaches ground elevation during the dry season. Additionally, the spatial and temporal variability of rainfall in Florida (MacVicar and Lin 1984) results in spatial and temporal variability in droughts (Duever et al. 1994). Consequently, it is necessary to identify and define the spatial extent of a particular drought being considered if meaningful conclusions are to be drawn, particularly for a species that uses the entire South Florida landscape.

It is certainly possible, although not always feasible, to measure the spatial extent of drying patterns within a given wetland. For many applications, however, it would be sufficient to at least identify drying patterns on a broader scale. We suggest that evaluations of drought effects on Snail Kite populations at least identify whether a particular drying event was a **local** event (i.e., a drying event occurring at a particular wetland or point in space), a **regional** event (i.e., a drying event occurring within a given defined region), or a **multi-regional** event (i.e., a drying event occurring across more than one defined regions).

For a preliminary exploration of the spatial relationships of droughts among wetlands within Snail Kite habitat we used water levels from major wetlands (where reliable water data were available) to determine whether or not a drought had occurred during each year from 1969-1994 (the years in which the annual Snail Kite survey were conducted). The specific gauges used for this analysis (and all subsequent analyses of hydrology) are presented in Appendix 8-1. We defined the intensity of a drought for a given area in a given year based on its standard deviation (as above). We considered any year in which the water levels were > 1 sd below the mean as a drought year and any year in which the water levels were >2 sd below the mean as an extreme drought. The 1977 minimum annual stage for Lake Kissimmee was not used to calculate the standard deviation because it was an extreme outlier (9.4 sd below the mean if 1977 value is not included) due to an intended drainage of the Lake for management. Inclusion of this value would have artificially inflated the variance and resulted in some biologically important droughts to have been overlooked (i.e., fewer years would have been scored as drought years because of the inflated variance).

The results from this analysis indicated that there is considerable variability in the spatial extent of droughts among the most frequently used habitats (Table 8-1). Some years (e.g., 1971) were relatively widespread droughts and encompassed many of the

Table 8-1. Drought intensity scores (standard deviations from mean annual minimum) for most major wetlands used by Snail Kites in Florida. Scores > 1 sd below mean are considred as drought years (bordered cells) and scores > 2 sd below mean are considred as extreme drought years (cells bordered with double line). Spatial extent of a drought can be evaluated by how many areas in a given year have scores > 1 sd below the mean.

YEAR	ENP[1]	BICY[2]	3A[3]	2A[4]	LOX[5]	WPB[6]	OKEE[7]	SJM[8]	KISS[9]	TOHO[10]	ETOHO[11]
1969	1.24	0.53	1.18	1.37	1.11	--	0.64	1.19	0.93	0.19	0.19
1970	-0.18	0.98	1.29	1.02	0.41	--	0.24	-0.46	0.41	0.20	0.21
1971	-1.63	-2.22	-1.28	-0.74	-2.23	--	-1.55	-1.66	-2.10	-2.31	-0.04
1972	-0.11	0.10	0.12	0.50	0.41	--	-0.11	0.09	0.65	-0.67	0.37
1973	-0.40	-0.79	-1.82	-0.96	-2.24	--	-0.32	0.25	0.84	0.24	-0.46
1974	-2.02	-1.48	-1.51	-0.61	0.04	--	-1.10	-1.96	0.76	1.06	2.58
1975	0.13	-1.72	-0.84	0.19	-0.64	--	-0.62	-1.06	1.04	0.49	--
1976	-0.10	-0.77	-0.04	1.69	0.43	--	-0.49	-1.22	-0.10	-0.17	0.52
1977	-0.19	-0.63	0.07	1.17	-0.36	--	-0.19	-0.08	-9.42	-0.24	-0.30
1978	0.59	-0.05	1.30	1.94	0.24	--	1.11	1.14	0.96	0.25	0.28
1979	0.94	-0.66	0.71	1.47	0.05	--	1.05	0.85	-0.67	-2.50	--
1980	1.10	1.54	1.28	0.94	0.34	--	0.78	-0.28	-1.00	0.25	-0.66
1981	0.31	-0.76	-1.15	-0.84	-0.63	-2.02	-1.88	-2.41	-0.98	0.28	-0.96
1982	0.62	0.53	-0.58	-0.38	0.72	0.94	-1.39	0.86	0.08	0.15	0.43
1983	1.38	1.41	0.61	-0.09	1.09	0.48	1.75	0.34	0.48	0.07	0.71
1984	0.84	1.26	0.48	-0.09	1.07	0.06	1.67	0.41	-0.76	-0.10	-0.40
1985	-0.29	0.31	-1.34	-1.43	0.58	1.15	-0.54	-0.16	1.07	0.26	0.53
1986	0.29	0.21	0.82	-0.24	1.12	0.85	-0.09	-1.26	0.21	0.28	0.17
1987	0.67	0.95	0.46	-0.62	0.75	-0.88	0.52	0.36	-2.96	-2.35	0.11
1988	0.55	0.83	0.61	-0.55	-0.29	0.30	1.16	0.36	0.04	0.04	0.12
1989	-2.02	-0.30	-1.67	-2.07	-2.31	-1.59	-1.04	0.37	0.02	0.28	-2.67
1990	-1.73	-0.52	-0.55	-1.12	-0.51	-1.16	-1.45	1.06	0.19	2.15	-2.42
1991	--	-0.40	-0.51	-0.12	-0.98	0.89	-0.31	1.01	-0.51	1.17	0.14
1992	--	-0.70	0.14	-0.79	0.12	-0.46	0.99	0.53	-0.37	0.40	0.60
1993	--	1.54	1.19	0.16	0.94	0.67	0.55	0.52	0.32	0.48	0.23
1994	--	0.82	1.02	0.23	0.78	0.76	0.63	1.19	1.44	0.08	0.71
1995	--	2.81	1.39	0.64	1.40	1.47	1.63	1.76	1.77	0.43	2.31

[1] *Everglades National Park*
[2] *Big Cypress National Preserve*
[3] *Water Conservation Area 3A*
[4] *Water Conservation Area 2A*
[5] *A.R.M. Loxahatchee National Wildlife Refuge*
[6] *City of West Palm Beach Water Catchement Area*
[7] *Lake Okeechobee*
[8] *Upper St. Johns Marsh*
[9] *Lake Kissimmee*
[10] *Lake Tohopekaliga*
[11] *East Lake Tohopekaliga*

major kite habitats within the range of Snail Kites in Florida, while others (e.g. 1985) were considerably more local in their spatial extent.

Temporal Extent-- The temporal extent of a drying event should also be considered when considering the effects of droughts. This includes both within-year extent (i.e., the duration of the drying event) and the between-year extent (i.e., whether or not drying events occurred in consecutive years). The duration of a given drying event may affect the survival of apple snails. Darby et al. (1996b, 1996c) found that average survival of apple snails experiencing a drying event was 3.9 weeks (±2.2 weeks sd) and 3.9 weeks (±3.1 weeks sd) for marshes in the upper St. Johns River Basin and Lake Kissimmee, respectively. Thus, not surprisingly, droughts of greater duration may have more of an impact on apple snail populations than those of short duration. Although research is lacking for post-drought recovery of apple snail populations, some less direct evidence (e.g., post-drought return rates) suggests that apple snail populations may take >1 year to recover to pre-drought population levels. Consequently, consecutive drought years also may slow the recovery process.

We used Lake Okeechobee as an example for examining the temporal extent of droughts from the period of 1969-1995. Using the definition (above) of a drought year being any year in which the minimum annual stage was <1 sd below the mean (i.e., minimum annual stage <11.17 ft MSL), Lake Okeechobee experienced six droughts during this period (Table 8-2.). Of these six droughts, there were two single-year events and two consecutive-year events of two years each (i.e., four droughts). The duration of these droughts (i.e., number of days below 11.17 ft MSL) ranged from 8-139 days. Thus, 1981 was a severe drought in intensity (-1.89 sd), was a two-year consecutive drought (followed by the 1982 drought), and had the longest duration at this level of intensity. Although not shown in this table, 1981 also had a large spatial extent. In contrast, the 1989 drought was relatively low intensity (-1.07 sd) and was of short duration at a intensity of 1 sd below the mean, although 1989 was also a two-year-consecutive drought (followed by the 1990 drought).

Table 8-2. The number of days that water stage was > 1 standard deviation below the average minimum stage for a 10-gauge average from Lake Okeechobee for each year from 1969-1994. This corresponds to a stage of < 11.17 ft MSL. The intensity for a given drought year is shown as the number of standard deviations below the mean.

Year	Drought	Intensity	No. Days
1969	No	--	--
1970	No	--	--
1971	Yes	-1.55	88
1972	No	--	--
1973	No	--	--
1974	Yes	-1.1	34
1975	No	--	--
1976	No	--	--
1977	No	--	--
1978	No	--	--
1979	No	--	--
1980	No	--	--
1981	Yes	-1.88	139
1982	Yes	-1.39	139
1983	No	--	--
1984	No	--	--
1985	No	--	--
1986	No	--	--
1987	No	--	--
1988	No	--	--
1989	Yes	-1.04	8
1990	Yes	-1.45	85
1991	No	--	--
1992	No	--	--
1993	No	--	--
1994	No	--	--

HYDROLOGIC REGIMES OF SNAIL KITE HABITAT

Hydroperiod-- a common measure of "wetness" in Florida is hydroperiod, or the proportion of time that a given area is inundated. Hydroperiod is usually expressed over a 12 month period (Fennema et al. 1994) as the number of days per year that an area is inundated or as a percentage (Olmstead and Loope 1984). Hydroperiod is somewhat misleading with respect to Snail Kite habitat because in most years the hydroperiod is approaching 100% (i.e., kite habitat does not dry out every year). Because Snail Kite habitat may be inundated for several consecutive years followed by a drying event, hydroperiod should be considered in longer time scales than annually (e.g., multiple-year averages). Thus, unless otherwise specified, our references to hydroperiod in this report represent averages over multiple years, rather than for a single given year.

There is no doubt that Snail Kites occur primarily in areas with relatively long hydroperiods. However, there has been considerable disagreement about how long of a hydroperiod is required. It has previously been suggested that Snail Kites require areas of continuous inundation (which implies 100% hydroperiod)(e.g., Howell 1932, Bent 1937, Stieglitz 1965, Stieglitz and Thompson 1967, Beissinger 1983, 1988). However, continuous inundation has been well documented to result in a loss of the woody vegetation (Craighead 1971, U.S.Department of Interior 1972, McPherson 1973, Worth 1983, Alexander and Crook 1984, Gunderson et al. 1988, Gunderson and Loftus 1993) used by kites for nesting, roosting, and foraging perches (Sykes et al. 1995). Continuous flooding also may kill sawgrass and other graminoid species (Gunderson 1994) that are an essential component of Snail Kite foraging habitat (Bennetts et al. 1994). Based on a 14 year (1969-1982) hydrologic assessment (U.S. Army of Engineers 1992), Bennetts et al. (1988) found Snail Kites in WCA-3A nesting in areas that had hydroperiods, ranging from approximately 84% to 99%. Our observations since that report are generally consistent and suggest that the distribution of hydroperiods for nesting kites ranges from approximately 80-99% with a peak at about 90%. Foraging Snail Kites during non-breeding periods, however, often use habitats ranging as low as ≈ 70% hydroperiod.

We believe that some perspectives about the requirement of continuous inundation for Snail Kite habitat have resulted from using inappropriate time scales. First, when an area dries out, there is no doubt that Snail Kites either disperse from that area or they will die. We also agree entirely that reproduction in that area will be reduced during the dry year and possibly for one or two years following the drying event depending on the intensity of the drought. This does not, however, preclude the possibility that the dispersing birds might reproduce in other areas that might be more suitable at that time. We also agree that if a drought is severe (i.e., high intensity, large spatial extent, and/or of long duration) a demographic response is likely (i.e., increased mortality and reductions in reproduction). These effects of a drying event have been cited (e.g., Beissinger 1983b) as reasons that areas should be kept permanently inundated. Unfortunately, this perspective ignores the fact that periodic drying events are necessary to maintain the plant communities that constitute Snail Kite habitat. The response of Snail Kites (or any species) during a "snapshot" event such as drying does not necessitate the need to manage an area so that the event does not occur. Periodic disturbance events such as fire, hurricanes, and drought are integral components of south Florida landscape patterns (Davis et al. 1994). Thus, the long-term maintenance of the habitat must be taken into account when considering such events. We certainly agree with previous authors that if drying events occur too frequently (i.e., annually), the habitat will be not support Snail Kites. However, a lack of periodic drying may preclude the persistence of many of the plant communities used by Snail Kites for foraging, nesting, and roosting.

The response of kites to prolonged inundation is likely to occur over a period of several years or even decades. Thus, a response to long-term habitat changes may not be as apparent as the dispersal of birds during a given drought year. For example, since 1969, the distribution of nesting Snail Kites in WCA-3A has shifted toward areas of shorter hydroperiod (Fig. 8-4), despite the fact that hydrologic conditions in WCA-3A have not changed substantially during this period (Fig. 8-5). Similar responses have also occurred at Lake Okeechobee and marshes of the Upper St Johns River (pers. obs.). In most longer-hydroperiod wetlands, our data suggest that Snail Kites have habitats available to them with longer hydroperiods than what they are using. Thus, long-term patterns of use by kites do not appear to support the previous suggestions of permanent inundation.

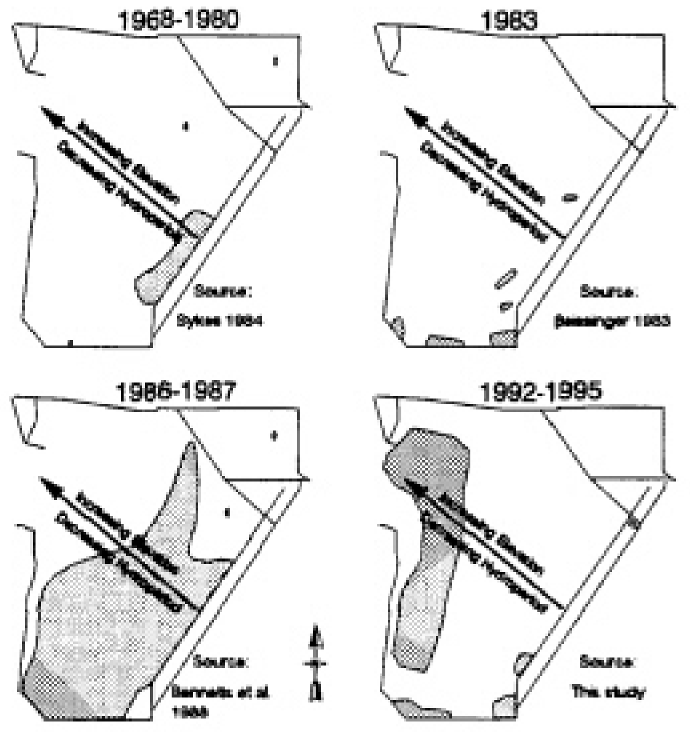


Figure 8-4. The reported nesting distribution of nesting Snail Kites (shaded) in Water Conservation Area 3A (WCA3A) from 1965 to present. It should be noted that birds nesting in southeastern WCA3A during this study were foraging primarily in Everglades National Park and the "Pocket" between the L-67A and L-67C levees, both of which have shorter hydroperiods than the nesting area.

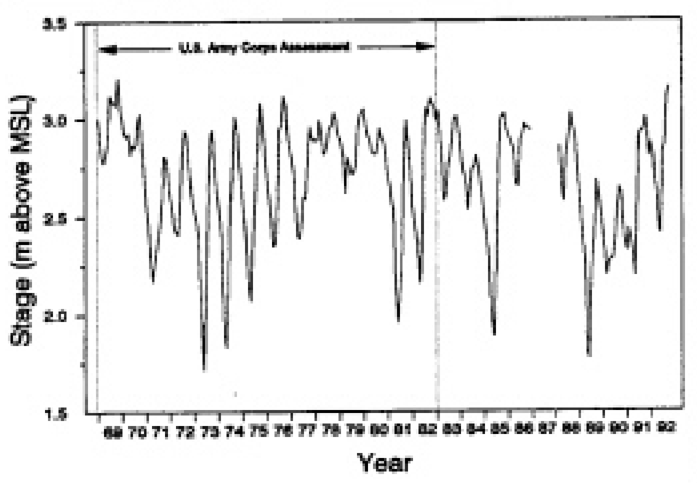


Figure 8-5. The average monthly water stage for gauge 3-28 in Water Conservation Area 3A (WCA-3A) for the period of 1969-1994. Shown for reference is the period of assessment (1969-1982) by the U.S. Army Corps. of Engineers (1992) used for previous assessments of Snail Kite use (Bennetts et al. 1988).

We also wish to emphasize that mosaic of habitats used Snail Kites is partially achieved by spatial heterogeneity within wetlands. Snail Kites will use shorter hydroperiod areas (e.g. wet prairies) of longer hydroperiod wetlands (i.e., wetlands of primarily slough or lacustrine communities)(see *The Hydrologic Window* below). They will also use longer hydroperiod areas (e.g., sloughs) of shorter hydroperiod wetlands (i.e., wet prairies). Thus, it is not essential that all of the wetlands considered as Snail Kite habitat be longer hydroperiod wetlands; rather that have a relatively long hydroperiod (e.g., > 85%) component.

Intervals Between Drying Events-- Because hydroperiod can be a misleading measure for assessing Snail Kite habitat (see above), the interval between drying events is sometimes used as an alternative measure (Bennetts et al. 1988, Beissinger 1995). This interval has generally been expressed as the average number of years between drying events (Bennetts et al. 1988, Beissinger 1995). Although this measure is probably better suited for evaluating Snail Kite habitat, caution is also needed for this measure to avoid misinterpretation. As with any discussion of drying events or droughts the definition of what constitutes an "event" needs to be clear (see *Drought Semantics)*. If we use our definition of a drought above as < 1 sd below the average minimum water stage, then during the period of 1969-1994 the average interval between droughts for WCA3A was 3.6 years (*note: only periods when a complete interval could be determined were used*). Lake Okeechobee had a similar interval of 3.8 years during this period. Beissinger (1995) suggested that populations are not viable unless the interval between droughts exceeds 4.3 years. However, the drought interval over the past 26 years in these two areas (the two areas most frequently used by kites during this period) has been less than 4.3 years and the population has been generally increasing.

We also emphasize that this interval does not represent the interval of drying events at the actual sites used by Snail Kites. Rather, it represents the interval between droughts of a specified intensity (1 < sd below the average minimum water stage) for the wetland as a whole. The interval between drying events at actual sites used by kites often is less. For example, most of the Snail Kites we observed (>90%) in WCA-3A were in areas of elevation >2.5 m. Drying events where the annual minimum stage was ≤2.5 m occurred at an average interval of 1.6 years from 1969-1994. However, this value was heavily influenced by a period of seven consecutive years that WCA3A dried to this elevation from 1971-1977. If this single 7-year period is excluded from this analysis, the average interval between drying events at 2.5 m elevation was 2.1 years. A similar assessment for Lake Okeechobee is more difficult because Snail Kites were more dispersed. However, the stage at 1 sd below the average minimum stage was 3.4 m (11.17 ft MSL). Very few, if any, kites were in habitats ≤ this elevation. Consequently, the average interval between drying events of the actual habitat used by kites on Lake Okeechobee would also have been substantially less than the 3.8 year average derived from using the 1 sd criteria. Bennetts et al. (1988) conducted an assessment of dry-down intervals for the elevations of habitats used by Snail Kites in the water conservation areas and found intervals ranging from 1.6-5.3 years. They also noted that the area with an interval of 5.3 years (WCA2A) had undergone a 9-year period of inundation that coincided with a decline of use in that area (although no causal relationship was established). Thus, although we generally agree with Beissinger (1995) that too short an interval between severe droughts (i.e., high intensity, large spatial extent, and/or of long duration) will result in population declines, we do not believe that this conclusion can be extended to imply that the frequency of drying events for a given local habitat (i.e., at the elevation actually used by kites) must be >4.3 years. We also have strong reservations about the specific values of dry-down intervals suggested by Beissinger (1995) to insure viable populations of Snail Kites because we question the validity of the parameter estimates used to derive these estimates (see *Monitoring Snail Kite Populations in Florida*), and he did not account for the spatial variability that exists in droughts (see discussion of *The Habitat Network* below).

We also point out that droughts probably do not occur at random time intervals. It is common for droughts to occur back to back in at least 2-consecutive year groups. Thus, although the average interval in WCA3A might be 3.6 years it includes several intervals of 1 (i.e., back to back drought years) and some intervals that are longer than the average.

Depth– There have been numerous reports of water depths used by Snail Kites for nesting (reviewed by Sykes et al. 1995). Based on data from this study, Bennetts et al (1988), and Brian Toland (unpubl. data) we found the average water depth at Snail Kite nests at the time of initiation was 60.4 cm (2.0 ft) ±26.5 cm (0.9 ft) sd (N=745)(Fig. 8-6). This is similar to previous reports, but requires some caveats. First this represents depths at the nest site, which are often in stands of sawgrass or willows. The wet prairie and slough habitats typically used for foraging tend to be slightly deeper (≈ 10 cm)(Bennetts et al. 1988). These data also have been collected during the nesting season. Water levels tend to be higher during the non-breeding season; however, during this period kites often move to different habitats, many of which have lower water levels (see *Seasonal Shifts in Habitat Use* in chapter on *Movements*). Thus, these levels may be a reasonable representation, but the variation may be greater than is indicated by these data.

South Florida wetland communities are influenced by depth as well as hydroperiod (U.S.D.I. 1972) and the interaction between these factors is probably more pronounced under the current system (Gunderson and Loftus 1993). Historically, the perimeter of wetland systems in Florida was a gradation from marshes into other habitats from more ephemeral marshes to uplands. As water volumes increased during the rainy season there was considerably more potential for water to expand laterally into the more ephemeral marshes (Fig. 8-7). Under the more recent compartmentalized system the perimeter of marshes is often constrained by levees. Thus, as water volumes increase, there is a relatively greater effect on depth because of the inability for water to move laterally. In addition, the impounding of water that was moving along an elevational gradient (e.g., from Lake Okeechobee to Florida Bay) also will result in increased depth behind the levees (Fig. 8-8). High water conditions also occurred historically; however, the current impounding of water artificially prolongs these conditions more than in the past (Gunderson and Loftus 1993). Thus, under the current system, longer hydroperiods are probably attained only in conjunction with greater depths than probably occurred in the natural (i.e., pre levee) system. Deep water as a result of these anthropogenic influences has resulted in dramatic changes in the biotic communities including a substantial loss of tree islands (Zaffke 1983, Worth 1987, Gunderson and Loftus 1993) and reductions in density of sawgrass (Hoffstetter and Parsons 1979). These changes can be detrimental to Snail Kite habitat.

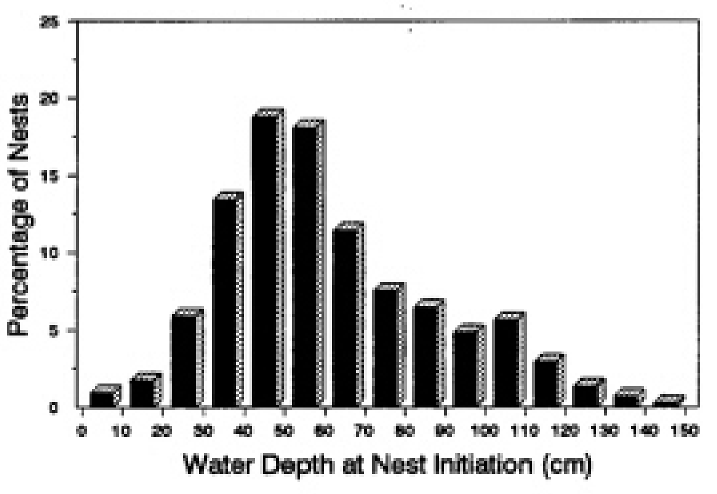


Figure 8-6. The percentage of Snail Kite nests (N=745) that were initiated in each 10 cm water depth class. Data are from Bennetts et al. (1988), B. Toland (unpubl. data), and this study.

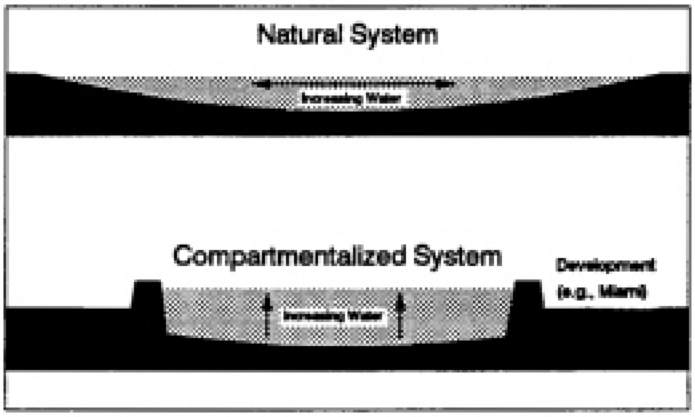


Figure 8-7. A conceptual illustration of how the compartmentalization of wetlands with levees increases depth by decreasing the potential for lateral movement of water.

THE HYDROLOGIC WINDOW

We believe that there has been considerable misunderstanding of the hydrologic conditions of Snail Kite habitat. In part, this misunderstanding may reflect disagreement among biologists as to what constitutes suitable hydrologic conditions for Snail Kites. We have discussed several points of disagreement in the preceding sections. However, some misunderstanding may also result because hydrologic conditions may influence Snail

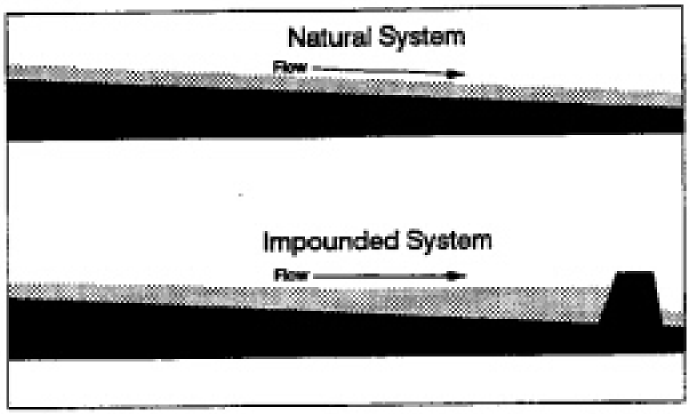


Figure 8-8. A conceptual illustration of how the impounding of wetlands with levees increases depth by buildup of water behind the levees.

Kite habitat at several spatial and temporal scales. For example, Snail Kites may respond to the long-term effects (e.g., the hydrologic regime) quite differently than short-term effects (e.g., current water levels). Our understanding of these differences that occur at different scales may be lost by merely describing Snail Kite habitat as being of relatively long hydroperiod. Consequently, we suggest a conceptual framework to express a more comprehensive viewpoint of the hydrologic conditions of Snail Kite habitat.

Central to our concept is that there is a "window" of hydrologic conditions in which Snail Kites usually occur. This window represents the combined effects of hydrology from all time scales at a given location. For simplicity, we will consider the effects of three time scales (in actuality the time scales form a continuum) that we will refer to as the (1) hydrologic regime, (2) intermediate hydro-history, and (3) current water levels. The hydrologic regime represents the water conditions that have occurred in an area over a period for at least several years. Although this regime could obviously be broken down further, here we are using it to represent changes that require a relatively long response time. It includes changes to soils (which may occur over centuries) as well as changes to the dominant vegetation communities (which may occur from <1 to several decades). The intermediate hydro-history refers to the conditions that have occurred within the previous few years. We are using it in this example to primarily represent the time since a local disturbance event (e.g., local drying) that may have influenced apple snail populations. Current water conditions are used in this example to represent local conditions (e.g., water depth) at a given point in time and space. These conditions may influence availability of food despite local abundance.

Next we wish to place our window within a given landscape. However, we first need to recognize that the location of our window within a wetland is not static, but is changing constantly as wetlands are changing at each of our time scales. To illustrate this concept we will first consider the window within a relatively long-hydroperiod wetland (WCA-3A). The effects of the hydrologic regime (long response-time effects) can be seen by examining the distribution Snail Kite nests in WCA-3A during the past several years (Fig. 8-9). We can see that the area used by kites in recent years is not the longest hydroperiod within WCA3A. Thus, with respect to the hydrologic regime, the current "window" currently is a relatively shorter hydroperiod portion of a long-hydroperiod wetland (Fig. 8-10). We can further see the effect of the intermediate hydro-history and current conditions by looking at the annual differences in nesting distribution (Fig. 8-11). The spatial distribution within WCA3A was similar for 1992, 1993, and 1994; however, 1992 had only 5 nests in WCA3A during that year. Most birds were nesting in the northern porion of their range in Florida. We suggest that this reflects the intermediate hydro-history of WCA3A. During 1989 and 1990 there were low water conditions in this area and 1991 was also relative low water; although not as low as the previous two years. Based on our observations of the few birds that nested in WCA3A during 1992, food was very limited. Although we did not collect any data on foraging during

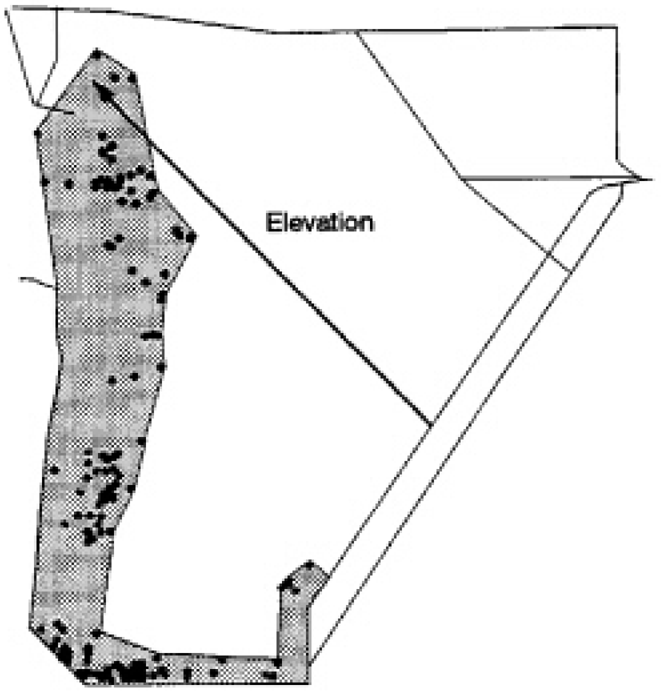


Figure 8-9. The distribution of Snail Kite nests (•) in Water Conservation Area 3A from 1992 through 1995. The shaded area represents the hydrologic regime currently used by nesting Snail Kites.

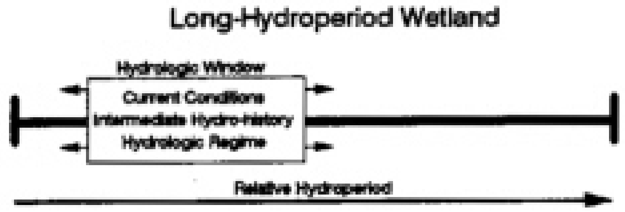


Figure 8-10. A conceptual hydrologic window for a long-hydroperiod wetland showing that in some cases (e.g., Water Conservation Area 3A) the areas currently used by Snail Kites are not the areas of the longest hydroperiod. This window can shift over time depending on the current hydrologic conditions, the intermediate hydro-history and the longer-term hydrologic regime.

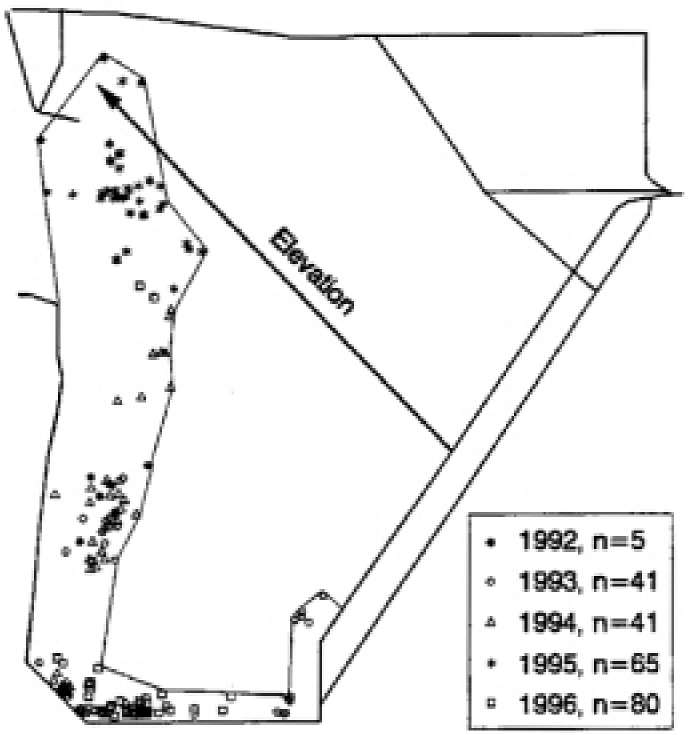


Figure 8-11. The distribution of Snail Kite nests in Water Conservation Area 3A during each year from 1992 through 1995.

1992, it was quite apparent from our observations that nesting birds were having a difficult time capturing snails. It was not unusual to observe birds spending > 30 minutes to capture snails compared to 1 or 2 minutes of foraging time in subsequent years (see *Effects of Food Resources on Movement*). We suggest that the extended period of low water preceding 1992 was a disturbance event that set snail populations back for at least one year post-drought. Consequently, the intermediate hydro-history was not very suitable for nesting in WCA3A during 1992.

The effect of current water conditions can also be seen in these data. The rainy season of 1994-1995 (including tropical storm Gordon) resulted in record high water levels for WCA3A. Most areas in WCA3A had depths > 1 m and many areas had depths > 1.5 m. The distribution of nesting kites during the 1995 nesting season reflects this high water event. The distribution of nesting kites (and our window of suitable hydrologic conditions) shifted dramatically to the north to an area (mostly within the Miccosukee Indian Reservation) of higher elevation, and consequently lower water depths, than had been observed during the previous 3 years. We believe that this shift in distribution resulted from the current conditions (i.e., water depth) being unsuitably high at that time. During the 1996 nesting season, kites shifted back to the south (Dreitz et al., unpubl. data), although many were still foraging in adjacent Everglades National Park and Big Cypress National Preserve where water depths had not been so extreme.

A quite different scenario occurred in the Stairstep Unit of Big Cypress National Preserve over this same time period that further illustrates our concept in a short-hydroperiod wetland. Wet prairie habitats within the Stairstep Unit are generally shorter hydroperiod than those which occur in WCA3A. Although birds have used this area regularly during the non-nesting season for foraging, we had no indication of nesting activity prior to 1995. This is not surprising because, except for the very wettest portions, these prairies dried out for short periods of time during most years. In contrast to WCA3A, the areas used by kites (primarily in Lostman's, Dixon, and East Sloughs were generally the longer hydroperiod habitats within this wetland (Fig. 8-12). During the nesting season of 1995, we observed 24 nests in this area. Thus, our window shifted from suitable foraging habitat during the non-nesting (rainy) season, to suitable nesting habitat during this high water event (Fig. 8-13). During 1996 when more typical spring dry downs occurred only 8 nests were found in this region. Thus, the window was shifting back down.

Our main point from these example is that not all Snail Kite habitat needs to be managed for some "optimal" hydroperiod. Spatial and temporal variation is an integral part of the Florida wetlands landscape and Snail Kites are well adapted to this variability. If all areas were managed as long hydroperiod wetlands, then Snail Kites would have limited habitat available during high water events. Similarly, if all areas were managed as short hydroperiod wetlands, then kites would only have habitat during high water events. We believe that it is this mosaic of hydrologic regimes and local conditions that enable kites to have habitat available during a variety of hydrologic conditions.

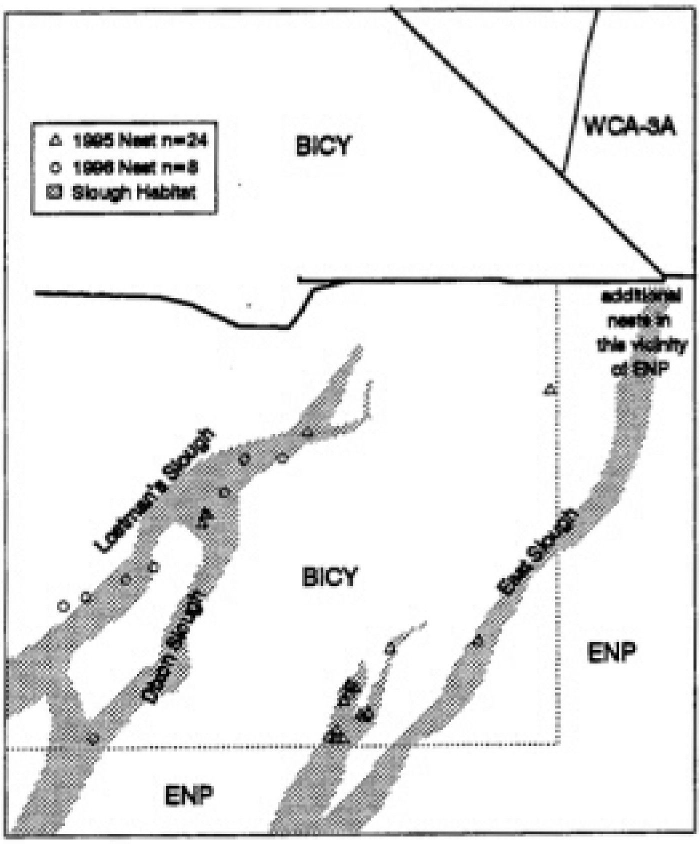


Figure 8-12. The distribution of Snail Kite nests in Big Cypress National Preserve during each year from 1992 through 1995 (no nests were observed from 1992-1994).

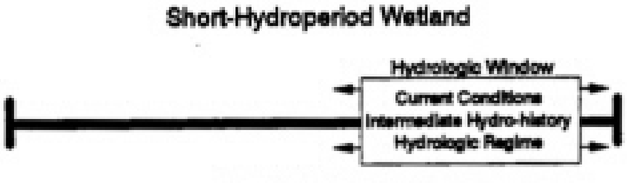


Figure 8-13. A conceptual hydrologic window for a short-hydroperiod wetland showing that in some cases (e.g., Big Cypress National Preserve) the areas currently used by Snail Kites are the areas of longer hydroperiod. This window can shift over time depending on the current hydrologic conditions, the intermediate hydro-history and the longer-term hydrologic regime.

Critical Habitat

CURRENT DESIGNATION

Critical habitat for the Snail Kite was determined in 1977 (Federal Register 42 [155]:40685-40688)(50 CFR Ch. 1 [10-1-94 edition])(USFWS 1986). It includes (1) St John's Reservoir, (2) Cloud Lake Reservoir, (3) Strazzulla Reservoir, (4) western portions of Lake Okeechobee, (5) A.R.M. Loxahatchee National Wildlife Refuge, (6) Water Conservation Area 2A, (7) Water Conservation Area 2B, (8) Water Conservation Area 3A south of Highway 84, and (9) a portion of Everglades National Park (Fig. 8-14).

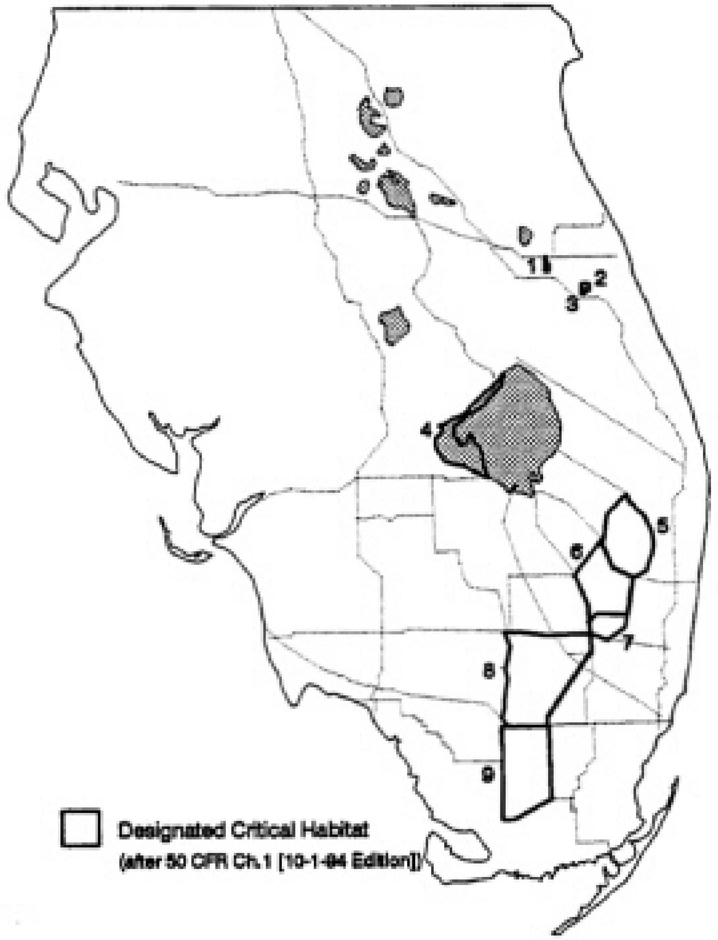


Figure 8-14. The currently designated critical habitat identified in the Snail Kite Recovery Plan (after 50 CFR Ch.1 [10-1-94 Edition]).

THE HABITAT NETWORK

Sykes (1983a) suggested the need to supplement existing protected habitat with "scattered islands" of habitat throughout the kites' range as a means of reducing the impacts of droughts. Takekawa and Beissinger (1989) also suggested that the currently designated critical habitat was inadequate because it lacked sufficient "drought-related" areas. Beissinger and Takekawa (1983) and Takekawa and Beissinger (1989) further suggested that habitats could be divided into primary, secondary, and drought-related habitats. They defined primary habitat as having been used extensively over the previous decade, while secondary habitats received irregular or sporadic use (Takekawa and Beissinger 1989). They defined drought-related habitats as having been used as a result of dry periods. Additionally, some management agencies have described

Snail Kite habitats relative to their function (e.g., "breeding habitat", "wintering habitat", or "drought habitat").

Our data are consistent with the views of these authors in that they indicate that the habitats used by Snail Kites in Florida are considerably more extensive than the currently-designated-critical habitat. Approximately 40% of the locations where we observed radio-transmittered Snail Kites were in habitats outside of the currently designated critical habitat. Additionally, 67% of the radio-transmittered adults used habitats outside of the critical habitat sometime during our observations. That only 67% of the birds we observed used areas outside of the critical habitat probably reflects the short duration of our observations. The number of areas used by kites was highly correlated with how long we observed the birds, and the duration of our observations for birds that had used areas outside of the currently designated critical habitat ($\bar{x}=356$ days, $n=106$) was significantly shorter than for birds who had not used areas outside of the critical habitat ($\bar{x}=267$ days, $n=53$)($t=-3.94$, $P< 0.001$). Thus, we believe that most, if not all, birds that live an average adult life span will use, and probably require, habitat outside of the currently designated critical habitat. Consequently, we strongly agree with the conclusions of Sykes (1983a) and Takekawa and Beissinger (1989) that smaller wetlands peripheral to the currently designated critical habitat need to be protected if Snail Kite populations are to persist. However, our data suggest that the concept of primary, secondary, and drought-related habitats needs to be revised. We believe that the emphasis of research during nesting and the inaccessibility of many areas has greatly limited our understanding of habitats used by kites. We would certainly agree with Sykes (1983a) and Takekawa and Beissinger (1989) that some habitats (e.g., Lake Okeechobee) have been used more consistently than others. We would also agree that some habitats are used more extensively during droughts. However, Snail Kite use of all habitats in Florida, including "primary" habitats, exhibits considerable fluctuation depending on local (and statewide) conditions and may at times have very few, if any, birds present. For example, during the annual count of 1994 (a high water year several years after the previous drought)(Bennetts et al. unpubl. data), no kites were found in WCA-2A (a "primary" habitat). During that same count 46 birds were counted at Lake Kissimmee (a "drought-related" habitat) and 43 were counted at Lostman's Slough of Big Cypress National Preserve. The latter area is not even listed as "primary", "secondary", or "drought-related" by Beissinger and Takekawa (1983) or Takekawa and Beissinger (1989); nor is it within the designated critical habitat (USFWS 1986). In addition, several of the "drought-related " habitats (e.g., Lake Kissimmee and Loxahatchee Slough [West Palm Beach water catchment area]) described by Beissinger and Takekawa (1983) and Takekawa and Beissinger (1989) have had kites present in every year that they have been included in the annual count regardless of whether or not it was a drought year. Approximately 25% of all our locations of radio-transmittered birds were in habitats considered to be "drought-related" habitats by Beissinger and Takekawa (1983) and/or Takekawa and Beissinger (1989) even though drought conditions did not occur during our study. Our data indicate that agricultural areas, agricultural and roadside canals, and peripheral marshes both seasonal and permanent (all described as "drought-related" areas) are used each year, primarily outside of the breeding season. We have even observed kites breeding in these "drought-related" habitats. Consequently, we believe that designations of specific habitats with respect to their function (e.g., "breeding habitat" or "drought habitat) can be misleading and under-represents the use of these habitats by Snail Kites. All habitats can be "drought" habitats, and most can be "breeding" breeding habitats. For example, if drought conditions exist in the northern portion of the kite's range, then birds inhabiting those areas might be using WCA-3A (a "primary" habitat) as a "drought" habitat. Similarly, when local conditions are good, birds will often breed in "drought-related" habitats. Designations based on relative use (e.g., "primary" and "secondary" habitats) can also be misleading because there are often substantial shifts in the distribution of birds over time. Consequently, land (and water) management planning may often use outdated information based on prior assessments of relative use. For example, most investigators working on Snail Kites today, agree that the habitat assessment of the Snail Kite Recovery Plan (U.S.F.W.S. 1986) is in need of revision even though it is only 10 years old.

Based on our data on the movements of Snail Kites from 1992-1995, we suggest that the use of habitats can be better characterized as an extensive network (Fig. 8-15). This network is comprised of habitats that may or may not be physically connected, but are connected through extensive movements of kites among the individual habitats. The network consists of local habitats ranging from large lake or marsh tracts to small agricultural ponds or canals. Some of the habitats may be used by hundreds of kites at a time, while others may be used by a single bird on rare occasions. Our data, as well as the annual count and numerous anecdotal observations and reports, suggest that the use of local habitats is highly variable over time. Even areas that are

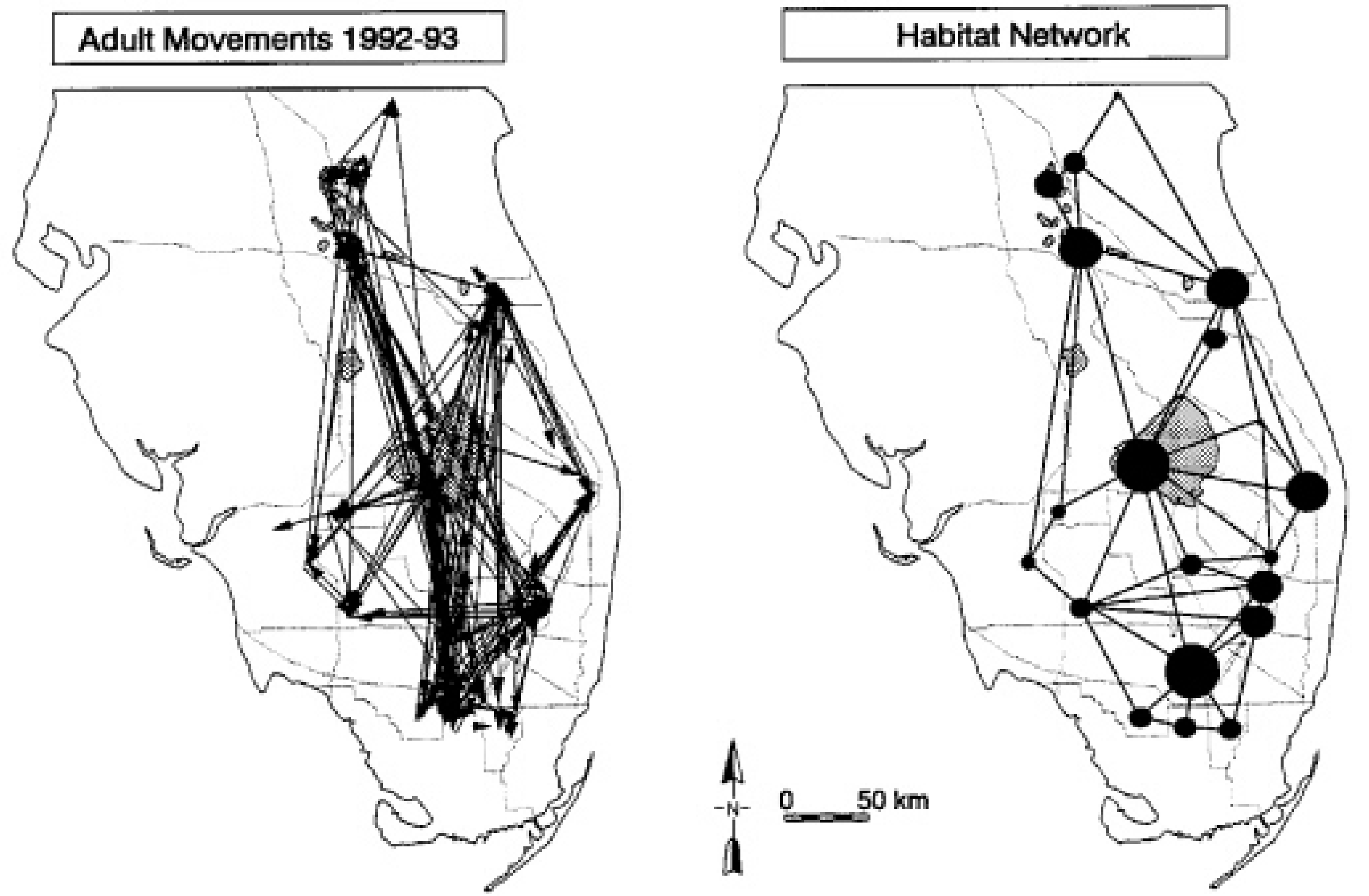


Figure 8-15. South Florida showing the inter-wetland movements of individual radio-tagged adult snail kites during 1992 and 1993. These movements illustrate a basic habitat network used by snail kites (also shown). We have shown only a limited subset of this network (and moments) to minimize cluttering, and because a complete synthesis of the peripheral habitats has not been done. The complete movements, and consequently the complete network, would include all movements and habitats used by kites throughout the state.

used consistently for a number of years have dramatic fluctuations in the number birds present at a given time. The number of birds using a given local habitat also fluctuates seasonally within years. Areas previously described as "secondary" or "drought-related" habitats may have numerous birds present at a time when "primary" habitats may have few birds (not always during droughts). Consequently, we suggest that the patterns of use are better described as a continuum that is highly variable in space and time.

We further hypothesize that the high mobility of Snail Kites enable them to extensively "sample" habitat quality throughout this network. Authors (e.g., Takekawa and Beissinger 1989) have previously suggested that drought induces high rates of dispersal in search of food. All evidence of which we are aware confirms that during droughts kites are more frequently found in areas peripheral to designated critical habitats (i.e., primary habitats described by Beissinger and Takekawa). However, our data suggest that the probability of moving from any given wetland to another may actually increase when food is more abundant. Movement probabilities showed an increasing trend each year since the 1989-1990 drought; movement probabilities also were higher during the summer months when food was more available. We hypothesize that high food availability affords kites the opportunity to broaden their "sample". From an evolutionary perspective, the more familiar an individual is with the potential habitats available, the better they might be able to find food in the event of a food shortage (e.g., from a severe drought).

META HABITATS: A HYPOTHESIS ABOUT THE RELATIONSHIP BETWEEN THE HABITAT NETWORK AND META-POPULATION STRUCTURE

We believe that there is a direct functional relationship between the extent of the habitat network described above and the stability and persistence of Snail Kite populations and their habitat. Here we describe a hypothesis about this relationship which is an extension of an existing hypothesis about population stability. We emphasize that existing data (much of which is presented in this report) strongly support that birds behave in the manner that we describe below; however, the relationship of this behavior to population dynamics remains untested and will be a focus of some modeling efforts currently underway.

Spreading of Risk-- Our hypothesis is really an extension of the concept of "Spreading of Risk" proposed by Den Boer (1968, 1981). Here the concept includes the integration of the spatial patterns and dynamics of Snail Kites and their habitat. The concept of spreading of risk, as proposed by Den Boer (1968), incorporates several key components:

1. *Habitats generally consist of a mosaic structure in which the population as a whole (i.e., the meta population) consists of smaller subpopulations (i.e., local populations).*

2. *Environments exhibit variability in local weather, food, predators, etc. (i.e., habitats are heterogeneous).*

3. *Environmental variability may lead to unequal survival and/or reproduction.*

4. *Consequently, the risk of wide fluctuation in animal numbers is spread unequally over the local populations within a meta population.*

5. *Thus, fluctuation at the meta-population scale is dampened because population dynamics of local populations are not completely synchronous (i.e., some local populations may be increasing while others are decreasing).*

The concept is perhaps more simply stated by the analogy of not having all of your eggs in one basket and that the baskets in which your eggs are in vary in quality over time.

The Meta Habitat Hypothesis-- We propose that the persistence and stability of the Florida Snail Kite population is enhanced by a mechanism similar to concept of spreading of risk. A key distinction is that Den Boer (1968) suggests that meta populations are divided into smaller local populations that respond **numerically** to variable environments (i.e., survival and reproduction differ among local populations); although he also suggested that migration among subpopulations would enhance stability. In contrast, our data suggest that the Florida population of Snail Kites is a single population, rather than a metapopulation comprised of local subpopulations. However, this population occurs, and moves freely, within a network of local habitats (i.e., a meta habitat comprised of local subhabitats). Thus, we suggest that the primary (but certainly not exclusive) population response of Snail Kites to a variable environment is **behavioral** (i.e., moving), rather than numerical. The buffering effect from spreading of risk results from the kites' ability to move to different habitats within the network as quality of local habitats fluctuate. Thus, risk is distributed across the landscape unequally among habitats through spatial extent and heterogeneity of habitat quality. We suggest that as droughts become increasingly widespread, the response becomes increasingly numerical (Fig. 8-16). Thus, we believe that our hypothesis represents an extreme case of the migration effect suggested by Den Boer (1968).

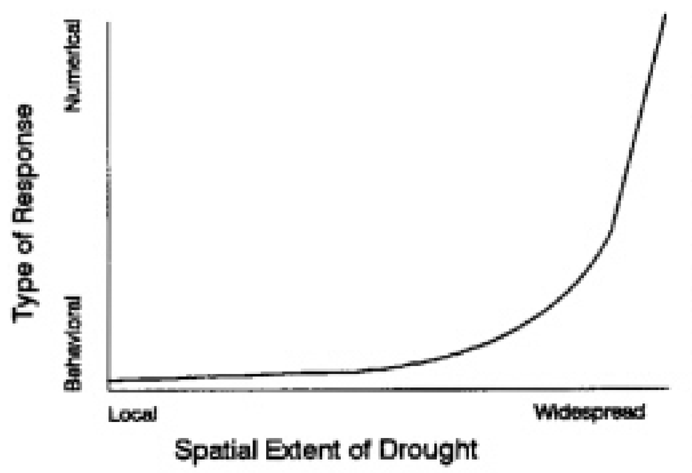


Figure 8-16. Hypothesized relationship bewteen the spatial extent of droughts and the type of response (behavioral or numerical) by Snail Kites in Florida.

We illustrate our hypothesis using 2 hypothetical scenarios (Fig. 8-17) representing the extremes of a continuum. In one scenario, we show the potential response to a local drying event (see discussion above on drought semantics). This can be result from local climatic conditions or be the result of a management action (e.g., Kissimmee Lake experienced a anthropogenic local drying event during 1996 as a result of a fishery restoration project). Under the scenario of a local drying event, birds that were using this habitat move (i.e., a behavioral response) in response to the drying event to other parts of the network that have more favorable conditions. Because most of the network is available as an alternative, there is unlikely to be a numerical response. That is, survival and reproduction are unlikely to be significantly influenced, even though the location of any nesting efforts may shift to alternative habitats. In the second scenario, we show an extreme widespread drought in which a large segment of the habitat network is unavailable. Under this scenario, the larger and more frequently-used alternative habitats may exhibit high concentrations of birds (e.g., the Kissimmee

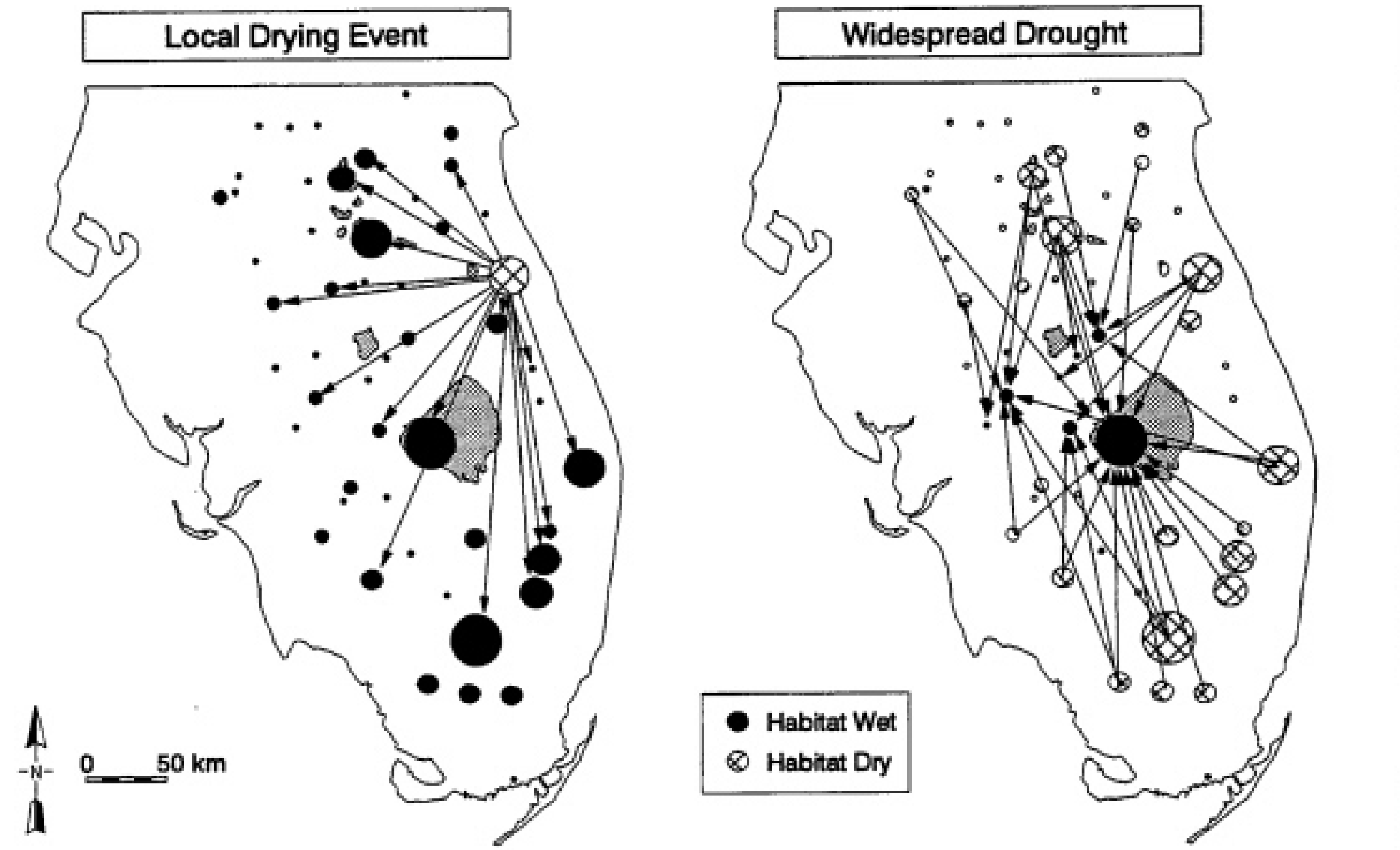


Figure 8-17. A hypothetical example illustrating our hypothesized responses to droughts of different spatial extent. A "local drying event" has relatively low spatial extent. Birds in the area of the drying event would likely move and could re-locate to any of the many habitats not experiencing drought conditions. During a "widespread drought" birds are displaced from all areas experiencing drought conditions and have a more limited number of suitable habitats available that are not experienceing drought conditions.

Chain of Lakes and Upper St. Johns River Basin during 1989-1990) and a greater proportion of the birds may move to smaller habitats more peripheral to the "critical" or "primary" habitats (i.e., the "drought related" habitats described by Beissinger and Takekawa [1983] and Takekawa and Beissinger [1989]). Thus the ability for the network to buffer a numeric response is weakened and survival and/or reproduction are more likely to be influenced. Most years are somewhere in between these extremes; however our data suggest that individual kites are extremely likely to move if conditions are not conducive to survival or reproduction.

Two critical assumptions of our hypothesis are that there is variability among habitat condition throughout the state and that animals move in response to this variability. Although several factors (e.g., hydrology and nutrients) undoubtedly have chronic effects on habitat quality, drought is probably the primary proximate effect. Spatial and temporal variability of droughts in Florida has been previously recognized (Duever et al. 1994) and we have already provided some evidence of variability among regions (see discussion of *Spatial Extent* of drought in this chapter). To further explore whether habitats exhibit spatial variability, we used Pearson's product moment correlation (SAS Inc. 1988) to determine the correlation of minimum annual stage for each of the 12 habitats used most frequently by radio-transmittered birds during this study for which we had sufficient water data. If habitats experience low water conditions synchronously (i.e., during the same years), then we would expect a high correlation among minimum annual water levels. Not surprisingly, there is generally a very high correlation among wetlands within the same region, less correlation between wetlands in nearby regions, and often no correlation between wetlands in distant parts of the Kite's range (Table 8-3). This result further supports our assumption of variability in habitat.

The second major assumption is that animals move in response to this variability. We have already shown that animals move throughout the state in the form of a network of habitats, but this in itself does not imply that birds move in response to variability in habitat conditions. Because no droughts occurred during our study, we are unable to test this assumption directly. However, the responses of Snail Kites to previous drought years during the past two decades does support this assumption. For example, our analysis indicated

Table 8-3. Pearson's Correlation Coefficients (r), probability > |r|, and sample size (N)(i.e., number of years we had water data for both areas) for the minum annual stage in each major wetland (for which we had water data) from 1969-1994. Wetland deignations are the same as in Table 8-1 and water level gauges used are presented in Appendix 6-4.

		3A	2B	2A	LOX	BICY	ENP	WPB	OKEE	SJM	KISS	TOHO	ETOHO
WCA3A	r	–	0.86	0.69	0.71	0.68	0.71	0.43	0.75	0.41	0.00	-0.13	0.18
	P>|r|	–	0.001	0.000	0.000	0.000	0.000	0.124	0.000	0.039	0.999	0.530	0.393
	N	26	10	26	26	26	22	14	26	26	26	26	24
WCA2B	r	0.86	–	0.78	0.60	0.73	0.76	0.55	0.65	-0.10	0.31	-0.19	0.55
	P>|r|	0.001	–	0.008	0.067	0.017	0.081	0.098	0.043	0.780	0.386	0.600	0.100
	N	10	10	10	10	10	6	10	10	10	10	10	10
WCA2A	r	0.69	0.78	–	0.44	0.15	0.53	0.57	0.44	0.15	-0.14	-0.20	0.32
	P>|r|	0.000	0.008	–	0.026	0.451	0.011	0.033	0.026	0.471	0.510	0.336	0.128
	N	26	10	26	26	26	22	14	26	26	26	26	24
LOX	r	0.71	0.60	0.44	–	0.66	0.66	0.59	0.53	0.21	0.14	0.02	0.47
	P>|r|	0.000	0.067	0.026	–	0.000	0.001	0.028	0.005	0.313	0.494	0.907	0.019
	N	26	10	26	26	26	22	14	26	26	26	26	24
BICY	r	0.68	0.73	0.15	0.66	–	0.64	0.50	0.63	0.47	0.13	0.06	0.01
	P>|r|	0.000	0.017	0.451	0.000	–	0.002	0.066	0.001	0.014	0.525	0.753	0.979
	N	26	10	26	26	26	22	14	26	26	26	26	24
ENP	r	0.71	0.76	0.53	0.66	0.64	–	0.49	0.71	0.33	0.01	-0.24	0.22
	P>|r|	0.000	0.081	0.011	0.001	0.002	–	0.154	0.000	0.130	0.964	0.272	0.357
	N	22	6	22	22	22	22	10	22	22	22	22	20
WPB	r	0.43	0.55	0.57	0.59	0.50	0.49	–	0.38	0.34	0.50	0.04	0.74
	P>|r|	0.124	0.098	0.033	0.028	0.066	0.154	–	0.179	0.230	0.069	0.894	0.002
	N	14	10	14	14	14	10	14	14	14	14	14	14
OKEE	r	0.75	0.65	0.44	0.53	0.63	0.71	0.38	–	0.51	0.06	-0.19	0.26
	P>|r|	0.000	0.043	0.026	0.005	0.001	0.000	0.179	–	0.008	0.762	0.351	0.227
	N	26	10	26	26	26	22	14	26	26	26	26	24
SJM	r	0.41	-0.10	0.15	0.21	0.47	0.33	0.34	0.51	–	0.11	0.08	-0.19
	P>|r|	0.039	0.780	0.471	0.313	0.014	0.130	0.230	0.008	–	0.588	0.710	0.366
	N	26	10	26	26	26	22	14	26	26	26	26	24
KISS	r	0.00	0.31	-0.14	0.14	0.13	0.01	0.50	0.06	0.11	–	0.32	0.16
	P>|r|	0.999	0.386	0.510	0.494	0.525	0.964	0.069	0.762	0.588	–	0.110	0.459
	N	26	10	26	26	26	22	14	26	26	26	26	24
TOHO	r	-0.13	-0.19	-0.20	0.02	0.06	-0.24	0.04	-0.19	0.08	0.32	–	-0.15
	P>|r|	0.530	0.600	0.336	0.907	0.753	0.272	0.894	0.351	0.710	0.110	–	0.496
	N	26	10	26	26	26	22	14	26	26	26	26	24
ETOHO	r	0.18	0.55	0.32	0.47	0.01	0.22	0.74	0.26	-0.19	0.16	-0.15	–
	P>|r|	0.393	0.100	0.128	0.019	0.979	0.357	0.002	0.227	0.366	0.459	0.496	–
	N	24	10	24	24	24	20	14	24	24	24	24	24

that the proportion of birds using the Everglades Region was relatively low following the drought in that region that preceded our study (see *Shifts in Regional Use* in chapter on *Movements*). Similar reports of such regional shifts have occurred during previous droughts. For example Takekawa and Beissinger (1989) reported that, during a 1985 drought, bird sightings in drought related habitats were increasing while numbers while water levels were decreasing in WCA-3A. They also reported a large concentration of birds in the Loxahatchee Slough Region during this drought (West Palm Beach Water Catchment Area). Our hydrologic analysis shows that during the 1985 drought, most of the Water Conservation Areas of the Everglades were effected; but the Loxahatchee Slough had remained relatively wet during that period. Similarly, during a more widespread drought in 1981, (Beissinger and Takekawa 1983) reported birds were heavily using "drought-related" habitats including lakes Kissimmee and Tohopekaliga. Our analysis showed that, particularly Lake Tohopekaliga, was relatively wet compared to other habitats during that drought.

Although our data on the monthly probability of movement did not indicate an effect of water levels, the levels during our study were relatively high. We did however, observe two instances where relatively low water levels were followed by subsequent dispersal of birds from that area. During 1993, water levels at Lake Okeechobee (Fig. 8-18) and the Upper St. Johns Marsh (Fig. 8-19) were at their lowest levels during this study. Although neither of these areas dried out to ground level, in both of these cases birds dispersed from these areas during the period of low water levels.

Our analyses of monthly movement probabilities did not indicate an effect of water levels and reported relationships between numbers of kites and water levels appear inconsistent. In addition to our analysis, Bennetts et al. (1994) reported relatively poor correlations between numbers of kites counted in WCAs 1 and 2A during the annual survey and water levels for those areas; however, a weak correlation was observed for WCA-3A. In contrast, Sykes (1983b) reported stronger correlations between kite numbers and water levels at Lake Okeechobee and WCA3A (for a shorter subset of the data reported by Bennetts et al. [1994]). Similarly Bennetts et al. (1995) found a relatively strong correlation between the number of kites counted and water levels in the Upper St. Johns marsh during their study and a previous study by B. Toland (Unpubl. data). The inconsistency of finding an effect of water levels probably should not be surprising because most years (including all during this study) are not drought years and there is considerable movement of kites that does not appear to be directly associated with water levels. This would tend to swamp out effects that might otherwise be observed. Based on an accumulation of evidence both quatitative and anecdotal, we believe that there is little doubt that Snail Kites move in response to low water conditions (i.e., droughts); however, they also move considerably even in the absence of droughts. Thus, we believe that more attention should proabably be paid to where they move, rather than if they move.

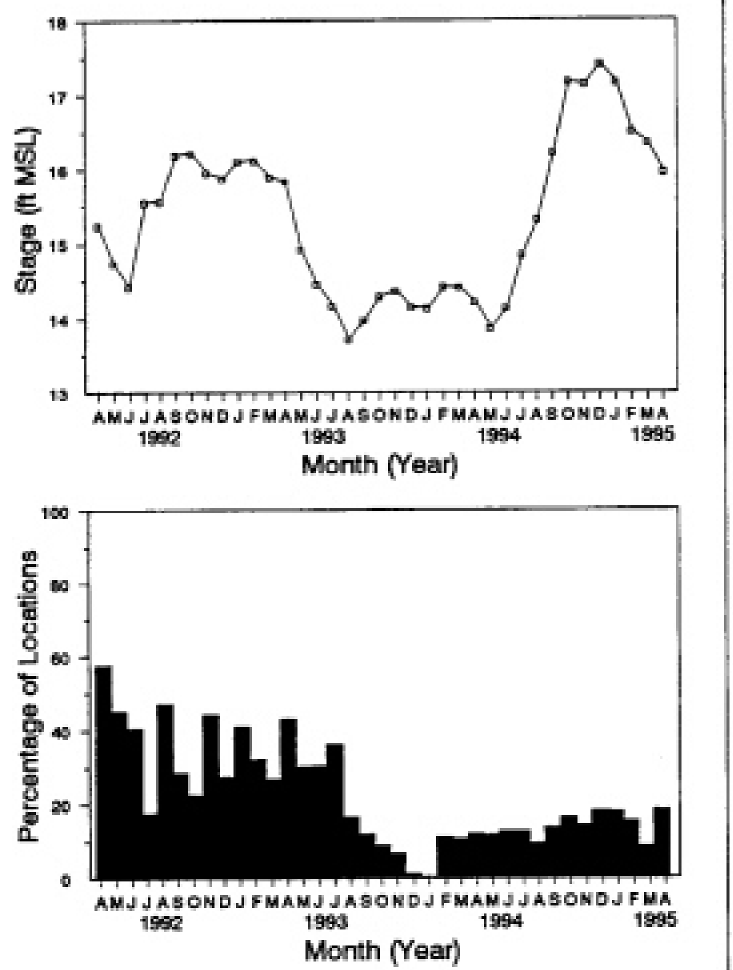


Figure 8-18. Average monthly water levels (Stage, ft MSL) at Lake Okeechobee (top) and the percentage of locations of radio-transmittered Snail Kites that were in the Okeechobee Region each month during this study (bottom).

Our hypothesis provides not only a mechanism for kites to survive periodic drought, but simultaneously provides a mechanism for long-term maintenance of the habitat (e.g., vegetation communities). Previous recommendations for the management of Snail Kites have emphasized the need for continuous flooding of habitats (e.g., Howell 1932, Bent 1937, Steiglitz 1965, Steiglitz and Thompson 1967, Beissinger 1983a, 1988). A conflicting concern is that continuous flooding without periodic drying results in a loss of tree islands and other woody vegetation used by Snail Kites for nesting, perching, and roosting (U.S.D.I. 1972, McPherson 1973, Worth 1983, Alexander and Crook 1984, Bennetts

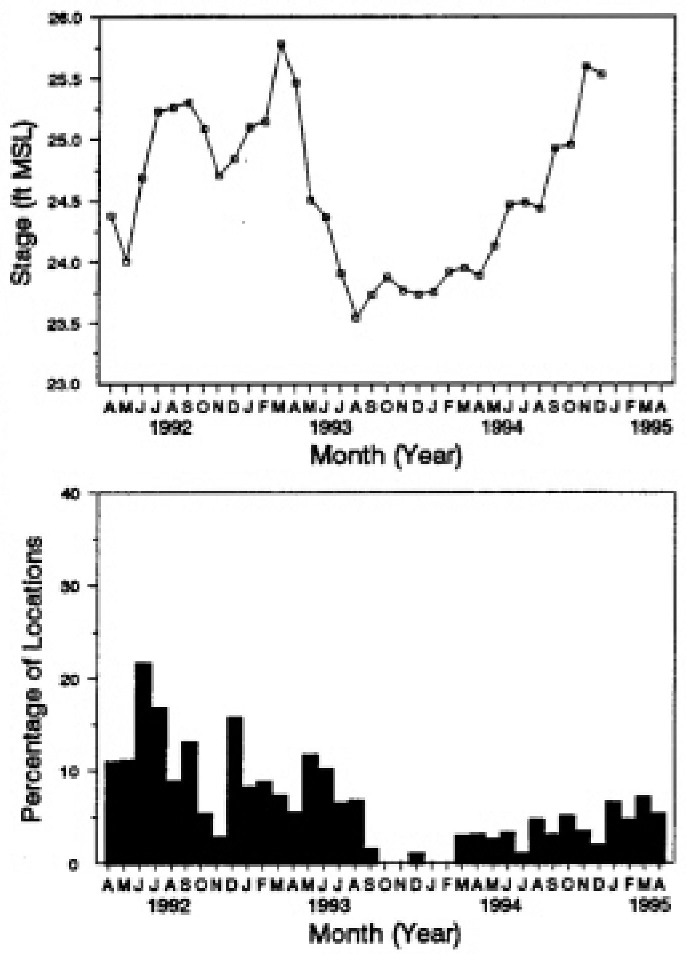


Figure 8-19. Average monthly water levels (Stage, ft MSL) at the Upper St. Johns Marsh (Blue Cypress Water Management Area (top) and the percentage of locations of radio-transmittered Snail Kites that were in the Upper St. Johns Region each month during this study (bottom).

et al 1994), as well as foraging habitat (e.g., wet prairies)(Pesnell and Brown 1979). Under our hypothesis, Snail Kite populations can persist (i.e., are buffered from catastrophic events) when periodic local drying events occur by moving to other habitats within the network that are not experiencing a local drying event.

PROTECTION OF HABITAT

Sykes (1983a) suggested that the loss of habitat has been the single most important factor responsible for decline of Snail Kites in Florida and further suggested that scattered areas of natural habitats throughout their historic range be preserved to reduce the impacts of drought conditions on populations. Takekawa and Beissinger (1989) also suggested that designated critical habitat lacked sufficient "drought-related" habitat components and that as many as possible of these areas must be preserved. We strongly agree with these suggestions, except that we believe that the importance of these habitats is not limited to drought years. As we have outline above, we believe that it is the extent of available habitat throughout a vast network that enables kites to persist. Consequently, we believe that the protection of only the currently designated critical habitat would be insufficient to maintain viable populations of Snail Kites over the long term. We have hypothesized, and anecdotal evidence strongly supports, that a key to the long term survival of Snail Kites is to have an extensive network of habitats, (including peripheral habitats), that enable kites to have some areas available (i.e., refugia) when the inevitable and periodic fluctuations in the quality of other habitats occur. Although we have some disagreement with previous authors about the specifics of how these habitats are used, the need to preserve an extensive network of peripheral habitats has been consistently suggested by biologists who have worked on this species (e.g., Stieglitz and Thompson 1967, Sykes 1983a, Beissinger and Takekawa 1983, Takekawa and Beissinger 1989, Bennetts et al. 1994).

Our concern about the spatial extent of the habitat network is not focused merely on the amount of wetland acreage available, although this is important. Rather, in order for the habitat network to function as a buffer for local events (e.g., drying events) that might otherwise be catastrophic, it is necessary that the habitats within the network have some asynchrony of these potentially devastating processes. If all habitats experienced drying events at the same time, there would be no potential to escape the demographic effects by moving to an alternative habitat (i.e., there would be no alternative habitats). The currently designated critical habitat is all located within the Everglades and Lake Okeechobee. We have shown (Table 8- 3) that drying events in these areas are all very highly correlated. The protection of additional areas that might be less correlated with the Everglades or Lake Okeechobee (e.g., the Kissimmee Chain-of-Lakes, Upper St. Johns River Basin, Loxahatchee Slough, and areas throughout the southwestern portions of the state) are therefore essential to the functioning network of habitats. The protection of peripheral areas to designated critical habitat as drought refugia was the major theme of a recent paper by Takekawa and Beissinger (1989); although we believe that the importance of these habitats extends beyond drought refugia.

The effects of habitat fragmentation on bird populations has received considerable focus in recent years (reviewed by Wiens 1989). Although our data show that Snail Kites are particularly mobile and have the ability to effectively use a relatively fragmented environment, there are still concerns of increasing fragmentation. For example, our data show that movements tend to occur more frequently in short increments. Consequently, small isolated habitats probably are less likely to be used by Snail Kites. Consequently, the protection of habitats peripheral to currently designated critical habitat should also be of ample size (habitats sufficient to support more than a handful of kites would probably require several thousand acres), or at least include several clusters of suitable smaller habitats in proximity, to reduce isolation effects.

It is also important to recognize that the quality of a given habitat is dependent on more than just having water at the time of a drought (e.g., apple snail populations, vegetation, size). Consequently, flooding an area when a drought occurs does not render it as suitable habitat. Suitable habitat is a result of current and past hydrology, vegetation, and apple snail populations. Snail Kite habitat characteristics have been extensively studied and were reviewed by Bennetts et al. (1994) and Sykes et al. (1995).

We also wish to make clear that our hypothesis about the habitat network does **not** imply that as peripheral wetlands are drained or degraded that Snail Kites will simply move elsewhere. Rather, it implies that having a vast network of habitat available is needed to ensure long-term survival of this species.

Habitat Quality, Nutrients, and Exotic Plant Invasions**–** Undoubtedly, the quality of habitat for Snail Kites is strongly influenced by both quantity and quality of water. Quantity of water was discussed in detail above. Although a lack of research has precluded strong inferences, it has been previously suggested that increased nutrient loadings may have a detrimental effect on apple snails (Davis 1994) and Snail Kites (Bennetts et al. 1994). Davis (1994) suggested that conversion of marshes to cattail may result in declines in apple snails. Additionally, Darby et al. (1996c) found low abundance of apple snails associated with substrates containing high flocculent debris. Such a substrate often occurs in cattail. Plant species that respond to nutrients (e.g., sawgrass, cattail, or water hyacinth) also may increase in biomass choking out the more open water used by kites for foraging. The availability of apple snails to kites requires sufficiently open water to enable visual detection. (Stieglitz 1965, Stieglitz and Thompson 1967, Sykes 1987c, Bennetts et al. 1988, 1994). Consequently, we can easily predict the deterioration of habitats for Snail Kites in which the open areas have been choked out by invading plants. In contrast, the relationships of apple snail populations to plant community changes is virtually unknown and research in this area is sorely needed.

Because Snail Kites commonly nest in *Melaleuca* (Bennetts and Kitchens 1995), a potential question that has been raised is whether or not the control of *Melaleuca* will be detrimental to Snail Kites. There has been no conclusive testing of whether nest sites are limiting for nesting kites; however, we believe that most biologists who have worked with Snail Kites would agree that food is probably a more important factor than nest site availability on Snail Kite reproduction. We also believe that the long term effects of *Melaleuca* on the foraging habitat (i.e., overtaking of open area foraging habitats) are more detrimental than the short-term benefits from the use of *Melaleuca* as a nesting substrate. Consequently, we believe that *Melaleuca* control is warranted, but may entail some short-term effects on nesting distribution. It is our unsubstantiated belief that the complete removal of *Melaleuca* will result in a shift in the distribution of some nesting activity (e.g., in WCA-2B). Regardless of the long-term detrimental impacts to the habitat, *Melaleuca* is a sturdy, well-protected nest substrate which is highly selected by Snail Kites (Bennetts et al. 1988) when it is present in light to moderate volumes.

Anthropogenic Influences**–** We believe that the "natural" system (i.e., prior to "water management") probably provided the best solution to maintaining Snail Kites as part of the Central and South Florida Ecosystem. However, the "natural" system no longer exists and we are constrained to do the best we can given the current and potential state of the system. In addition to long-term water management (i.e., schedules), there are often situations in which short-term drying events are prescribed. In recent years such events have been prescribed for reasons such as aquatic weed control, fishery restoration, agricultural needs, and habitat restoration.

Several factors should be considered when evaluating the potential of a management-induced drying event. In additional to the "drought" factors discussed above (e.g., intensity, spatial extent, and temporal extent), the hydrologic status of the full habitat network should be considered. For example, if drought conditions are occurring in other regions of kite habitat then a management induced drying event should be avoided or at least postponed. a situation in which this type of conflict is likely to occur is for agricultural needs. When there is a shortage of water for agriculture, it is likely to be during a drought when there is a general shortage of water in the system.

The timing of a management induced drying event should also be considered. For example, if water levels need to be reduced in an area used by nesting kites, then it should initiated prior to the nesting season so that birds are induced to seek alternative nesting locations, rather than having their nests destroyed as a result of the drying event. Waiting until after the nesting season is also an alternative; however, obtaining desired water levels may be problematic given that the end of the nesting season usually coincides with the onset of the rainy season.

South Florida Ecosystem Restoration and Snail Kites

Early assessments of South Florida ecosystem restoration suggested that serious conflicts existed between alternatives that were being considered at that time and the recovery of Snail Kites. We believe that the current directions and goals of the restoration process are not in conflict and will even improve the recovery of Snail Kites in Florida. This conclusion, however, does not come without caveats. Previous assessments expressed concern primarily about increased frequency of drying events in WCA-3A as a result of more water being distributed east of the L-67 levee. It was further suggested that a pool of water needed to be maintained in southern WCA-3A in order to serve as drought refugia in this region. We agree entirely with these early assessments that areas of long hydroperiod (e.g., >90%) must be a part of this ecosystem if viable populations Snail Kites are to persist. However, we strongly disagree that the solution to maintaining long hydroperiod areas are best achieved by maintaining an impounded pool in southern WCA-3A. In fact, we believe that maintaining these deep (e.g., >1.3-1.5 m) impounded pools will result in nesting habitat degradation due to a loss of woody vegetation (Gunderson et al. 1988, Gunderson and Loftus 1993) and degradation of foraging habitat due to a loss of wet prairie communities (Gunderson 1994). In the historic system increasing volumes of water undoubtedly resulted in more lateral expansion than increased depth compared to the current system (because of an absence of constraining levees). Consequently, long hydroperiods were maintained with less of the "bathtub" effect than currently exists. We believe that goals such as restoring more of the spatial extent and re-establishing the hydrologic integrity (e.g., sheet flows)(Weaver et al. 1993, South Florida Ecosystem Working Group 1994) will help maintain the long hydroperiod components of these wetlands with less habitat degradation that exists under the current system.

The senior author of this report (REB) previously suggested that a substantial lag time (e.g., 10 years) might be required for Snail Kites to re-establish themselves in areas where long hydroperiods were restored (Bennetts et al. 1988). This suggestion was based on the time it took for substantial numbers of Snail Kites to be reported in the WCAs after completion of the impounding levees, which was confounded by a series of particularly dry years. Data from this study (e.g., use of the North East Shark River Slough and Big Cypress National Preserve) have indicated that Snail Kites can rapidly respond suitable habitats that are large enough or in proximity to other well-used habitats. Consequently, the spatial redistribution of hydrologic regimes (e.g., shifting of water into historic flow-ways) will probably not have a major impact, provided that suitable long hydroperiod areas are maintained as part of this ecosystem. The halting and reversing of exotic plant an animal invasions have also been identified as part of the South Florida Ecosystem recovery efforts (South Florida Ecosystem Working Group 1994). The effects of exotic plants on Snail Kite habitat have been previously discussed (see *Snail Habitat Quality, Nutrients, and Exotic Plant Invasions*). We believe that achieving these recovery goals will be beneficial and probably necessary for the long-term maintenance of Snail Kite habitat.

The reduction of water and airborne nutrients and contaminants also has been identified as a goal of the recovery efforts. We have previously discussed nutrients (see *Snail Habitat Quality, Nutrients, and Exotic Plant Invasions*), but contaminants present another problem. Mercury is one of the most widely known contaminant problems in Central and South Florida. Some investigation has been conducted on mercury levels in apple snails (Eisemann et al., in press), and found relatively low levels ($\bar{x} = 0.063$, n =62) compared to other species in the region (Eisemann et al., in press). However, the bioaccumulation of these low levels in Snail Kites has not been investigated.

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APPENDICES

Appendix 3-1. *Primary notation, symbols, and abbreviations used throughout this report.*

Symbols for Parameters

Symbol	Name	Definition within the context of this report
α	alpha	Type I error rate (i.e., probability of falsely rejecting a null hypothesis (H_o) that is true).
β	beta	Type II error rate (i.e., probability of failing to rejecting a null hypothesis (H_o) that is false).
θ	theta	Used as a "wildcard" term for any parameter
Φ	phi	The probability of surviving from time t to $t + 1$, conditional upon the animal being alive at time t.
p	p	The probability of resighting an animal, conditional upon that animal being alive and in the study area.
ψ	psi	The probability of being in a different location between times t and $t + 1$, conditional upon the animal being alive at both times and its location known.

Subscripts and Descriptive Symbols

i, j, t	Used to denote an individual animal, time, or location of a parameter. For example, Φ_t might denote survival at tme t.
ˆ	A hat above a symbol denotes that the symbol represents an estimate of the parameter, rather than the true parameter. For example, $\hat{\Phi}$ denotes an estimate of survival.
·	A dot used as a subscript for a parameter denotes that the parameter is constant over the range of potential effects of the model (e.g., time). This does not imply that there are no differences associated with that effect, but rather, that separate parameter estimation for that effect is not supportable with our data.

Abbreviations

AIC	Akaike's Information Criteria
CJS	Cormack-Jolly-Seber
DEV	Deviance
GOF	Goodness-of-fit
LRT	Likelihood ratio test
MLE	Maximum Likelihood Estimator
MLS	Mean Life Span
MSL	Mean Sea Level
np	The number of estimable parameters in a model.
SY	Study Year (15 April of SY to 14 April of SY + 1)

Appendix 3-1. Cont.

Abbreviations for Wetlands

BICY	Big Cypress National Preserve
ENP	Everglades National Park
ETOHO	East Lake Tohopekaliga
HOLEY	Holey Land Wildlife Management Area
KISS	Lake Kissimmee
LOX	A.R.M. Loxahatchee National Wildlife Refuge (WCA-1)
OKEE	Lake Okeechobee
NESRS	North East Shark River Slough (East Everglades)
SJM	St. Johns Marsh (Blue Cypress Water Management Area and Blue Cypress Marsh Water Conservation Area)
TOHO	Lake Tohopekaliga
WCA1	Water Conservation Area 1 (A.R.M. Loxahatchee National Wildlife Refuge)
WCA2A	Water Conservation Area 2A
WCA2B	Water Conservation Area 2B
WCA3A	Water Conservation Area 3A
WCA3B	Water Conservation Area 3B
WPB	City of West Palm Beach Water Catchment Area (Lake Park Reservoir)(part of the Loxahatchee Slough)
PERIF	Peripheral Wetlands (misc. wetlands peripheral to one listed above)

Abbreviations for Regions

EVER	Everglades and Big Cypress (includes WCAs, ENP, BICY, LOX, HOLEY, and the C111 Basin)
OKEE	Okeechobee (includes OKEE)
LOXSL	Loxahatchee Slough (includes WPB and surrounding City of West Palm Beach properties, Corbitt Wildlife Management Area, Pal-Mar Water Control District, and wetlands within Pratt-Whitney properties)
USJ	Upper St. Johns River Basin (includes SJM, St. Johns Reservoir, and scattered privately owned wetlands within the basin)
KISS	Kissimmee Chain-of-Lakes (Includes KISS, TOHO, ETOHO, and other Lakes within the Kissimmee Chain.
PERI	Peripheral (Includes scattered remnants of natural wetlands outside of the primary drainage basins listed above. Also includes scattered man-made or man-altered wetlands [e.g., canals, roadside ditches, agricultural retention ponds, etc.).

Appendix 3-2. *Formula for the Kaplan Meier estimator of survival and its corresponding estimate of variance (Kaplan and Meier 1958, Cox and Oakes 1984, Pollock et al. 1989, White and Garrott 1990). All estimates were derived using a modified (for our specific data)version of the SAS code provided by White and Garrott (1990).*

The Kaplan-Meier estimator is an extension of a binomial estimator such that the probability of surviving from time $j - 1$ *to* j is estimated as:

$$\hat{\Phi}_j = \frac{r_j - d_j}{r_j}$$

where r_j is the number of animals at risk of dying in the interval between j and $j - 1$ (i.e., the number alive at the start of the inteval) and d_j is the number of animals that died during the interval. Thus, the probabilty of surviving over all intervals is estimated as:

$$\hat{\Phi}_j = \prod_{j=1}^{n_0} \frac{r_j - d_j}{r_j}$$

Cox and Oakes (1984) provide an estimate for the variance of $\hat{\Phi}_j$ as:

$$Var(\hat{\Phi}_j) = \frac{(\hat{\Phi}_j)^2(1 - \hat{\Phi}_j)}{r_j}$$

and an approximate (1 - α) confidence interval is constructed as:

$$\hat{\Phi} \pm z_{\alpha}\sqrt{Var(\hat{\Phi})}$$

where $z_{\alpha} = 1.96$ for $\alpha = 0.05$ (White and Garrott 1990).

Appendix 3-3. Formula for three versions of the log-rank test (Cox and Oakes 1984). All test statistics were derived using a modified (for our specific data) version of the SAS code provided by White and Garrott (1990).

Let d_{1j} and d_{2j} denote the number of deaths and r_{1j} and r_{2j} denote the number of animals at risk from samples 1 and 2 (i.e., comparison group), respectively at time *j*. The first variation is such that the expected value and variance of d_{1j} are given as:

$$E(d_{1j}) = \frac{d_j r_{1j}}{r_j}$$

and

$$var_1(d_{1j}) = \frac{d_j r_{1j} r_{2j}(r_j - d_j)}{r^2(r_j - 1)}$$

(Pollock et al. 1989a). The log-rank test is then derived by combining the results from each contingency table as an approximate chi-square test statistic with 1 degree of freedom such that:

$$\chi^2 = \frac{\left[\sum_{j=1}^{k} d_{1j} - \sum_{j=1}^{k} E(d_{1j})\right]^2}{\sum_{j=1}^{k} var_1(d_{1j})}$$

The second variation of the log-rank test is estimated as above except that the variance of d_{1j} is estimated as:

$$var_2(d_{1j}) = \frac{r_1 r_2 d_j}{r_j^2}$$

This test is slightly more conservative (i.e., less likely to make a Type I error, but has lower power)(Cox and Oakes 1984, Pollock et al. 1989, White and Garrott 1990).

The third variation variation estimates the variance of d_{ij} as:

$$var_3(d_{1j}) = \left[\frac{1}{\sum_{j=1}^{k} \frac{d_j r_{1j}}{r_j}} + \frac{1}{\sum_{j=1}^{k} \frac{d_j r_{2j}}{r_j}}\right]^{-1}$$

and is even more conservative (Cox and Oakes 1984, Pollock et al. 1989, White and Garrott 1990). The SAS program described by White and Garrott (1990) to compute the Kaplan-Meier estimates also computes each of these log-rank test statistics.

Appendix 3-4*. Binomial estimator used for estimating movement probabilities and their corresponding variance.*

Our estimate of movement probability was based on a binomial distribution such that the probability of being at a different location between times t and $t + 1$ ($\hat{\psi}_t$) is:

$$\hat{\psi} = \frac{m_t}{n}$$

where m_t is the number of animals that were in a different location (i.e., wetland) between times t and $t + 1$, and n is the number of animals alive and their location known at both times. The variance of $\hat{\psi}_t$ is estimated as:

$$Var(\hat{\psi}) = \frac{\hat{\psi}\,(1 - \hat{\psi})}{n}$$

and a 95% confidence interval is estimated as:

$$\hat{\psi} \pm z_{\alpha}\sqrt{Var(\hat{\psi})}$$

where $z_{0.05} = 1.96$ for $\alpha = 0.05$ (White and Garrott 1990).

Appendix 4-1. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), standard error (SE) of the estimate, and 95% confidence intervals for survival estimates of adult and juvenile Snail Kites during each study year (SY)(April 15 to April 14). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate of either age class occurred. The number of animals at risk of dying (r_j) changes as a result of animals having been captured, having been censored, and having died. We have not shown all changes in r_j because of the high frequency of such changes (i.e., 203 such changes for this appendix).*

Appendix 4-1a. Estimates for SY 1992.

	Adults				Juveniles			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/92	1.000	11	--	--	1.000	4	--	--
06/12/92	1.000	36	--	--	0.960	25	0.039	0.883 - 1.000
07/07/92	1.000	42	--	--	0.916	22	0.057	0.805 - 1.000
07/20/92	1.000	41	--	--	0.871	20	0.070	0.733 - 1.000
07/25/92	1.000	40	--	--	0.825	19	0.080	0.668 - 0.981
04/11/93	0.962	26	0.038	0.888-1.000	0.825	12	0.080	0.668 - 0.981
04/14/93	0.962	25	0.038	0.888-1.000	0.825	12	0.080	0.668 - 0.981

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this age class ranged from 11-43 ($\bar{x}$=27.8) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this age class ranged from 4-25 ($\bar{x}$=16.4) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-1b. Estimates for SY 1993.

	Adults				Juveniles			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/93	1.000	56	--	--	1.000	14	--	--
04/28/93	1.000	59	--	--	0.929	14	0.069	0.794 - 1.000
05/04/93	1.000	66	--	--	0.867	15	0.088	0.695 - 1.000
08/07/93	0.984	64	0.016	0.954 - 1.000	0.867	26	0.088	0.695 - 1.000
11/13/93	0.963	47	0.026	0.913 - 1.000	0.867	20	0.088	0.695 - 1.000
12/18/93	0.934	33	0.038	0.860 - 1.000	0.867	12	0.088	0.695 - 1.000
01/05/94	0.903	30	0.048	0.809 - 0.997	0.867	11	0.088	0.695 - 1.000
02/10/94	0.858	20	0.063	0.734 - 0.982	0.867	9	0.088	0.695 - 1.000
04/14/94	0.858	16	0.063	0.734 - 0.982	0.867	8	0.088	0.695 - 1.000

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this age class ranged from 16-76 ($\bar{x}$=53.0) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this age class ranged from 8-30 ($\bar{x}$=18.9) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-1c. Estimates for SY 1994.

	Adults				Juveniles			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/94	1.000	54	--	--	1.000	4	--	--
05/15/94	1.000	74	--	--	0.941	17	0.057	0.829 - 1.000
05/18/94	1.000	74	--	--	0.882	16	0.078	0.729 - 1.000
05/21/94	1.000	74	--	--	0.833	18	0.088	0.661 - 1.000
05/21/94	1.000	75	--	--	0.789	19	0.094	0.606 - 0.973
06/08/94	1.000	76	--	--	0.750	20	0.097	0.560 - 0.940
06/09/94	1.000	76	--	--	0.711	19	0.099	0.516 - 0.905
06/14/94	1.000	76	--	--	0.687	30	0.099	0.493 - 0.881
06/17/94	0.987	78	0.013	0.962 - 1.000	0.687	31	0.099	0.493 - 0.881
06/21/94	0.987	75	0.013	0.962 - 1.000	0.643	31	0.097	0.452 - 0.833
06/29/94	0.987	74	0.013	0.962 - 1.000	0.598	29	0.096	0.411 - 0.786
08/13/94	0.987	72	0.013	0.962 - 1.000	0.548	23	0.094	0.364 - 0.732
09/15/94	0.987	71	0.013	0.962 - 1.000	0.523	22	0.093	0.341 - 0.705
10/11/94	0.972	66	0.019	0.934 - 1.000	0.523	20	0.093	0.341 - 0.705
01/01/95	0.972	58	0.019	0.934 - 1.000	0.496	19	0.092	0.316 - 0.676
01/21/95	0.972	55	0.019	0.934 - 1.000	0.468	18	0.091	0.290 - 0.646
01/25/95	0.955	55	0.026	0.904 - 1.000	0.439	16	0.090	0.263 - 0.615
01/28/95	0.937	54	0.031	0.876 - 0.997	0.439	15	0.090	0.263 - 0.615
01/28/95	0.919	53	0.035	0.851 - 0.988	0.439	15	0.090	0.263 - 0.615
02/15/95	0.883	51	0.042	0.801 - 0.965	0.439	15	0.090	0.263 - 0.615
04/14/95	0.883	48	0.042	0.801 - 0.965	0.439	15	0.090	0.263 - 0.615

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this age class ranged from 48-78 ($\bar{x}$=66.6) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this age class ranged from 4-31 ($\bar{x}$=17.7) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-2. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), standard error (SE) of the estimate, and 95% confidence intervals for survival estimates of adult male and female Snail Kites during each study year (SY)(April 15 to April 14). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate of either sex class occurred. The number of animals at risk of dying (r_j) changes as a result of animals having been captured, having been censored, and having died. We have not shown all changes in r_j because of the high frequency of such changes (i.e., 137 such changes for this appendix).*

Appendix 4-2a. Estimates for SY 1992.

	Female				Male			
Date	$\hat{\Phi}$	r_j^1	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j^2	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/92	1.000	5	--	--	1.000	6	--	--
04/11/93	1.000	14	--	--	0.917	12	0.080	0.760 - 1.000
04/14/93	1.000	14	--	--	0.917	11	0.080	0.760 - 1.000

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this sex class ranged from 5-22 ($\bar{x}$=15.0) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this sex class ranged from 6-21 ($\bar{x}$=13.7) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-2b. Estimates for SY 1993.

	Female				Male			
Date	$\hat{\Phi}$	r_j^1	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j^2	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/93	1.000	29	--	--	1.000	27	--	--
08/07/93	0.969	32	0.031	0.908-1.000	1.000	32	--	--
11/13/93	0.928	24	0.049	0.832-1.000	1.000	23	--	--
12/18/93	0.866	15	0.075	0.719-1.000	1.000	18	--	--
01/05/94	0.866	13	0.075	0.719-1.000	0.941	17	0.057	0.829-1.000
02/10/94	0.866	11	0.075	0.719-1.000	0.837	9	0.111	0.619-1.000
04/14/94	0.866	10	0.075	0.719-1.000	0.837	6	0.111	0.619-1.000

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this sex class ranged from 10-40 ($\bar{x}$=26.9) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this sex class ranged from 6-36 ($\bar{x}$=24.8) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-2c. Estimates for SY 1994.

	Female				Male			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/94	1.000	27	--	--	1.000	19	--	–
10/11/94	1.000	30	--	--	0.967	30	0.033	0.902-1.000
01/25/95	0.962	26	0.038	0.888-1.000	0.967	26	0.033	0.902-1.000
01/28/95	0.962	25	0.038	0.888-1.000	0.929	26	0.048	0.835-1.000
01/29/95	0.962	26	0.038	0.888-1.000	0.892	25	0.059	0.777-1.000
02/15/95	0.962	25	0.038	0.888-1.000	0.815	23	0.075	0.668-0.962
04/14/95	0.962	25	0.038	0.888-1.000	0.815	21	0.075	0.668-0.962

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this sex class ranged from 25-38 ($\bar{x}$=31.1) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this sex class ranged from 19-32 ($\bar{x}$=27.7) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-3. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), and standard error (SE) of the estimate for survival of adult Snail Kites captured from each region during each study year (SY)(April 15 to April 14). Regions are Everglades (EVER), Lake Okeechobee (OKEE), Kissimmee Chain-of-Lakes (KISS), Upper St. Johns River (USJ), and Loxahatchee Slough (LOXSL). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate occurred. The number of animals at risk of dying (r_j) changes as a result of animals having been captured, having been censored, and having died.. We have not shown all changes in r_j because of the high frequency of such changes. Confidence intervals are not shown for clarity of presentation (i.e., in order to fit all estimates in a single table); however, 95% confidence intervals can be estimated as $\hat{\Phi} \pm 1.96\,SE(\hat{\Phi})$.*

Appendix 4-3a. Estimates for SY 1992.

	EVER			OKEE			KISS			USJ			LOXSL		
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[3]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[4]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[5]	SE ($\hat{\Phi}$)
04/15/92	1.000	3	--	1.000	6	--	1.000	1	--	1.000	1	--	1.000	0	--
04/11/93	1.000	13	--	0.950	20	0.049	1.000	11	--	1.000	7	--	1.000	6	--
04/14/93	1.000	14	--	0.950	19	0.049	1.000	12	--	1.000	7	--	1.000	6	--

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 2-14 ($\bar{x}$=6.4) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 6-20 ($\bar{x}$=14.5) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-12 ($\bar{x}$=6.7) during this study year.*

[4] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-7 ($\bar{x}$=4.9) during this study year.*

[5] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-7 ($\bar{x}$=2.6) during this study year.*

Appendix 4-3b. Estimates for SY 1993.

	EVER			OKEE			KISS			USJ			LOXSL		
Date	$\hat{\phi}$	r_j[1]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[2]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[3]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[4]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[5]	SE ($\hat{\phi}$)
04/15/93	1.000	14	--	1.000	18	--	1.000	11	--	1.000	7	--	1.000	6	--
08/07/93	1.000	15	--	0.952	21	0.046	1.000	15	--	1.000	7	--	1.000	7	--
11/13/93	0.923	13	0.074	0.952	14	0.046	1.000	12	--	1.000	4	--	1.000	6	--
12/18/93	0.923	8	0.074	0.952	9	0.046	1.000	10	--	1.000	2	--	0.833	6	0.152
01/05/94	0.923	8	0.074	0.952	8	0.046	0.875	8	0.117	1.000	2	--	0.833	6	0.152
02/10/94	0.923	5	0.074	0.952	3	0.046	0.750	7	0.153	1.000	1	--	0.833	4	0.152
04/14/94	0.923	21	0.074	0.952	5	0.046	0.750	8	0.153	1.000	3	--	0.833	3	0.152

[1] *Infrequent changes in* $\hat{\phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 5-21 (*$\bar{x}$*=12.2) during this study year.*

[2] *Infrequent changes in* $\hat{\phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 3-27 (*$\bar{x}$*=13.8) during this study year.*

[3] *Infrequent changes in* $\hat{\phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 5-16 (*$\bar{x}$*=11.6) during this study year.*

[4] *Infrequent changes in* $\hat{\phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 1-10 (*$\bar{x}$*=4.8) during this study year.*

[5] *Infrequent changes in* $\hat{\phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 3-7 (*$\bar{x}$*=5.1) during this study year.*

Appendix 4-3c. Estimates for SY 1994.

	EVER			OKEE			KISS			USJ			LOXSL		
Date	$\hat{\phi}$	r_j[1]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[2]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[3]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[4]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[5]	SE ($\hat{\phi}$)
04/15/94	1.000	25	--	1.000	5	--	1.000	10	--	1.000	3	--	1.000	3	--
10/11/94	1.000	26	--	1.000	12	--	0.947	19	0.051	1.000	3	--	1.000	1	--
01/25/95	1.000	25	--	1.000	12	--	0.880	14	0.081	1.000	2	--	1.000	1	--
01/28/95	1.000	25	--	0.909	11	0.087	0.880	14	0.081	1.000	2	--	1.000	1	--
01/29/95	1.000	25	--	0.909	11	0.087	0.812	13	0.099	1.000	2	--	1.000	1	--
02/15/95	1.000	25	--	0.808	9	0.123	0.744	12	0.111	1.000	2	--	1.000	1	--
04/14/95	1.000	25	--	0.808	8	0.123	0.744	12	0.111	1.000	2	--	1.000	0	--

[1] *Infrequent changes in $\hat{\phi}$ may result in poor representation of r_j. r_j for this region ranged from 25-34 ($\bar{x}$=28.2) during this study year.*

[2] *Infrequent changes in $\hat{\phi}$ may result in poor representation of r_j. r_j for this region ranged from 5-12 ($\bar{x}$=10.5) during this study year.*

[3] *Infrequent changes in $\hat{\phi}$ may result in poor representation of r_j. r_j for this region ranged from 10-19 ($\bar{x}$=15.5) during this study year.*

[4] *Infrequent changes in $\hat{\phi}$ may result in poor representation of r_j. r_j for this region ranged from 2-3 ($\bar{x}$=2.5) during this study year.*

[5] *Infrequent changes in $\hat{\phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-3 ($\bar{x}$=1.8) during this study year.*

Appendix 4-4. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), and standard error (SE) of the estimate for survival of juvenile Snail Kites fledged from each region during each study year (SY)(April 15 to April 14). Regions are Everglades (EVER), Lake Okeechobee (OKEE), Kissimmee Chain-of-Lakes (KISS), Upper St. Johns River (USJ), and Loxahatchee Slough (LOXSL). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate occurred. The number of animals at risk of dying (r_j) changes as a result of animals having been captured, having been censored, and having died.. We have not shown all changes in r_j because of the high frequency of such changes. Confidence intervals are not shown for clarity of presentation (i.e., in order to fit all estimates in a single table); however, 95% confidence intervals can be estimated as $\hat{\Phi} \pm 1.96\ SE(\hat{\Phi})$.*

Appendix 4-4a. Estimates for SY 1992.

	EVER			OKEE			KISS			USJ			LOXSL		
Date	$\hat{\Phi}$	r_j^1	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^2	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^3	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^4	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j	SE ($\hat{\Phi}$)
04/15/92	1.000	1	--	1.000	2	--	1.000	1	--	1.000	2	--	--[5]	--[5]	--[5]
06/12/92	0.750	4	0.217	1.000	9	--	1.000	0	--	1.000	2	--	--[5]	--[5]	--[5]
07/07/92	0.750	3	0.217	1.000	9	--	0.833	6	0.152	1.000	4	--	--[5]	--[5]	--[5]
07/20/92	0.500	3	0.250	1.000	7	--	0.833	6	0.152	1.000	4	--	--[5]	--[5]	--[5]
07/25/92	0.500	3	0.250	1.000	7	--	0.833	5	0.152	0.750	4	0.217	--[5]	--[5]	--[5]
04/14/93	0.500	1	0.250	1.000	6	--	0.833	3	0.152	0.750	3	0.217	--[5]	--[5]	--[5]

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-4 ($\bar{x}$=2.7) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 2-10 ($\bar{x}$=7.0) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-6 ($\bar{x}$=3.6) during this study year.*

[4] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-5 ($\bar{x}$=2.5) during this study year.*

[5] *There were insufficient data to estimate survival in this region.*

Appendix 4-4b. Estimates for SY 1993.

	EVER			OKEE			KISS			USJ			LOXSL		
Date	$\hat{\phi}$	r_j[1]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[2]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[3]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[4]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j	SE ($\hat{\phi}$)
04/15/93	1.000	10	--	1.000	3	--	1.000	0	--	1.000	0	--	--[5]	--[5]	--[5]
04/28/93	0.900	10	0.095	1.000	3	--	1.000	0	--	1.000	0	--	--[5]	--[5]	--[5]
04/14/94	0.900	7	0.095	1.000	2	--	1.000	0	--	1.000	1	--	--[5]	--[5]	--[5]

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 7-12 ($\bar{x}$=10.4) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 2-10 ($\bar{x}$=4.9) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-4 ($\bar{x}$=2.1) during this study year.*

[4] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-5 ($\bar{x}$=3.5) during this study year.*

[5] *There were insufficient data to estimate survival in this region.*

Appendix 4-4c. Estimates for SY 1994.

	EVER			OKEE			KISS			USJ			LOXSL		
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[3]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j	SE ($\hat{\Phi}$)
04/15/94	1.000	4	--	1.000	0	--	1.000	0	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
05/15/94	0.923	13	0.074	1.000	2	--	1.000	2	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
05/18/94	0.846	12	0.100	1.000	2	--	1.000	2	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
05/21/94	0.846	11	0.100	0.500	2	0.354	1.000	4	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
05/25/94	0.781	13	0.112	0.500	1	0.354	1.000	4	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
06/08/94	0.716	12	0.120	0.500	3	0.354	1.000	4	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
06/09/94	0.716	11	0.120	0.500	3	0.354	0.750	4	0.217	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
06/14/94	0.671	16	0.120	0.500	3	0.354	0.750	10	0.217	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
06/23/94	0.671	18	0.120	0.500	3	0.354	0.583	9	0.198	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
06/29/94	0.597	18	0.118	0.500	3	0.354	0.583	7	0.198	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
07/27/94	0.559	16	0.116	0.500	1	0.354	0.583	6	0.198	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
08/13/94	0.522	15	0.114	0.500	1	0.354	0.583	6	0.198	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
09/15/94	0.485	14	0.112	0.500	1	0.354	0.583	6	0.198	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
01/01/95	0.485	13	0.112	0.500	1	0.354	0.467	5	0.190	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
01/21/95	0.485	13	0.112	0.500	1	0.354	0.350	4	0.174	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
01/25/95	0.485	13	0.112	0.500	1	0.354	0.175	2	0.151	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
04/14/95	0.485	13	0.112	0.500	1	0.354	0.175	2	0.151	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 4-18 ($\bar{x}$=12.2) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-3 ($\bar{x}$=1.5) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-10 ($\bar{x}$=4.4) during this study year.*

[4] *There were insufficient data to estimate survival in this region.*

Appendix 4-5. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), and standard error (SE) of the estimate for survival of adult Snail Kites present in each region during each study year (SY)(April 15 to April 14). Regions are Everglades (EVER), Lake Okeechobee (OKEE), Kissimmee Chain-of-Lakes (KISS), Upper St. Johns River (USJ), and peripheral habitats (PERI). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate occurred. The number of animals at risk of dying (r_j) changed as a result of animals having been captured, having moved to a different region, having been censored, and having died.. We have not shown all changes in r_j because of the high frequency of such changes. Confidence intervals are not shown for clarity of presentation (i.e., in order to fit all estimates in a single table); however, 95% confidence intervals can be estimated as $\hat{\Phi} \pm 1.96\ SE(\hat{\Phi})$.*

Appendix 4-5a. Estimates for SY 1992.

	EVER			OKEE			KISS			USJ			PERI		
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[3]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[4]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[5]	SE ($\hat{\Phi}$)
04/15/92	1.000	0	--	1.000	6	--	1.000	2	--	1.000	1	--	1.000	0	--
04/11/93	1.000	12	--	0.955	22	0.044	1.000	7	--	1.000	3	--	1.000	1	--
04/14/93	1.000	13	--	0.955	21	0.044	1.000	8	--	1.000	3	--	1.000	1	--

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-15 ($\bar{x}$=6.4) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-22 ($\bar{x}$=11.7) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-8 ($\bar{x}$=3.7) during this study year.*

[4] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-6 ($\bar{x}$=3.3) during this study year.*

[5] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-6 ($\bar{x}$=2.5) during this study year.*

Appendix 4-5b. Estimates for SY 1993.

	EVER			OKEE			KISS			USJ			PERI		
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j[3]	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j	SE ($\hat{\Phi}$)
04/15/93	1.000	13	--	1.000	20	--	1.000	7	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
08/07/93	1.000	30	--	0.933	15	0.064	1.000	6	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
12/18/93	1.000	14	--	0.933	0	0.064	1.000	6	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
01/05/94	1.000	15	--	0.933	0	0.064	0.800	5	0.179	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
01/19/94	0.857	7	0.132	0.933	0	0.064	0.800	5	0.179	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
04/14/94	0.857	20	0.132	0.933	2	0.064	0.800	10	0.179	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]

[1] *Infrequent changes in* $\hat{\Phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 4-30 (*$\bar{x}$*=13.9) during this study year.*

[2] *Infrequent changes in* $\hat{\Phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 0-26 (*$\bar{x}$*=10.9) during this study year.*

[3] *Infrequent changes in* $\hat{\Phi}$ *may result in poor representation of* r_j. r_j *for this region ranged from 3-13 (*$\bar{x}$*=7.2) during this study year.*

[4] *There were insufficient data to estimate survival in this region.*

Appendix 4-5c. Estimates for SY 1994.

	EVER			OKEE			KISS			USJ			PERI		
Date	$\hat{\Phi}$	r_j^1	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^2	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^3	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^4	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^5	SE ($\hat{\Phi}$)
04/15/94	1.000	23	--	1.000	2	--	1.000	9	--	1.000	2	--	1.000	0	--
10/19/94	1.000	23	--	0.923	13	0.074	1.000	8	--	1.000	3	--	1.000	1	--
11/13/94	0.950	20	0.049	0.923	11	0.074	1.000	7	--	1.000	3	--	1.000	0	--
02/02/95	0.950	23	0.049	0.923	11	0.074	0.750	4	0.217	0.667	3	0.272	1.000	0	--
02/07/95	0.950	26	0.049	0.923	11	0.074	0.750	4	0.217	0.667	3	0.272	0.500	2	0.354
02/23/95	0.950	24	0.049	0.659	7	0.166	0.750	1	0.217	0.667	2	0.272	0.500	2	0.354
04/14/95	0.950	21	0.049	0.659	6	0.166	0.750	4	0.217	0.667	2	0.272	0.500	1	0.354

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 16-35 ($\bar{x}$=24.7) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 2-13 ($\bar{x}$=9.0) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-16 ($\bar{x}$=8.1) during this study year.*

[4] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-3 ($\bar{x}$=2.3) during this study year.*

[5] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-7 ($\bar{x}$=2.7) during this study year.*

Appendix 4-6. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), and standard error (SE) of the estimate for survival of juvenile Snail Kites present in each region during each study year (SY)(April 15 to April 14). Regions are Everglades (EVER), Lake Okeechobee (OKEE), Kissimmee Chain-of-Lakes (KISS), Upper St. Johns River (USJ), and peripheral habitats (PERI). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate occurred. The number of animals at risk of dying (r_j) changed as a result of animals having been captured, having moved to a different region, having been censored, and having died.. We have not shown all changes in r_j because of the high frequency of such changes. Confidence intervals are not shown for clarity of presentation (i.e., in order to fit all estimates in a single table); however, 95% confidence intervals can be estimated as $\hat{\Phi} \pm 1.96\ SE(\hat{\Phi})$.*

Appendix 4-6a. Estimates for SY 1992.

	EVER			OKEE			KISS			USJ			PERI		
Date	$\hat{\Phi}$	r_j^1	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^2	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^3	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^4	SE ($\hat{\Phi}$)	$\hat{\Phi}$	r_j^5	SE ($\hat{\Phi}$)
04/15/92	1.000	1	--	1.000	2	--	1.000	0	--	1.000	1	--	1.000	0	--
07/07/92	1.000	2	--	1.000	7	--	1.000	4	--	1.000	5	--	0.000	1	--
07/20/92	0.750	4	0.217	1.000	7	--	1.000	5	--	1.000	3	--	0.000	0	--
07/25/92	0.750	4	0.217	1.000	7	--	1.000	4	--	0.667	3	0.272	0.000	0	--
04/14/93	0.750	2	0.217	1.000	6	--	1.000	1	--	0.667	0	0.272	0.000	0	--

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 1-4 ($\bar{x}$=2.8) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 2-9 ($\bar{x}$=6.8) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-5 ($\bar{x}$=2.7) during this study year.*

[4] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-5 ($\bar{x}$=2.1) during this study year.*

[5] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-2 ($\bar{x}$=0.6) during this study year.*

Appendix 4-6b. Estimates for SY 1993.

	EVER			OKEE			KISS			USJ			PERI		
Date	$\hat{\phi}$	r_j^1	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j^2	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j^3	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j	SE ($\hat{\phi}$)
04/15/93	1.000	7	--	1.000	3	--	1.000	0	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
04/28/93	0.800	5	0.179	1.000	2	--	1.000	0	--	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]
04/14/94	0.800	4	0.179	1.000	0	--	1.000	1	0.179	--[4]	--[4]	--[4]	--[4]	--[4]	--[4]

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 4-11 ($\bar{x}$=7.2) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-9 ($\bar{x}$=3.8) during this study year.*

[3] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-4 ($\bar{x}$=1.0) during this study year.*

[4] *There were insufficient data to estimate survival in this region.*

Appendix 4-6c. Estimates for SY 1994.

	EVER			OKEE			KISS			USJ			PERI		
Date	$\hat{\phi}$	r_j[1]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j[2]	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j	SE ($\hat{\phi}$)	$\hat{\phi}$	r_j	SE ($\hat{\phi}$)
04/15/94	1.000	4	--	--[3]	--[3]	--[3]	1.000	0	--	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
05/24/94	0.923	13	0.074	--[3]	--[3]	--[3]	1.000	4	--	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
05/26/94	0.839	11	0.104	--[3]	--[3]	--[3]	1.000	4	--	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
06/16/94	0.839	14	0.104	--[3]	--[3]	--[3]	0.900	10	0.095	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
06/21/94	0.787	16	0.110	--[3]	--[3]	--[3]	0.900	9	0.095	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
06/30/94	0.787	16	0.110	--[3]	--[3]	--[3]	0.700	9	0.145	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
07/07/94	0.688	16	0.110	--[3]	--[3]	--[3]	0.700	4	0.145	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
07/12/94	0.626	11	0.121	--[3]	--[3]	--[3]	0.700	4	0.145	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
08/03/94	0.578	13	0.121	--[3]	--[3]	--[3]	0.700	5	0.145	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
08/23/94	0.536	14	0.119	--[3]	--[3]	--[3]	0.700	4	0.145	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
09/22/94	0.495	13	0.117	--[3]	--[3]	--[3]	0.700	4	0.145	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
01/01/95	0.495	9	0.117	--[3]	--[3]	--[3]	0.525	4	0.187	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
01/25/95	0.495	11	0.117	--[3]	--[3]	--[3]	0.262	2	0.208	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
02/02/95	0.495	11	0.117	--[3]	--[3]	--[3]	0.000	1	--	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]
04/14/95	0.495	10	0.117	--[3]	--[3]	--[3]	0.000	0	--	--[3]	--[3]	--[3]	--[3]	--[3]	--[3]

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 4-16 ($\bar{x}$=10.8) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this region ranged from 0-10 ($\bar{x}$=3.5) during this study year.*

[3] *There were insufficient data to estimate survival in this region.*

Appendix 4-7. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), standard error (SE) of the estimate, and 95% confidence intervals for survival estimates of adult Snail Kites in marsh and lake habitats during each study year (SY)(April 15 to April 14). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate of either age class occurred. The number of animals at risk of dying (r_j) changed as a result of animals having been captured, having moved to a different habitat type (e.g., lake to marsh), having been censored, and having died. We have not shown all changes in r_j because of the high frequency of such changes.*

Appendix 4-7a. Estimates for SY 1992.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/92	1.000	1	--	--	1.000	8	--	--
04/11/93	1.000	19	--	--	0.967	30	0.033	0.902-1.000
04/14/93	1.000	20	--	--	0.967	28	0.033	0.902-1.000

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 1-22 ($\bar{x}$=11.8) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 8-30 ($\bar{x}$=15.0) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-7b. Estimates for SY 1993.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/93	1.000	20	--	--	1.000	27	--	--
08/07/93	1.000	37	--	--	0.952	21	0.046	0.861-1.000
12/18/93	0.947	19	0.051	0.847-1.000	0.952	5	0.046	0.861-1.000
01/05/94	0.947	22	0.051	0.847-1.000	0.762	5	0.174	0.420-1.000
01/19/94	0.874	13	0.084	0.709-1.000	0.762	4	0.174	0.420-1.000
04/14/94	0.874	22	0.084	0.709-1.000	0.762	11	0.174	0.420-1.000

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 7-37 ($\bar{x}$=20.0) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 3-39 ($\bar{x}$=17.5) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-7c. Estimates for SY 1994.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/94	1.000	25	--	--	1.000	11	--	--
10/19/94	1.000	33	--	--	0.950	20	0.049	0.854-1.000
11/13/94	0.963	27	0.036	0.891-1.000	0.950	17	0.049	0.854-1.000
02/02/95	0.932	31	0.047	0.841-1.000	0.887	15	0.076	0.737-1.000
02/07/95	0.901	30	0.544	0.794-1.000	0.887	12	0.076	0.737-1.000
02/23/95	0.901	27	0.544	0.794-1.000	0.709	10	0.127	0.459-0.960
04/14/95	0.901	25	0.544	0.794-1.000	0.709	10	0.127	0.459-0.960

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 20-43 ($\bar{x}$=30.6) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 5-25 ($\bar{x}$=17.0) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-8. *Survival estimates ($\hat{\Phi}$), number of animals at risk of dying during interval j (r_j), standard error (SE) of the estimate, and 95% confidence intervals for survival estimates of juvenile Snail Kites in marsh and lake habitats during each study year (SY)(April 15 to April 14). Estimates are shown only for the starting date, ending date, and dates where a change in survival estimate of either age class occurred. The number of animals at risk of dying (r_j) changed as a result of animals having been captured, having moved to a different habitat type (e.g., lake to marsh), having been censored, and having died. We have not shown all changes in r_j because of the high frequency of such changes.*

Appendix 4-8a. Estimates for SY 1992.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/92	1.000	2	--	--	1.000	2	--	--
07/07/92	0.889	9	0.105	0.683-1.000	1.000	11	--	--
07/20/92	0.778	8	0.139	0.506-1.000	1.000	11	--	--
07/25/92	0.648	6	0.165	0.324-0.972	1.000	11	--	--
04/14/93	0.648	5	0.165	0.324-0.972	1.000	7	--	--

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 2-11 ($\bar{x}$=5.7) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 2-14 ($\bar{x}$=9.5) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-8b. Estimates for SY 1993.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/93	1.000	8	--	--	1.000	3	--	--
04/28/93	0.857	7	0.132	0.598-1.000	1.000	2	--	--
05/04/93	0.714	6	0.171	0.380-1.000	1.000	4	--	--
04/14/94	0.714	5	0.171	0.380-1.000	1.000	0	--	--

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 5-16 ($\bar{x}$=5.7) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 0-13 ($\bar{x}$=4.9) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 4-8c. Estimates for SY 1994.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\Phi}$	r_j[1]	SE ($\hat{\Phi}$)	95% C.I.[1]	$\hat{\Phi}$	r_j[2]	SE ($\hat{\Phi}$)	95% C.I.[3]
04/15/94	1.000	4	--	--	1.000	0	--	--
05/24/94	0.929	14	0.689	0.794-1.000	1.000	6	--	--
05/26/94	0.851	12	0.097	0.660-1.000	1.000	6	--	--
05/31/94	0.851	10	0.097	0.660-1.000	0.833	6	0.152	0.535-1.000
06/07/94	0.766	10	0.119	0.533-0.999	0.833	6	0.152	0.535-1.000
06/16/94	0.766	15	0.119	0.533-0.999	0.769	13	0.153	0.469-1.000
06/21/94	0.721	17	0.120	0.485-0.957	0.769	12	0.153	0.469-1.000
06/30/94	0.721	16	0.120	0.485-0.957	0.641	12	0.152	0.343-0.939
07/07/94	0.631	16	0.121	0.394-0.868	0.641	7	0.152	0.343-0.939
07/12/94	0.574	11	0.123	0.333-0.814	0.641	7	0.152	0.343-0.939
08/03/94	0.529	13	0.121	0.292-0.767	0.641	6	0.152	0.343-0.939
08/23/94	0.492	14	0.118	0.260-0.723	0.641	5	0.152	0.343-0.939
09/22/94	0.456	14	0.115	0.231-0.682	0.641	5	0.152	0.343-0.939
09/23/94	0.456	12	0.115	0.231-0.682	0.513	5	0.167	0.185-0.841
01/25/95	0.456	14	0.115	0.231-0.682	0.342	3	0.179	0.000-0.692
02/02/95	0.456	14	0.115	0.231-0.682	0.171	2	0.150	0.000-0.466
04/14/95	0.456	13	0.115	0.231-0.682	0.171	1	0.150	0.000-0.466

[1] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 4-17 ($\bar{x}=11.8$) during this study year.*

[2] *Infrequent changes in $\hat{\Phi}$ may result in poor representation of r_j. r_j for this habitat ranged from 0-13 ($\bar{x}=4.9$) during this study year.*

[3] *Estimates > 1.00 have been truncated to 1.00.*

Appendix 6-1. *Estimates of cumulative natal dispersal ($\hat{\psi}$), number of animals at "risk" of dispersal (i.e., sample size of juveniles in their natal wetland) during interval j (r_j), standard error (SE) of the estimate, and 95% confidence intervals for estimates of $\hat{\psi}$ during each study year (SY)(April 15 to April 14). Estimates were derived using a Kaplan-Meier estimator. Estimates are shown only for the starting date, ending date, and dates where a change in estimates occurred. The number of animals at risk (r_j) changed as a result of animals having been captured, having dispersed, having been censored, and having died. We have not shown all changes in r_j because of the high frequency of such changes.*

	1992				1993				1994			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
04/15	0.000	3	--	--	0.000	13	--	--	0.000	4	--	--
04/18	0.000	3	--	--	0.067	15	0.064	0.000-0.193	0.000	4	--	--
04/26	0.000	5	--	--	0.138	13	0.091	0.000-0.317	0.000	5	--	--
04/28	0.000	8	--	--	0.354	12	0.128	0.104-0.604	0.000	5	--	--
05/13	0.000	8	--	--	0.354	12	0.128	0.104-0.604	0.063	16	0.061	0.000-0.181
05/19	0.000	18	--	--	0.392	17	0.126	0.146-0.638	0.063	16	0.061	0.000-0.181
05/23	0.000	17	--	--	0.422	20	0.123	0.181-0.663	0.063	17	0.061	0.000-0.181
05/26	0.000	17	--	--	0.422	20	0.123	0.181-0.663	0.115	18	0.076	0.000-0.264
05/31	0.000	17	--	--	0.422	20	0.123	0.181-0.663	0.167	17	0.088	0.000-0.339
06/02	0.000	17	--	--	0.422	20	0.123	0.181-0.663	0.271	16	0.103	0.069-0.473
06/03	0.048	21	0.046	0.000-0.139	0.454	18	0.120	0.219-0.690	0.271	14	0.103	0.069-0.473
06/05	0.095	20	0.064	0.000-0.221	0.454	17	0.120	0.219-0.690	0.271	14	0.103	0.069-0.473
06/10	0.095	20	0.064	0.000-0.221	0.454	17	0.120	0.219-0.690	0.316	16	0.106	0.108-0.525
06/11	0.095	22	0.064	0.000-0.221	0.479	22	0.117	0.249-0.709	0.316	16	0.106	0.108-0.525
06/12	0.095	22	0.064	0.000-0.221	0.504	21	0.114	0.280-0.728	0.316	21	0.106	0.108-0.525
06/14	0.095	22	0.064	0.000-0.221	0.504	21	0.114	0.280-0.728	0.343	26	0.105	0.136-0.549
06/26	0.186	20	0.084	0.022-0.350	0.504	21	0.114	0.280-0.728	0.343	25	0.105	0.136-0.549
06/28	0.186	18	0.084	0.022-0.350	0.528	21	0.111	0.310-0.746	0.343	25	0.105	0.136-0.549
07/01	0.186	17	0.084	0.022-0.350	0.552	19	0.108	0.341-0.764	0.343	25	0.105	0.136-0.549
07/04	0.234	17	0.091	0.054-0.413	0.552	18	0.108	0.341-0.764	0.343	23	0.105	0.136-0.549
07/07	0.282	16	0.097	0.090-0.473	0.552	18	0.108	0.341-0.764	0.371	23	0.105	0.166-0.576

Appendix 6-1. Cont.

	1992				1993				1994			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
07/09	0.282	16	0.097	0.090-0.473	0.552	18	0.108	0.341-0.764	0.428	22	0.103	0.227-0.630
07/14	0.282	16	0.097	0.090-0.473	0.552	18	0.108	0.341-0.764	0.514	20	0.098	0.321-0.707
07/19	0.282	16	0.097	0.090-0.473	0.552	18	0.108	0.341-0.764	0.547	15	0.097	0.356-0.737
07/27	0.282	16	0.097	0.090-0.473	0.552	18	0.108	0.341-0.764	0.611	14	0.093	0.428-0.794
07/30	0.282	13	0.097	0.090-0.473	0.612	14	0.102	0.413-0.811	0.611	14	0.093	0.428-0.794
08/06	0.282	13	0.097	0.090-0.473	0.702	11	0.090	0.525-0.879	0.611	14	0.093	0.428-0.794
08/12	0.282	13	0.097	0.090-0.473	0.702	11	0.090	0.525-0.879	0.644	12	0.091	0.465-0.822
08/13	0.337	13	0.104	0.132-0.542	0.702	10	0.090	0.525-0.879	0.644	11	0.091	0.465-0.822
08/23	0.337	13	0.104	0.132-0.542	0.702	10	0.090	0.525-0.879	0.676	11	0.088	0.503-0.849
09/05	0.392	12	0.109	0.178-0.607	0.768	9	0.082	0.608-0.928	0.676	10	0.088	0.503-0.849
09/08	0.392	11	0.109	0.178-0.607	0.801	7	0.076	0.651-0.951	0.676	10	0.088	0.503-0.849
09/14	0.447	11	0.113	0.227-0.668	0.801	4	0.076	0.651-0.951	0.709	10	0.085	0.541-0.876
09/26	0.503	10	0.114	0.279-0.726	0.801	3	0.076	0.651-0.951	0.709	9	0.085	0.541-0.876
09/29	0.503	10	0.114	0.279-0.726	0.801	3	0.076	0.651-0.951	0.741	9	0.082	0.581-0.901
10/01	0.503	9	0.114	0.279-0.726	0.867	3	0.074	0.722-1.000	0.741	9	0.082	0.581-0.901
10/03	0.503	9	0.114	0.279-0.726	0.934	2	0.060	0.816-1.000	0.741	9	0.082	0.581-0.901
10/04	0.503	9	0.114	0.279-0.726	0.934	2	0.060	0.816-1.000	0.773	8	0.078	0.621-0.925
10/26	0.558	9	0.114	0.334-0.781	0.934	1	0.060	0.816-1.000	0.773	7	0.078	0.621-0.925
11/10	0.558	9	0.114	0.334-0.781	0.934	1	0.060	0.816-1.000	0.806	7	0.073	0.663-0.949
11/11	0.558	9	0.114	0.334-0.781	0.934	1	0.060	0.816-1.000	0.838	6	0.068	0.705-0.971
04/14	0.558	6	0.114	0.334-0.781	0.934	0	0.060	0.816-1.000	0.838	5	0.068	0.705-0.971

[1] *Estimates < 0.00 have been truncated to 0.00 and estimates > 1.00 have been truncated to 1.00.*

Appendix 6-2. *Estimates of cumulative natal dispersal ($\hat{\psi}$), number of animals at "risk" of dispersal (i.e., sample size of juveniles in their natal wetland) during interval j (r_j), standard error (SE) of the estimate, and 95% confidence intervals for estimates of $\hat{\psi}$ from northern and southern regions during each study year (SY)(April 15 to April 14). Estimates were derived using a Kaplan-Meier estimator. Estimates are shown only for the starting date, ending date, and dates where a change in estimates occurred. The number of animals at risk (r_j) changed as a result of animals having been captured, having dispersed, having been censored, and having died. We have not shown all changes in r_j because of the high frequency of such changes.*

Appendix 6-2a. Estimates for SY 1992.

	Northern Regions				Southern Regions			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
04/15/92	0.000	1	--	--	0.000	3	--	--
04/19/92	0.111	9	0.105	0.000-0.316	0.000	13	--	--
04/21/92	0.222	8	0.139	0.000-0.494	0.000	13	--	--
06/26/92	0.222	9	0.139	0.000-0.494	0.167	12	0.108	0.000-0.378
07/04/92	0.319	8	0.152	0.022-0.617	0.167	10	0.108	0.000-0.378
07/07/92	0.417	7	0.158	0.106-0.726	0.167	10	0.108	0.000-0.378
08/13/92	0.533	5	0.164	0.212-0.855	0.167	9	0.108	0.000-0.378
09/05/92	0.650	4	0.159	0.338-0.962	0.167	9	0.108	0.000-0.378
09/14/92	0.767	3	0.143	0.487-1.000	0.167	9	0.108	0.000-0.378
09/26/92	0.883	2	0.109	0.669-1.000	0.167	9	0.108	0.000-0.378
10/26/92	0.883	1	0.109	0.669-1.000	0.259	9	0.129	0.005-0.513
01/10/93	0.883	0	0.109	0.669-1.000	0.259	6	0.129	0.005-0.513
04/14/93	0.883	0	0.109	0.669-1.000	0.259	6	0.129	0.005-0.513

[1] *Estimates < 0.00 have been truncated to 0.00 and estimates > 1.00 have been truncated to 1.00.*

Appendix 6-2b. Estimates for SY 1993.

	Northern Regions				Southern Regions			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
04/15/93	0.000	0	--	--	0.000	13	--	--
04/18/93	0.000	0	--	--	0.067	15	0.064	0.000 0.193
04/26/93	0.000	0	--	--	0.138	13	0.091	0.000 0.317
04/28/93	0.000	0	--	--	0.354	12	0.128	0.103-0.604
05/19/93	0.000	5	--	--	0.408	12	0.128	0.157-0.658
05/23/93	0.000	8	--	--	0.457	12	0.126	0.209-0.705
06/03/93	0.143	7	0.132	0.000-0.402	0.457	11	0.126	0.209-0.705
06/11/93	0.143	6	0.132	0.000-0.402	0.491	16	0.123	0.250-0.732
06/13/93	0.143	6	0.132	0.000-0.402	0.525	15	0.119	0.291-0.759
06/28/93	0.143	8	0.132	0.000-0.402	0.561	13	0.116	0.334-0.788
07/01/93	0.143	7	0.132	0.000-0.402	0.598	12	0.112	0.379-0.817
07/29/93	0.250	8	0.153	0.000-0.550	0.598	7	0.112	0.379-0.817
07/30/93	0.357	7	0.165	0.034-0.680	0.598	7	0.112	0.379-0.817
08/04/93	0.464	6	0.168	0.134-0.794	0.655	7	0.109	0.440-0.870
08/06/93	0.571	5	0.165	0.247-0.895	0.655	6	0.109	0.440-0.870
09/05/93	0.786	4	0.135	0.520-1.000	0.655	5	0.109	0.440-0.870
09/08/93	0.786	2	0.135	0.520-1.000	0.724	5	0.107	0.514-0.934
10/01/93	1.000	1	--	--	0.724	2	0.107	0.514-0.934
10/03/93	1.000	0	--	--	0.862	2	0.111	0.644-1.000
04/14/94	1.000	0	--	--	0.862	2	0.111	0.644-1.000

[1] *Estimates < 0.00 have been truncated to 0.00 and estimates > 1.00 have been truncated to 1.00*

Appendix 6-2c. Estimates for SY 1994.

	Northern Regions				Southern Regions			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
04/15/94	0.000	0	–	–	0.000	4	–	–
05/13/94	0.000	2	–	–	0.071	14	0.069	0.000 0.206
05/26/94	0.000	5	–	–	0.143	13	0.094	0.000 0.326
05/31/94	0.000	5	–	–	0.214	12	0.110	0.000 0.429
06/02/94	0.000	5	–	–	0.357	11	0.128	0.106-0.608
06/09/94	0.200	5	0.179	0.000-0.551	0.357	11	0.128	0.106-0.608
06/14/94	0.200	10	0.179	0.000-0.551	0.397	16	0.126	0.149-0.645
07/09/94	0.500	7	0.177	0.153-0.846	0.397	15	0.126	0.149-0.645
07/14/94	0.500	5	0.177	0.153-0.846	0.518	15	0.119	0.285-0.750
07/19/94	0.600	5	0.167	0.272-0.928	0.518	10	0.119	0.285-0.750
07/27/94	0.600	4	0.167	0.272-0.928	0.614	10	0.113	0.393-0.835
08/12/94	0.600	4	0.167	0.272-0.928	0.663	8	0.109	0.449-0.875
08/23/94	0.700	4	0.152	0.401-0.999	0.663	7	0.109	0.449-0.875
09/14/94	0.700	3	0.152	0.401-0.999	0.711	7	0.103	0.508-0.913
09/29/94	0.700	3	0.152	0.401-0.999	0.759	6	0.097	0.569-0.948
10/04/94	0.800	3	0.130	0.544-1.000	0.759	5	0.097	0.569-0.948
11/10/94	0.800	2	0.130	0.544-1.000	0.807	5	0.088	0.633-0.981
11/11/94	0.800	2	0.130	0.544-1.000	0.855	4	0.078	0.701-1.000
01/22/95	0.800	1	0.130	0.544-1.000	0.855	3	0.078	0.701-1.000
04/14/95	0.800	1	0.130	0.544-1.000	0.855	3	0.078	0.701-1.000

[1] *Estimates <0.00 have been truncated to 0.00 and estimates $>$ 1.00 have been truncated to 1.00*

Appendix 6-3. *Estimates of cumulative natal dispersal ($\hat{\psi}$), number of animals at "risk" of dispersal (i.e., sample size of juveniles in their natal wetland) during interval j (r_j), standard error (SE) of the estimate, and 95% confidence intervals for estimates of $\hat{\psi}$ from marsh and lake habitats during each study year (SY)(April 15 to April 14). Estimates were derived using a Kaplan-Meier estimator. Estimates are shown only for the starting date, ending date, and dates where a change in estimates occurred. The number of animals at risk (r_j) changed as a result of animals having been captured, having dispersed, having been censored, and having died. We have not shown all changes in r_j because of the high frequency of such changes.*

Appendix 6-3a. Estimates for SY 1992.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
04/15/92	0.000	2	–	–	0.000	2	–	–
06/03/92	0.077	13	0.074	0.000-0.222	0.000	9	–	–
06/04/92	0.154	12	0.100	0.000-0.350	0.000	9	–	–
06/26/92	0.154	12	0.100	0.000-0.350	0.222	9	0.139	0.000-0.494
07/04/92	0.224	12	0.114	0.001-0.448	0.222	6	0.139	0.000-0.494
07/07/92	0.224	11	0.114	0.001-0.448	0.352	6	0.165	0.027-0.676
08/13/92	0.302	10	0.126	0.054-0.549	0.352	4	0.165	0.027-0.676
09/05/92	0.379	9	0.134	0.117-0.642	0.352	4	0.165	0.027-0.676
09/14/92	0.379	8	0.134	0.117-0.642	0.514	4	0.187	0.146-0.881
09/26/92	0.379	8	0.134	0.117-0.642	0.676	3	0.182	0.319-1.000
10/26/92	0.457	8	0.138	0.186-0.727	0.676	2	0.182	0.319-1.000
04/14/93	0.457	5	0.138	0.186-0.727	0.676	1	0.182	0.319-1.000

[1] *Estimates <0.00 have been truncated to 0.00 and estimates > 1.00 have been truncated to 1.00.*

Appendix 6-3b. Estimates for SY 1993.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
04/15/93	0.000	3	--	--	0.000	10	--	--
04/18/93	0.000	3	--	--	0.083	12	0.080	0.000-0.240
04/26/93	0.333	3	0.272	0.000-0.867	0.083	10	0.080	0.000-0.240
04/28/93	0.333	2	0.272	0.000-0.867	0.358	10	0.144	0.075-0.641
05/19/93	0.333	6	0.272	0.000-0.867	0.417	11	0.142	0.137-0.696
05/23/93	0.333	7	0.272	0.000-0.867	0.462	13	0.138	0.190-0.733
06/03/93	0.444	6	0.248	0.000-0.931	0.462	12	0.138	0.190-0.733
06/11/93	0.444	10	0.248	0.000-0.931	0.506	12	0.134	0.244-0.769
06/12/93	0.444	10	0.248	0.000-0.931	0.551	11	0.129	0.298-0.804
06/28/93	0.444	11	0.248	0.000-0.931	0.596	10	0.124	0.353-0.838
07/01/93	0.444	10	0.248	0.000-0.931	0.641	9	0.118	0.410-0.872
07/29/93	0.514	8	0.227	0.069-0.959	0.641	7	0.118	0.410-0.872
07/30/93	0.514	7	0.227	0.069-0.959	0.692	7	0.112	0.473-0.911
08/04/93	0.583	7	0.205	0.181-0.985	0.744	6	0.104	0.539-0.948
08/06/93	0.583	6	0.205	0.181-0.985	0.795	5	0.095	0.608-0.981
09/05/93	0.583	5	0.205	0.181-0.985	0.897	4	0.070	0.760-1.000
09/08/93	0.667	5	0.180	0.313-1.000	0.897	2	0.070	0.760-1.000
10/01/93	0.667	2	0.180	0.313-1.000	1.000	1	--	--
10/03/93	0.833	2	0.148	0.542-1.000	1.000	0	--	--
04/14/94	0.833	1	0.148	0.542-1.000	1.000	0	--	--

[1] *Estimates <0.00 have been truncated to 0.00 and estimates >1.00 have been truncated to 1.00*

Appendix 6-3c. Estimates for SY 1994.

	Marsh Habitat				Lake Habitat			
Date	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]	$\hat{\psi}$	r_j	SE ($\hat{\psi}$)	95% C.I.[1]
04/15/94	0.000	0	--	--	0.000	4	--	--
05/13/94	0.000	4	--	--	0.083	12	0.080	0.000-0.240
05/26/94	0.000	5	--	--	0.154	13	0.100	0.000-0.350
05/31/94	0.000	5	--	--	0.224	12	0.114	0.001-0.448
06/02/94	0.000	5	--	--	0.365	11	0.130	0.111-0.620
06/09/94	0.143	7	0.132	0.000-0.402	0.365	9	0.130	0.111-0.620
06/14/94	0.143	12	0.132	0.000-0.402	0.411	14	0.128	0.159-0.662
07/07/94	0.143	10	0.132	0.000-0.402	0.456	13	0.126	0.209-0.703
07/09/94	0.314	10	0.151	0.017-0.611	0.456	12	0.126	0.209-0.703
07/14/94	0.314	8	0.151	0.017-0.611	0.592	12	0.116	0.363-0.820
07/19/94	0.429	6	0.164	0.107-0.750	0.592	9	0.116	0.363-0.820
07/27/94	0.429	5	0.164	0.107-0.750	0.683	9	0.107	0.473-0.892
08/12/94	0.429	5	0.164	0.107-0.750	0.728	7	0.101	0.530-0.925
08/23/94	0.543	5	0.166	0.217-0.869	0.728	6	0.101	0.530-0.925
09/14/94	0.543	4	0.166	0.217-0.869	0.773	6	0.094	0.590-0.957
09/29/94	0.543	4	0.166	0.217-0.869	0.819	5	0.085	0.651-0.986
10/04/94	0.657	4	0.159	0.345-0.969	0.819	4	0.085	0.651-0.986
11/10/94	0.771	3	0.141	0.494-1.000	0.819	4	0.085	0.651-0.986
11/11/94	0.771	2	0.141	0.494-1.000	0.864	4	0.075	0.717-1.000
04/14/95	0.771	1	0.141	0.494-1.000	0.864	3	0.075	0.717-1.000

[1] *Estimates < 0.00 have been truncated to 0.00 and estimates > 1.00 have been truncated to 1.00*

Appendix 6-4. *Water gauges used for hydrologic analyses of individual wetlands in this report. Also shown is the agency that maintains records of the gauge.*

Wetland	Wetland Abbr.	Gauge(s)	Agency
Big Cypress National Preserve	BICY	NP-34	Big Cypress National Preserve
Everglades National Park	ENP	NP-33	Everglades National Park
East Lake Tohopekaliga	ETOHO	S-59_H	South Florida Water Management District
Lake Kissimmee	KISS	Lake Kissimmee	U.S. Geological Survey, Water Resources Division
Lake Okeechobee	OKEE	Okeechobee 10-station average	U.S. Army Corps of Engineers
St. Johns Marsh	SJM	S-251E (within study-period effects) Blue Cypress Lake (long-term hydrologic regimes)	St. Johns River Water Management District
Lake Tohopekaliga	TOHO	Lake Tohopekaliga	U.S. Geological Survey, Water Resources Division
Loxahatchee National Wildlife Refuge	LOX	CA1-7	U.S. Army Corps. Of Engineers
Water Conservation Area 2A	WCA2A	CA2-17	U.S. Army Corps. Of Engineers
Water Conservation Area 2B	WCA2B	2B-Y	South Florida Water Management District
Water Conservation Area 3A	WCA3A	CA3-28	U.S. Army Corps. Of Engineers
West Palm Beach Water Catchment Area	WPB	3-Gauge Average (CNTL3, CNTL4, STA7)	City of West Palm Beach