

POPULATION ECOLOGY AND CONSERVATION OF THE SNAIL KITE

By

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POPULATION ECOLOGY AND CONSERVATION OF THE SNAIL KITE

By

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My research was articulated around three primary goals: (1) determine the current status of the Snail Kite (*Rostrhamus sociabilis*) population in Florida; (2) provide information about population ecology relevant to conservation of the Snail Kite; (3) make recommendations that will help Snail Kite recovery.

I found that the Snail Kite population declined dramatically in recent years. Estimates of stochastic population growth rate and probabilities of quasi extinction suggested that the Snail Kite population in Florida was at high risk of extinction. The sharp decline observed after 2001 was mostly associated with a multiregional drought that occurred in 2001 and affected movement, survival and reproduction. The occurrence of this disturbance allowed us to evaluate hypotheses related to the effect of droughts on demography and movement of Snail Kites. Only a small proportion of kites escaped a regional drought by moving to refugia (wetlands less affected by drought). Many individuals died after the drought. During drought, adult survival dropped by 16%, while juvenile survival dropped by 86% (possibly because juveniles were less likely to reach refugia). Although kites exhibit extensive exploratory behavior, particularly among contiguous wetlands, they also show high levels of annual site tenacity during the breeding season, especially to their place of birth. Fidelity to breeding and natal sites has been given

relatively little attention in the past. However, I found that fidelity to the natal region could have significant effects on movement patterns and survival, and could influence the whole dynamics of the kite population.

Although the 2001 drought had a considerable effect on survival, reproduction, and abundance, our results suggest that the lack of recovery after 2002 was predominantly caused by lack of recruitment. We found evidence that both habitat conversion (caused by prolonged hydroperiod and increased water depth during the Fall), and the increase in frequency of drying events (during the Spring and Summer), especially in Water Conservation Area 3A (WCA3A), could be responsible for the observed reduction in population growth rate. Finally, I present a set of management recommendations to promote Snail Kite recovery.

CHAPTER 1 INTRODUCTION

Why Study the Snail Kite?

Natural ecosystems provide societies with goods and services worth trillions of dollars annually, and also perform “life-support services” essential to the persistence of humanity (Daily et al. 1997). These services include purification of air and water, detoxification, decomposition of wastes, and regulation of climates, to list a few (Daily et al. 1997). Yet, most natural ecosystems suffer from escalating destruction caused by human activities. The multiplication of ecosystem restoration efforts around the world reveals some level of recognition of the problem.

The Everglades ecosystems in south Florida are currently the site of one of the largest and most ambitious ecosystem restoration projects ever undertaken (Mitsch and Gosselink 2000). A major multi-billion dollar restoration project of the Everglades (the Comprehensive Everglades Restoration Plan, CERP) is being implemented by the U.S. Army Corps of Engineers, the U.S. Fish and Wildlife Service, and the state of Florida to restore this ecosystem. Restoration of the Everglades is gathering enormous attention both nationally and internationally (The Economist 2005). If this project succeeds, it is likely to become a model for other large ecosystem restoration projects throughout the world (The Economist 2005). The primary objective of this restoration project is to improve the quality of native habitats and increase diversity and abundance of native plants and animals (RECOVER 2005). The principal idea of the restoration is to act on two primary stressors of the system: hydrology and water quality (RECOVER 2005). Conservation biologists and managers have selected a number of indicator species as measures of success of the restoration (RECOVER 2005; Niemi and McDonald 2004). The Snail Kite (*Rostrhamus sociabilis plumbeus*) is one of the indicator species that was selected by the CERP work team (RECOVER 2005).

There are at least six justifications to list the Snail Kite as an important indicator of Everglades restoration. First, the Snail Kite is a wetland dependent species. Kites forage and nest preferentially in habitats dominated by plant communities that CERP strives to restore (RECOVER 2005). Second, Snail Kites respond numerically (e.g., change in mortality rates) and behaviorally (e.g., change in movement rates) to changes in hydrological conditions (the primary stressor modified by CERP). The response of kites to changes in hydrological conditions is measurable (e.g., estimates of reproductive parameters, movement, etc.). Third, the Snail Kite population experienced some dramatic decline after the drainage and fragmentation of the Everglades, to the point that it was listed as federally endangered in 1967. The recovery of endangered species is also one of the tasks of CERP (RECOVER 2005). Fourth, because of the charismatic nature of this species, the Snail Kite is an indicator that can ease communication with the public. Fifth, the geographic range of the Snail Kite in Florida encompasses most of the wetlands that CERP will attempt to restore (RECOVER 2005). Sixth, the monitoring of the Snail Kite is one of the few programs in Florida that is long term (> 15 years) and accounts for detectability and spatial variation (Bennetts et al. 1999b; Yoccoz et al. 2001).

Background Information on Snail Kites

The Snail Kite is a medium size raptor which is restricted to the American continent and Cuba. The Snail Kite belongs to the Order of the *Falconiformes*, the Family of the *Accipitridae*, the Subfamily of the *Buteoninae* and the Genus *Rostrhamus* (Lerner and Mindell 2005). Three subspecies have been recognized: *R. s. plumbeus* is found in Florida and Cuba, whereas *R. s. sociabilis*, and *R. s. major* range from Central to South America. Beissinger (1998) has questioned this classification, which is based on morphometric measurements.

The Snail Kite in Florida is restricted to the remaining wetlands that used to constitute the historic Kissimmee-Okeechobee-Everglades watershed. The Snail Kite is a wetland dependent

species that feeds almost exclusively on freshwater Apple Snails *Pomacea paludosa* (Beissinger 1988). Kites are sensitive to change in hydrological conditions, partly because snail availability is tightly linked to hydrology (Beissinger 1995). The occurrence of droughts in particular reduces snail availability drastically, and therefore affects kites movement and demography (i.e., during drought kites must move or die) (Bennetts and Kitchens 2000). Conversely, aside from some possible short term benefits for juvenile survival (Bennetts et al. 2002), prolonged hydroperiod, flooding events or drought suppression may, in the longer term, degrade the vegetation communities that support both kite foraging and nesting habitats (Kitchens et al. 2002), making the management of kite habitat a complex endeavor.

Since 1930, the network of wetlands occupied by kites has changed dramatically. It has been reduced approximately by half of its original size, and has been severely fragmented (Kitchens et al. 2002). In 1967 the Snail Kite from Florida and Cuba was first listed as endangered pursuant to the Endangered Species Conservation Act (USFWS 1999).

Since its listing as an endangered species the Snail Kite population in Florida has been monitored using quasi-systematic annual count surveys (Bennetts and Kitchens 1997). In the early seventies counts were less than 200, but increased approximately to 1000 birds in 1995. However, Bennetts et al. (1999b) criticized that monitoring technique, arguing that these counts were of limited value, if not misleading, because detection probabilities were not accounted for. Since 1992 a capture-mark-recapture study was initiated to provide robust estimates of vital rates (i.e., survival, reproduction, movement) and population size. This protocol was coupled to an extensive radiotelemetry protocol between 1992 and 1995 to provide more precise estimates of movement and survival (Bennetts et al. 1999a).

Dreitz et al. (2002) provided the first estimates of population size that accounted for detection, and their estimates (from 1997 to 2000) were four to five times greater than the recovery target set by the USFWS in 1999. Estimates of Dreitz et al. (2002) during the study period also indicated a fairly stable population. Under the objectives set by the recovery plan of 1999, these figures were encouraging.

Objectives and Outline

My research was articulated around three primary goals:(1) determine the current status of the Snail Kite population in Florida; (2) provide information about population ecology relevant to conservation of the Snail Kite; (3) make clear recommendations that will help Snail Kite recovery.

- In Chapter 2, I provided new information related to the status of the Snail Kite in Florida. Based on a recently proposed estimator of abundance (i.e., the superpopulation approach), I presented estimates of population size and population growth rates for the last 9 years. In Chapter 2 I also emphasized the importance of accounting for major sources of variation when estimating demographic parameters.
- In Chapter 3, I examined how Snail Kites perceive and move through the landscapes of Florida. I also examined the link between movement and survival, and investigated the relevance of fragmentation and habitat destruction to Snail Kite conservation.
- In Chapter 4, I focused on some important behavioral components that determine movement and survival of kites. In particular, I looked at how fidelity to the natal site influenced movement and survival. At the end of the chapter, I emphasized the importance of considering fidelity to the natal site for management.
- In Chapter 5, I used matrix population models to estimate projected population growth rates and probability of quasi-extinction. I also evaluated competing hypotheses explaining changes in population growth rates. At the end of the chapter, I provided a set of recommendations for management of Snail Kite habitat.
- In the final chapter (Chapter 6), I synthesized the information presented in chapters 1 through 5, and provided some perspectives for future work on the Snail Kite.

CHAPTER 2
IMPORTANCE OF WELL-DESIGNED MONITORING PROGRAMS FOR THE
CONSERVATION OF ENDANGERED SPECIES: CASE STUDY OF THE SNAIL KITE

Introduction

Monitoring natural populations is often a necessary step to establish the conservation status of species and to help improve management decisions (Yoccoz et al. 2001). However, many monitoring programs do not effectively address two important components of variation in monitoring data: spatial variation and detectability, which ultimately may limit the utility of monitoring in identifying declines and improving management (Yoccoz et al. 2001).

Detectability refers to the probability that an animal will be detected if it is present in the sampled area (Williams et al. 2002). Many sources of variation may affect detectability (e.g., observer effect, environmental conditions), and monitoring data that do not take detectability into account will typically lead to biased estimates (Williams et al. 2002). Spatial variation is another source of variability of monitoring data. It results from the inability to sample the entire area of interest (i.e., inference is drawn from selected spatial units that are only a fraction of the area of interest; this is a problem when the areas sampled are not representative of the entire area) (Williams et al. 2002).

The principle that monitoring programs should take detectability and spatial variation into consideration is gaining some support among wildlife biologists (see Williams et al. 2002). However, analyses using uncorrected counts continue to be published in major journals (reviewed in Rosenstock et al. 2002; Conn et al. 2004). The continued controversy around the value of uncorrected count-based indexes results partly from the fact that monitoring programs that estimate detectability are often more labor intensive (Conn et al. 2004). Some authors have argued that when the focus is on population change rather than population size, uncorrected count-based indexes may be sufficient, but for this latter statement to be correct, detectability

should remain constant over time, which is rarely the case when monitoring mobile organisms (Conn et al. 2004). The principle that it is crucial to estimate detection and to account for spatial variation when monitoring animal populations appears to take even longer to be accepted by some managers. This is problematic because recovery plans for many endangered species are still based on monitoring programs that ignore these primary sources of variations (e.g., Cape Sable Seaside Sparrow *Ammodramus maritimus mirabilis*, Wood Stork *Mycteria americana*, see USFWS (1999)).

We used the monitoring of the Snail Kite (*Rostrhamus sociabilis plumbeus*) in Florida to illustrate the importance of considering detectability and spatial variation. The Snail Kite feeds almost exclusively on freshwater snails and, thus, is considered a wetland-dependent species (Beissinger 1988). In the United States the Snail Kite is restricted to the remaining wetlands of central and south Florida (Dreitz et al. 2002). Because the availability of snails to kites is strongly dependent on hydrological conditions, variations in water levels are likely to influence kite behavior and demography (Beissinger and Takekawa 1983). Droughts affect kite behavior and demography by reducing snail availability to kites (Beissinger and Takekawa 1983).

The drainage of the Everglades that began in the early 1930s and was followed by wetland destruction led to the collapse of the kites in Florida (USFWS 1999). In 1967 the Snail Kite was first listed as endangered pursuant to the U.S. Endangered Species Conservation Act (ESA) (USFWS 1999). Three primary quantitative recovery criteria were set by the U.S. Fish and Wildlife Service (USFWS) in 1999 on which to base reclassification of the Snail Kite from endangered to threatened (USFWS 1999): (1) “the 10-year average for the total population size is estimated as ≥ 650 , with a coefficient of variation (CV) less than 20% for the pooled data” (USFWS 1999); (2) “no annual population estimate is less than 500”; and (3) “the rate of

increase to be estimated annually or biannually and over the 10 year period will be greater than or equal to 1.0, sustained as a 3-year running average” (USFWS 1999). These criteria, however, were set in reference to data obtained from uncorrected counts (USFWS 1999). Since 1965 several agencies have been conducting kite surveys throughout the designated critical kite habitats (reviewed in Bennetts et al. 1999b). One major weakness of most count surveys is that detectability is not considered (Bennetts et al. 1999b). Hereafter we used the term “counts” to refer to uncorrected counts, which basically correspond to the number of animals counted during a survey. These counts represent an unknown fraction of the target population (i.e., detection probability is not taken into account, see Williams et al. 2002). In contrast, the terms “estimate of population size” and “estimate of superpopulation size” correspond to population parameters of interest that take detectability into consideration.

Dreitz et al. (2002) provided the first estimates of population size that accounted for detection, and their estimates (from 1997 to 2000) were four to five times greater than the target set by the USFWS in 1999. Estimates of Dreitz et al. (2002) during the study period also indicated a fairly stable population. Under the objectives set by the recovery plan of 1999, these figures were encouraging. However, estimates presented in this study indicate that criteria set by the recovery plan in 1999 need revision and that count surveys of populations that occupy large landscapes may be dangerously misleading.

Using a recent estimator of superpopulation size, we examined the implications of carefully considering detection probabilities and spatial variation when making inference about changes in population size and number of young produced. In this study, the superpopulation consisted of all kites that had a non-zero probability of being detected over the course of the sampling year (Dreitz et al. 2002). The superpopulation approach employed in our study and in

Dreitz et al. (2002) was based on capture-mark-resighting analyses. This approach allowed for the estimation of superpopulation size that takes into account detectability and spatial variation (Williams et al. 2002). This approach makes use of capture-mark-resight models such as Cormack-Jolly-Seber models (CJS) (Dreitz et al. 2002).

There are six primary steps used in this study. 1) We estimated superpopulation size for young and adults separately. 2) Based on these estimates, we examined changes in abundances by estimating population growth rates, and we looked for population decline. 3) We then compared count data with superpopulation estimates. Since detection probabilities for counts are typically < 1.0 , counts will often underestimate the “true” population size (Williams et al. 2002). 4) We computed one type of detection probability (denoted P) as the ratio of the number of kites counted over the estimated superpopulation size, and examined how detection varied over time for two types of count surveys. If this detection estimate varied substantially over time, then count-based indexes could be very misleading. For instance, if detection increases over time (e.g., because of additional field personnel), population growth rates derived from counts may suggest that the population is growing, or remains stable, while in fact, the “true” population is decreasing. Note that detection probability based on the ratio statistic (P) is different from detection probability (denoted p) directly estimated using capture-mark-resight models such as the CJS (Williams et al. 2002). 5) We examined the recovery criteria that the USFWS set for kites to determine whether these criteria were met or were close to being met based on two types of monitoring data, one that considered detection and spatial variation (superpopulation approach), and another that did not (i.e., count data). 6) Finally, we examined the implications of addressing detectability and spatial sampling for the conservation of kites and other endangered species.

Methods

Study Area

The Snail Kite population in Florida has been described as geographically isolated (Martin et al. 2006; Dreitz et al. 2002). Kites occupy the remaining wetlands of the Kissimmee-Okeechobee-Everglades freshwater watershed. The sampled units we used are identical to the units Dreitz et al. (2002) used and encompassed major kite habitats (Figure 2-1). Although kites may temporarily emigrate to unsampled areas, it is unlikely that they will not return to the major wetlands included in the survey during some portion of the sampling period (Dreitz et al. 2002).

Sampling Methods

Marking protocol

Multiple, consecutive surveys of Snail Kites from airboats were conducted during the peak of the breeding season (March through June) throughout the areas sampled from 1992 to 2005. During surveys, workers located nests and banded young kites when they were ready to fledge (~25 days). A total of 1806 young were marked between 1992 and 2005. Prior to 1995, 134 kites were marked as adults (> 1 year) (Bennetts and Kitchens 2000). Additionally, 76 kites were marked as young prior to 1992. Kites were marked with alpha-numeric bands.

Population survey protocol

Our protocol for population surveys from 2001 to 2005 followed that described by Dreitz et al. (2002) and was part of the same Florida Cooperative Fish and Wildlife Research Unit (FCFWRU) kite-monitoring program. Four to six consecutive surveys from airboats were conducted at 2- to 4-week intervals throughout the designated wetland units from 25 February to 30 June. From 2001 to 2003, the surveys started between 1 March and 8 March and ended between 15 June and 19 June. In 2004 and 2005, the surveys started between 25 February and 1 March and ended between 27 June and 30 June. During each survey we inspected every sighted

kite with binoculars and spotting scopes. We categorized each observed individual as: (1) marked if the kite carried a band that could be uniquely identified; (2) unmarked if the sighted kite did not carry an identifiable band; or (3) unknown if the banding status of the kite could not be determined.

Analysis

Superpopulation size estimates of adults

We used the superpopulation approach (Schwarz and Arnason 1996) generalized by Schwarz and Stobo (1997) into a robust design framework. This approach allows for movement during secondary occasions (i.e., between surveys within a year, see Dreitz et al. 2002). Dreitz et al. (2002) were the first to apply this method to the Snail Kite. All notations follow Dreitz et al. (2002). The superpopulation approach estimated the total number of kites present in the sampled area for at least some of the surveys during the sampling period (surveys within a year were denoted $i=1, 2, \dots, n$). For any given year (denoted j), we referred to this estimate as the superpopulation estimate for each year (\hat{N}_j^*).

$$\hat{N}_j^* = \hat{N}_{1j} + \sum_{i=1}^{n-1} \hat{B}_{ij}, \quad (\text{Eq. 2-1})$$

where \hat{N}_{1j} is the estimated abundance of the first survey in year j . The \hat{N}_{ij} is estimated as

$$\hat{N}_{ij} = \frac{m_{ij} + u_{ij}}{\hat{p}_{ij}}, \quad (\text{Eq. 2-2})$$

where m_{ij} is the number of marked kites and u_{ij} the number of unmarked kites at each survey i in year j . Kites whose banding status was unknown were excluded from this analysis. The \hat{p}_{ij} (sighting probability) is the estimated probability of sighting a kite given that it was present in

survey i of year j . Given the constraint, $p_{1j} = p_{2j}$, abundance can be estimated for all surveys within year j .

The \hat{B}_{ij} is the estimate of the number of new kites entering the sampled area (between survey i and $i+1$) from areas not sampled on each survey

$$\hat{B}_{ij} = \hat{N}_{i+1,j} - \hat{N}_{ij} \hat{\phi}_{ij}, i > 0, \quad (\text{Eq. 2-3})$$

where $\hat{\phi}_{ij}$ (apparent survival) is the estimated probability of not dying and not permanently emigrating to an area not sampled between surveys i and $i+1$ of year j . Given the constraint $p_{1j} = p_{2j}$, \hat{B}_{ij} can be estimated for $i = 1, \dots, (n-1)$.

As in Dreitz et al. (2002) we used the CJS model implemented in program MARK to estimate $\hat{\phi}_{ij}$ and \hat{p}_{ij} (Cooch and White 2005). We analyzed each annual capture-recapture data set separately to obtain estimates of ϕ_i and p_i within a year. We preferred this approach to a multigroup approach (used in Dreitz et al. 2002) because the date for the within year surveys did not match exactly from one year to the other. Unlike Dreitz et al. (2002) the number of sampling surveys in our study varied between four and six (we note that the number of sampling surveys should not affect the superpopulation estimate as long as the sampling periods remain similar). Although we ended our surveys before 30 June in 2001, 2002 and 2003, our data indicates that all surveys conducted after the second week of June did not affect estimates of superpopulation size. Indeed, removing the last survey for years when surveys ended on approximately 30 June, did not affect the estimate of abundance. This can be explained by the fact that by the end of the sampling season, it is unlikely that many birds will enter the sampled areas for the first time (i.e., most birds have already done so before the last survey).

For model selection among CJS models, we used QAIC_c, which corresponds to the Akaike information criterion (AIC) corrected for small sample size and extrabinomial variation (Burnham and Anderson 2002). We ran four CJS models for each year. Models that assumed ϕ_i and p_i remained constant between surveys were denoted with a subscripted dot (.). Conversely, models that allowed ϕ_i and p_i to vary among surveys were denoted with a subscripted t . Thus, the four models were denoted: $\phi.p.$, $\phi.p_t$, $\phi_t.p.$, and $\phi_t.p_t$. As recommended by Burnham and Anderson (2002), we used model-averaged estimates of ϕ and p . The purpose of estimating ϕ and p with CJS models was primarily to compute estimates of superpopulation size. Confidence intervals of estimates of superpopulation size were computed with the same parametric bootstrap procedure (500 simulations) described in Dreitz et al. (2002).

The assumptions for the superpopulation model are similar to the ones required for the more widely known Jolly-Seber model (Williams et al. 2002). In particular, homogeneity of rates among animals are assumed. The superpopulation model also assumes that all members of the superpopulation unavailable until t will exhibit similar probability of being available for capture at $t + 1$. The Goodness of fit test (test 2 + test 3) implemented in program RELEASE, which tests for homogeneity of ϕ_i and p_i and for lack of independence of survival and capture events (Burnham et al. 1987), is also applicable for the superpopulation model (Williams et al. 2002). There is no evidence of heterogeneity or lack of independence for ϕ_i and p_i when probability p is > 0.05 (Cooch and White 2005). Burnham and Anderson (2002) indicate that model structure is acceptable for extra-binomial factor $\hat{c} < 4$, and they suggest to adjust for extrabinomial variation if $\hat{c} > 1$. We computed \hat{c} with program RELEASE (Burnham et al. 1987).

Estimation of population growth rate

Annual population growth rate (λ_j), was estimated as:

$$\hat{\lambda}_j = \frac{\hat{N}_{j+1}^*}{\hat{N}_j^*}, \quad (\text{Eq. 2-4})$$

We then computed the arithmetic average of all the $\hat{\lambda}_j$ over the last 8 years (1998 to 2005) and a 3-year running average (denoted $\hat{\lambda}_{j-(j+2)}$).

Estimation of the number of young produced

We used the superpopulation approach described above to estimate the number of young produced in any given year (hereafter referred as young) for the entire superpopulation (denoted \hat{N}_{Yj}^*). For this analysis m_{ij} and u_{ij} (see Eq. 2-2) included exclusively kites that were hatched in year j . We used this approach only in 2004 and 2005 because we began recording m_{ij} and u_{ij} for the young in 2004. There was not enough band resight information of young in 2004 and 2005 to estimate ϕ_{ij} and p_{ij} that were specific to that particular age class. Therefore, we used ϕ_{ij} and p_{ij} computed for adults to estimate the number of young produced in 2004 and 2005.

Detection probabilities for number of young produced every year

Only a proportion of the total number of young produced were detected and marked every year. To estimate the proportion of young marked during each year (i.e., detection probability of young), we used the following estimator (see Williams et al. 2002):

$$\hat{P}_{Yj} = \frac{C_{Yj}}{\hat{N}_{Yj}^*}, \quad (\text{Eq. 2-5})$$

where \hat{P}_{Yj} is the detection probability of young in year j , C_{Yj} is the number of young observed and marked in year j (hereafter referred as the number of young marked). The \hat{P}_{Yj} differed from survey-specific \hat{p}_{ij} (directly estimated with CJS models).

Count data

We used two types of count survey data that we subsequently compared to estimates of superpopulation size: first count (FC), and maximum count (MC). For FC we used the first FCFWRU annual count survey (total number of birds counted during the first survey) as an indicator of annual abundance. We used the first annual count survey because it was always conducted at the same date (1 March \pm 1 week). Many agencies, including the Florida Fish and Wildlife Conservation Commission use this type of format for surveys in which a designated study area is sampled annually (typically at the same time of year). The MC was annual count data of the maximum count obtained for any of the FCFWRU surveys within a sampling season. MC and FC included: marked, unmarked and unknown kites. However, because in 1997 unknown birds were not reported, all analyses related to FC and MC data focused on the period 1998 to 2005.

Average number of kites and growth rate based on count data

We computed the arithmetic average for the two sets of count data (\bar{C}). We also used these count data sets to compute annual growth rate based on counts (λ_{cj}). λ_{cj} were estimated as follow (see also Williams et al. 2002):

$$\hat{\lambda}_{cj} = \frac{C_{j+1}}{C_j}, \quad (\text{Eq. 2-6})$$

We then computed the 8-years arithmetic average of all the $\hat{\lambda}_{cj}$; as well as the 3-year running average denoted: $\hat{\lambda}_{cj-(j+2)}$.

Detection probabilities for FC and MC

Monitoring based on counts typically assumes detection probability to equal 1.0; however, in practice, this assumption is rarely met (Williams et al. 2002).

We determined the detection probability of Snail Kites using both FC and MC surveys by computing the ratio of the number of kites counted in a given year j (C_j) (using either FC or MC), over the estimated superpopulation size for that same year (\hat{N}_j^*):

$$\hat{P}_j(FC) = \frac{C_j(FC)}{\hat{N}_j^*} \quad \text{and} \quad \hat{P}_j(MC) = \frac{C_j(MC)}{\hat{N}_j^*}, \quad (\text{Eq. 2-7})$$

We emphasize that $\hat{P}_j(FC)$ and $\hat{P}_j(MC)$ differed from survey specific \hat{p}_{ij} (directly estimated with CJS models).

We also established, for each type of survey (FC and MC), the increase in detection probabilities (in percentage) necessary to obtain an average count of kites (\bar{C}) ≥ 650 .

Estimates of Precision and Magnitude of the Difference between Estimates

We used the delta method to compute the variances of derived estimates (Williams et al. 2002). 95% confidence intervals (95% CI) of any parameter θ that was not strictly positive (e.g., estimate of magnitude of the difference, see below) were computed as follows: 95% CI [$\hat{\theta}$] = $\hat{\theta} \pm t_{0.025,df} * \widehat{SE}[\hat{\theta}]$, where $\widehat{SE}[\hat{\theta}]$ is the estimated standard error of $\hat{\theta}$ and $t_{0.025,df}$ is the upper 97.5 percentile point of the t distribution on df (Burnham and Anderson 2002). As recommended by Burnham and Anderson (2002), for any parameter θ that is strictly positive (e.g., population size), we used an approximation for computing 95% CI [$\hat{\theta}$] that is based on a lognormal distribution (p. 259 Burnham and Anderson 2002). The magnitude of the difference between two estimates (\widehat{MD}) was estimated by computing the arithmetic difference between estimates (Cooch and White 2005).

Results

Population Size and Average Population Growth Rate

Estimates of $\hat{\phi}_{ij}$ and \hat{p}_{ij} were obtained with model averaging of models $\phi.p.$, $\phi.p_t$, $\phi_t.p.$, and $\phi_t.p_t$ for each year (estimates of $\hat{\phi}_{ij}$, \hat{p}_{ij} and other survey-specific parameter estimates used to compute estimates of superpopulation size are available on-line see Table A-1 in Appendix A). There was no need to adjust for lack of fit of the most general model in 2002, 2003, 2004 and 2005, because \hat{c} was ≤ 1 , and test 2 + test 3 from RELEASE were all non significant ($p > 0.05$). In 2001, the test 2 + test 3 was significant ($p = 0.02$). Therefore, we adjusted for lack of fit of the most general model in 2001 ($\hat{c} = 2.2$). Estimates of superpopulation size (\hat{N}_j^*) from 1997 to 2000 were obtained from Dreitz et al. (2002), whereas estimates from 2001 to 2005 are the results of the present study. Estimates of superpopulation size between 1997 and 2000 were fairly constant and relatively high (Dreitz et al. 2002; Figure 2-2). Superpopulation size estimates decreased sharply during the interval 2000-2002, but there was an apparent stabilization, or even slight increase (but note the 95% CI overlap) in 2004 and 2005. The average superpopulation size for the last 9 years (1997 to 2005) was 2254 (95% CI = 2124 to 2392). Estimates of the 8-year average growth rate based on superpopulation estimates was 0.93 (95% CI = 0.84 to 1.03). Estimates of annual growth rate based on superpopulation estimates were > 1 , in 1998, 2003 and 2004 (Table 2-1). Estimates of the 8-year average growth rate was 1.11 (95% CI = 0.91 to 1.37) based on FC; and 0.99 (95% CI = 0.86 to 1.12) based on MC. Estimates of the 3-year running average growth rate based on superpopulation estimates and on MC were > 1 for $\hat{\lambda}_{02-04}$ only (Table 2-1). Estimates of the 3-year running average growth rate based on FC was < 1 for $\hat{\lambda}_{00-02}$ only (Table 2-1).

Average Number of Kites Before and After Decline Based on the Superpopulation Approach

Estimates of superpopulation size suggests three major periods: a pre-decline period (1997 to 2000), a decline period (2000 to 2002) and a post decline period (2002 to 2005) (Figure 2-2). We computed the average number of kites during the pre and post decline periods.

Prior to decline (1997 to 2000), the average number of kites based on the superpopulation estimator was 3157 (95% CI = 2909 to 3426). After decline (2002 to 2005) the average number of kites was 1407 (95% CI = 1278 to 1550). There was a substantial decrease between before and after decline ($\widehat{MD} = 1750$; 95% CI = 1457 to 2041). This represented a 55% decrease (95% CI = 46% to 67%) when compared with predecline levels.

Average Number of Kites Before and After Decline Based on Count Data

Average number of kites before decline (1998 to 2000) based on FC data was 397 kites (95% CI = 164 to 959) and 403 (95% CI = 316 to 514) after decline (2002 to 2005). Therefore, FC data showed a slight increase in kite numbers between the intervals 1998 to 2000 and 2002 to 2005; however, the difference was not biologically significant ($\widehat{MD} = 6$; 95% CI = -220 to 208). Based on MC data average number of kites (\bar{C}) before decline (1998 to 2000) was 600 (95% CI = 462 to 779) and after decline (2002 to 2005) was 410 (95% CI = 337 to 499). Although 95% CI intervals of \bar{C} overlapped, MC data showed a substantial decrease in kite numbers between the intervals 1998 to 2000 and 2002 to 2005, ($\widehat{MD} = 190$; 95% CI = 82 to 298). This represented a 32% decrease (95% CI = 20% to 51%).

Average Number of Kites and Growth Rate Based on Count Data

The average number of kites counted with FC and MC for the last 8 years (1998 to 2005, but excluding 2001), was 401 kites (95% CI = 319 to 503) for FC and 491 kites (95% CI = 392 to 616) for MC. The CV was 0.09 for MC and FC.

Estimates of annual growth rate based on FC were < 1 in 2000 and 2002 (Table 2-1).

Estimates of annual growth rate based on MC were < 1 from 1999 to 2002 (Table 2-1).

Number of Young

There was a sharp decline in the number of young marked starting in 1999 (Figure 2-3). The average number of young marked from 1992 to 1998 was 200 (95% CI = 145 to 277), whereas the average number of young marked between 1999 and 2005 was 61 (95% CI = 38 to 96). The difference was substantial ($\widehat{MD} = 139$; 95% CI = 75 to 204). This represented a 70% decrease (95% CI = 41% to 100%).

The number of young produced in 2004 and 2005 based on the superpopulation approach were $\widehat{N}_{Y2004}^* = 414$ and $\widehat{N}_{Y2005}^* = 55$. The detection probabilities in 2004 and 2005 were $\widehat{P}_{Y2004} = 0.16$ and $\widehat{P}_{Y2005} = 0.35$. Estimates of confidence intervals could not be computed because sample size of resighting of young kites was too small.

Detection Probabilities for FC and MC

An increase of 63% in detection probability was necessary to obtain an average count > 650 for the FC survey; an increase of 33% in detection probability was necessary to reach a similar target based on the MC survey data (Table 2-1). Detection estimates increased over the years for both types of surveys (Table 2-1).

Discussion

Population Decline

Our results based on the superpopulation approach indicate that the population of Snail Kites in Florida declined sharply between 2000 and 2002 (Figure 2-2). Although estimates were slightly higher for 2004 and 2005, there was no evidence of a substantial recovery. The reduction in the estimated average kite abundance before and after decline was substantial (55% reduction

in abundance). The method we used to estimate the superpopulation size of kites was also useful in obtaining the number of young produced per breeding season. Although this parameter is difficult to estimate in the wild, it is often needed to evaluate the viability of threatened populations. For instance, the superpopulation approach is an appealing method to compute reliable estimates of fertility rates, which are critical to correctly parameterize many types of population viability analyses (Morris and Doak 2002).

We only had data to compute estimates of the number of young produced for 2 years (2004 and 2005). We also used these estimates to compute the proportion of young marked during these 2 years (i.e., detection of young). The fact that detection of young varied substantially in 2004 and 2005 suggests that one should be cautious in using the number of young marked as an indicator of the number of young produced. However, we believe detection estimates for these 2 years corresponded to extreme values. We expected low detection probability for 2004 because birds bred unusually early, which meant a large proportion of birds fledged before they could be marked. Conversely, in 2005 we invested an unprecedented effort in nest searching and marking young, which led to higher detection. Unless detection declined significantly between the intervals 1992-1998 and 1999-2005, we expect the observed number of young marked to be representative of an important decline in the number of young produced. We believe detection is likely to have increased in recent years because we invested more effort in nest-searching activities than in earlier years. An increase in detection implies that the reduction in the number of young produced in recent years is even more severe than is apparent in Figure 3-3. Models used to obtain the number of young produced assumed that estimates of ϕ_{ij} and p_{ij} for young and adults were similar. Appropriate sample size of resighting of young kites should be collected

in the future to check the assumption that adult estimates of ϕ_{ij} and p_{ij} provide a reasonable approximation to estimate the number of young produced.

Problems Associated with Counts and Implications for Recovery Plans

Identifying population decline is critical to the process of species conservation. In practice, it is often the documentation of population decline below a critical threshold that leads to the classification of species as endangered under the ESA. Additionally, identifying a reduction in population size may prevent unsubstantiated downlisting. The legal protection offered by the ESA is in many cases essential to the persistence of many species at risk of extinction (Doremus and Pagel 2001). Our results provide a compelling example of the risks associated with setting recovery targets that are based on deficient monitoring programs. Next we explain how some of the current recovery targets presented in the Snail Kite recovery plan (USFWS 1999) could be met (even with a declining population) if monitoring does not account for major sources of error such as detection.

One of the major recovery criteria listed in the plan states that the 10-year average population size should be > 650 . Even the most recent superpopulation estimates obtained during our study indicated that the actual Snail Kite population size may be twice this number. This suggests that although the 8-year-average counts obtained with FC and MC were all below the recovery target set by the USFWS (i.e., 650 kites), it is likely that by increasing the search effort (e.g., increase in the number of field personnel), more than 650 kites could have been counted during these surveys. In fact, an increase of 33% in detection probability (i.e., the proportion of kites counted from the “true” population size) during MC counts and 63% during the FC counts would have boosted the average number of kites counted over a period of 8 years to above the 650 target (Table 2-1). In both cases CV was < 0.2 (i.e., $< 20\%$). The second recovery criterion

states that kite numbers should not fall below 500 for any given year. This condition would not have been met for the FC count with detection increased by 63%, because the count in 1998 would be 460 (but increasing detection from 0.09 to 0.16 in 1998 would have brought the count for that year to 501). Similarly, this condition would not have been met for the MC count with detection increased by 33%, because the count in 2003 would be 463 (but increasing detection from 0.30 to 0.43 in 2003 would have brought the count for that year to 501).

The third recovery criterion stipulates that the 3-year running average should not be < 1.0 over a period of 10 years. Out of the five averages that could be computed for the last 8 years of data for the FC count, only one value fell below 1.0. Reducing the proportion of birds that were observed in 2001 from 0.19 to 0.11 (see Table 2-1), would have pushed all values of the running average for the FC count above 1.0 (although the lower CI of these values may have fallen below 1.0, nothing is mentioned in the recovery plan about parameter uncertainty of growth rate estimates). One can think of scenarios that would cause such a reduction in the proportion of kites counted. For example, dry conditions could reduce airboat access to wetlands used by kites.

Finally, when computing the 8-year average of growth rate for the superpopulation, the FC count and the MC count, we found that the growth rate was < 1.0 for the superpopulation and the MC count but was > 1.0 for the FC count (in all cases lower 95% CI were < 1.0). The fact that the estimate of the average growth based on FC data was > 1.0 , even though the population was declining, is most likely due to the increase in detection probabilities over the years (Table 2-1). This increase in detection probability was also observed for the MC data, and resulted in an inflated 8-years average growth rate for the MC survey as well. The observed increase in detection probabilities over time could be due to an increase in the number of field personnel in recent years (since 2002).

A particularly disturbing fact regarding count data is that, despite the drop in kite abundance (55% based on the superpopulation approach) the FC count did not indicate a reduction in kite numbers. The MC count, however, indicated a reduction in kite numbers. The MC count may be less biased than FC because for every sampling year the maximum count will be closer to the true abundance than any other single count. This is because all counts underestimate true abundance, therefore the maximum count should be the closest to the true abundance than any other count. However, since both types of counts ignored detection and did not deal effectively with sampling variation they were therefore biased. The FC count (i.e., single annual count) is by far the most common type of count survey. The format of the FC count was very similar to the surveys conducted by the Florida Fish and Wildlife Conservation Commission (FFWCC) between 1995 and 2004, except that the FFWCC annual count took place during the midwinter (December to February), and was restricted to fewer wetlands (FFWCC unpublished data). This spatial restriction also increases potential for errors associated with spatial variation.

Thus, by simply varying the proportion of kites observed during counts (i.e., detection) three major recovery criteria in the Snail Kite recovery plan were close to being met based on a monitoring that relied on counts (e.g., FC) in spite of an alarming decrease in estimated population size and reduced reproduction.

Our primary purpose was not to set new recovery criteria for the Snail Kite (although our study strongly suggests that existing criteria are in need of revisions), and we point out that several authors have proposed promising approaches to set more appropriate criteria (e.g., Gerber and DeMaster 1999; Morris and Doak 2002). Instead, we emphasize the critical importance of designing monitoring programs that address major, common sources of errors,

because reliability of the recovery criteria will strongly depend on the quality of the monitoring data.

Importance of Monitoring to Diagnose Causes of Decline

Although the identification of population decline is an important step, it is evidently only part of the process of protecting a species. A next step should be to diagnose the cause of decline, or alternatively, factors limiting growth. In the case of kites, the drought that occurred in 2001 appears to coincide with the population decline and strongly affected adult and juvenile survival (Martin et al. 2006). However, the drought affected kite survival only temporarily (1 to 2 years, see Martin et al. 2006). The lack of evident recovery four years after this natural disturbance suggests that factors affecting reproduction and recruitment may prevent growth. The drastic reduction in the number of young kites marked (70% decrease), suggests that factors limiting reproduction may deserve more attention than they have received in the past. However, rigorous evaluation of the causes of decline and factors limiting growth needs to be performed.

Hypotheses related to disease, predation, food availability and nest substrate should probably be the focus of future investigations (see Peery et al. 2004, Martin et al. unpublished). The multiple competing hypotheses approach (MCH) provides an appealing framework to disentangle the factors that could potentially affect population growth of threatened species (Williams et al. 2002; Peery et al. 2004). Ideally, monitoring programs designed to tease apart ecological hypotheses using MCH, will incorporate both spatial variation and detectability. Addressing spatial variation is particularly important to effectively assess hypotheses related to spatial dynamics (Yoccoz et al. 2001). This may be of particular relevance to the management of spatially structured populations of species that occupy large landscapes (Yoccoz et al. 2001).

Conclusion

A growing number of ecologists are recognizing the value of using designs that incorporate both detectability and spatial sampling because (1) they allow for better parameter estimates, and (2) because they favor more effective evaluation of ecological hypotheses (reviewed in Yoccoz et al. 2001). As illustrated by our results, these sampling design issues are extremely relevant to the protection of endangered species. Indeed, ignoring detectability and spatial variation may lead to dangerously inappropriate management decisions (e.g., unsubstantiated downlisting). Nonetheless, considerable resources continue to be invested in monitoring programs that ignore these sources of variability, and many recovery plans continue to rely on these flawed programs. Given the immediate risks of extinction faced by an increasing number of species, it is urgent for managers and conservation biologists to rigorously revisit these recovery plans and monitoring programs that do not effectively address spatial sampling and detectability.

Table 2-1. Estimates of Snail Kites annual population growth rates; and 3-year running average of growth rates.

Parameter ^a	Year (j)						
	1998	1999	2000	2001	2002	2003	2004
<u>Annual rates</u>							
$\hat{\lambda}_j$ (S)	1.14 ^b	0.77 ^b	0.73 ^b	0.69	0.83	1.29	1.05
$\hat{\lambda}_{cj}$ (FC)	1.26	1.57	0.69	1.09	0.77	1.25	1.17
$\hat{\lambda}_{cj}$ (MC)	1.18	0.83	0.85	0.89	0.83	1.16	1.17
<u>Average rates</u>							
$\hat{\lambda}_{j-(j+2)}$ (S)	0.88 ^b	0.73 ^b	0.75 ^b	0.94	1.05	-	-
$\hat{\lambda}_{cj-(j+2)}$ (FC)	1.17	1.12	0.85	1.04	1.06	-	-
$\hat{\lambda}_{cj-(j+2)}$ (MC)	0.95	0.85	0.86	0.96	1.05	-	-

^aParameter explanations: $\hat{\lambda}_j$, estimates of annual population growth rate based on superpopulation estimates (S); $\hat{\lambda}_{cj}$, estimates of annual population growth based on first-count surveys (FC) and maximum count survey (MC); $\hat{\lambda}_{j-(j+2)}$, 3-year running average growth rate based on $\hat{\lambda}_j$ (S); $\hat{\lambda}_{cj-(j+2)}$, 3-year running average growth rate based on $\hat{\lambda}_{cj}$ (FC) and $\hat{\lambda}_{cj}$ (MC).

^bComputed using data from Dreitz et al. (2002).

Table 2-2. Estimates of detection probability of Snail Kites for first-count surveys (FC) and maximum count surveys (MC) for each year between 1998 and 2005^a.

Detection	Year (j)								\bar{C}
	1998	1999	2000	2001	2002	2003	2004	2005	
$\hat{P}_j(FC)$	0.09	0.10	0.20	0.19	0.30	0.28	0.27	0.30	399
$\hat{P}_j(FC)+63\%*\hat{P}_j(FC)$	0.15	0.16	0.33	0.31	0.49	0.45	0.44	0.49	651
$\hat{P}_j(MC)$	0.18	0.19	0.20	0.23	0.30	0.30	0.27	0.30	490
$\hat{P}_j(MC)+33\%*\hat{P}_j(MC)$	0.24	0.25	0.27	0.31	0.40	0.40	0.36	0.40	654

^a Estimates were obtained by computing the ratio count over superpopulation size for each year (j). The \bar{C} corresponds to the average number of kites counted using the estimated detection for FC ($\hat{P}_j(FC)$) and for MC ($\hat{P}_j(MC)$) and the detection probabilities that were increased by 63% for the FC surveys ($\hat{P}_j(FC)+63\%*\hat{P}_j(FC)$) and 33% for the MC surveys ($\hat{P}_j(MC)+33\%*\hat{P}_j(MC)$).

^b Detection probabilities from 1998 to 2000 were computed using estimates of superpopulation size published in Dreitz et al. (2002).

^b Computed using data from Dreitz et al. (2002).

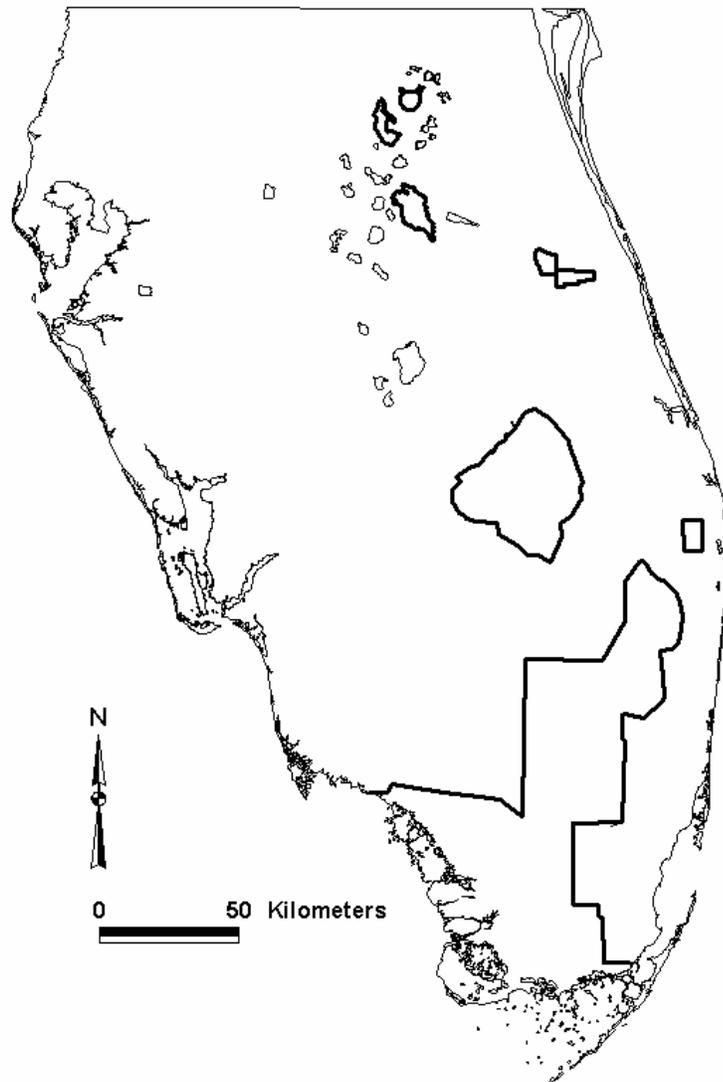


Figure 2-1. Map of the wetlands that were sampled to obtain both counts and capture-resighting information of Snail Kite for the estimation of population size. Thick black line delimits areas sampled by the Florida Cooperative Fish and Wildlife Research Unit.

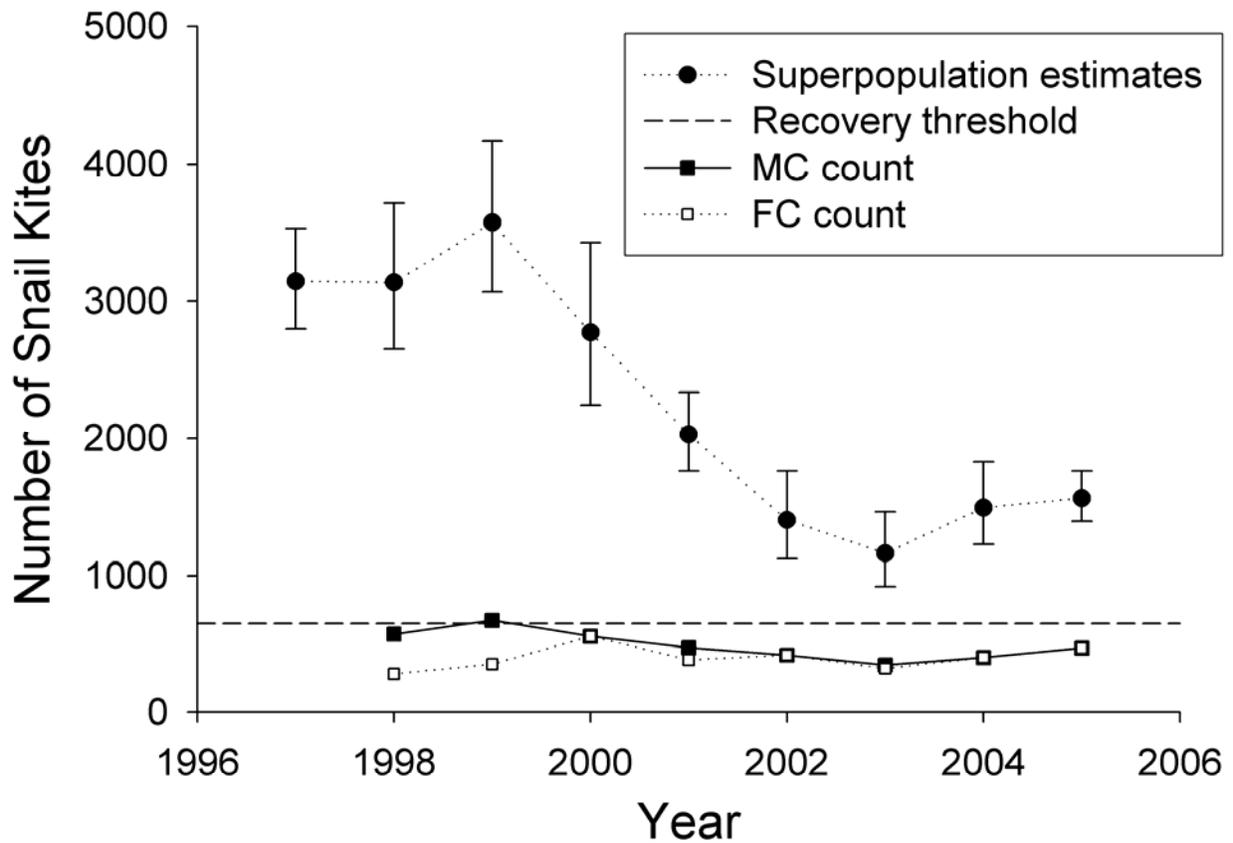


Figure 2-2. Comparison of the estimates of population size of Snail Kites (using the superpopulation approach) with annual counts. Data for three count surveys are plotted in the figure: (1) first count survey (FC); (2) maximum count survey. Kite numbers and estimates of population size from 1997 to 2000 were obtained from Dreitz et al. (2002), while estimates from 2001 to 2005 were results of the present study. Error bars correspond to 95% confidence intervals. The recovery target for Snail Kites (650 birds), set by the USFWS in 1999 is also presented.

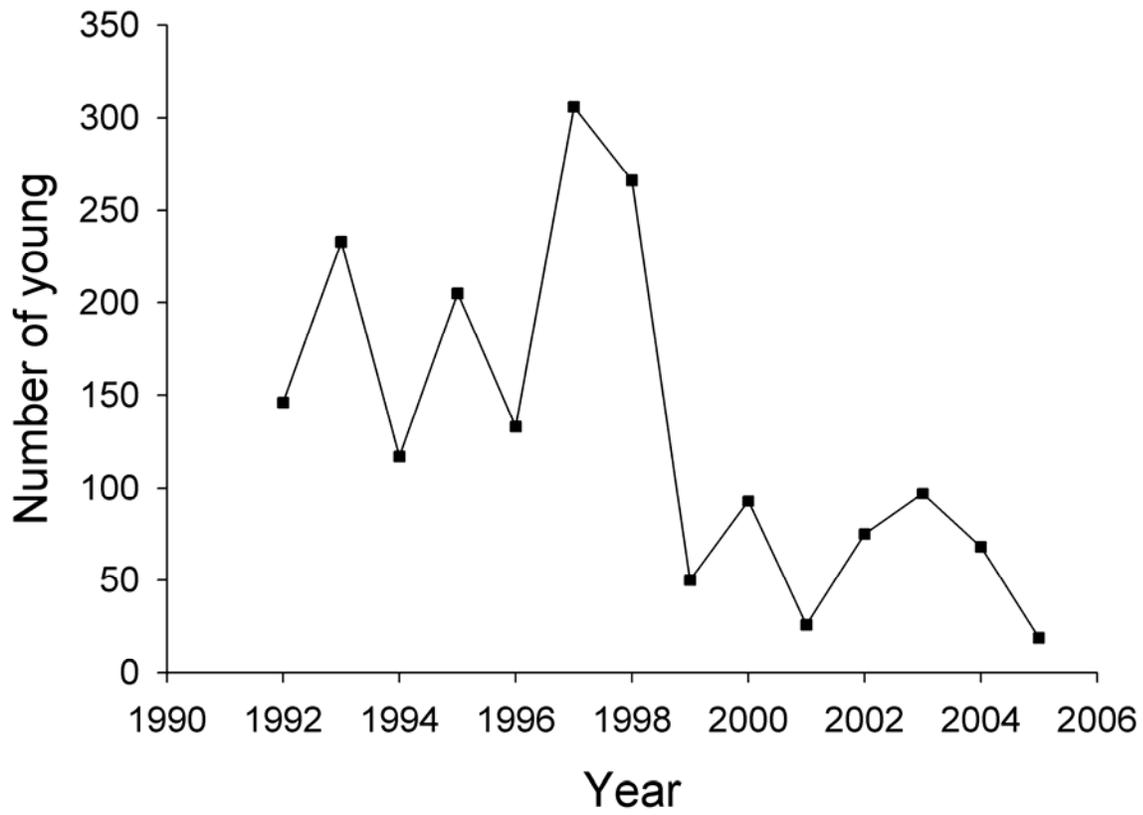


Figure 2-3. Number of young (i.e., nestlings close to fledging) Snail Kites marked every year from 1992 to 2005.

CHAPTER 3
MULTISCALE PATTERNS OF MOVEMENT IN FRAGMENTED LANDSCAPES AND
CONSEQUENCES ON DEMOGRAPHY OF THE SNAIL KITE IN FLORIDA

Introduction

Habitat loss and fragmentation are major factors affecting populations of many organisms (Holt and Debinski, 2003). One detrimental effect is reduced movement of these organisms (Holt and Debinski 2003; Smith and Hellmann 2002). This may have important population consequences given that movement is a fundamental process driving the dynamics of fragmented populations, as it connects local populations through emigration and immigration (Hanski 1999; Clobert et al. 2001).

To assess how movement influences the dynamics of spatially-structured populations, we need to understand how animals perceive, move through, and learn about the landscapes they occupy (Hanski 2001). We also need to evaluate the relative importance of critical factors governing movement processes at a pertinent spatio-temporal scales. Patch size, distance between patches, and patch quality are major factors influencing the movement of many animal populations in spatially structured systems (Hanski 1999). Several studies have demonstrated the effect of distance on movement (e.g., Haddad 1999; Hanski 2001). Theoretical models of metapopulation dynamics commonly assume greater emigration from smaller patches (Hanski 2001; Schtickzelle and Baguette 2003), and higher immigration toward larger habitat patches because of the more frequent encounters of moving animals with patch boundaries (**patch boundary effect**) (Lomolino 1990; Hanski 2001).

Fragmentation and habitat reduction reduce patch size and increase the linear distance between patches: both alterations are likely to decrease movement (Holt and Debinski 2003). Creating areas unsuitable for foraging or breeding (i.e., **matrix**) between or around habitats may also decrease survival (Schtickzelle and Baguette 2003).

Despite the importance of providing robust quantitative demographic and movement estimates of populations inhabiting fragmented landscapes (Hanski 2001; Williams, Nichols and Conroy 2002), few empirical estimates exist, especially for vertebrates using large landscapes.

From 1992 to 2004, we studied an isolated population of Snail Kites (*Rostrhamus sociabilis*) restricted to Florida. The Snail Kite is a raptor that feeds almost exclusively on freshwater apple snails *Pomacea paludosa* (Beissinger 1988). The kite's restricted diet makes it a wetland-dependent species. Since wetlands in Florida have been severely reduced (Davis and Ogden 1994; Kitchens et al. 2002) since the early 1930s, the population is now confined to the remaining fragments of wetlands extending from the southern end to the centre of the state (Figure 3-1).

Because the availability of apple snails to kites is related to hydrologic conditions, variations in water levels are likely to influence Snail Kite behaviour and demography. In particular, snail availability to kites is greatly reduced during droughts (Beissinger 1995). Beissinger (1986) and DeAngelis and White (1994) described the hydrologic environment used by kites as highly spatially-temporally variable. In such a variable environment, one might expect kites to show nomadic tendencies (Bennetts and Kitchens 2000). Bennetts and Kitchens (2000) developed a conceptual model of kite movement along a food resource gradient. They hypothesized that when food is scarce (during drought), kites move to refugia habitats or die. When food is abundant exploratory movements can be done at minimum risk of starvation. During droughts, kites that have previously explored wetlands throughout their range are less likely to search randomly for alternative habitats, and thus are less likely to starve. Their model also suggests that when food is superabundant, occasional territorial defence may occur for short periods of time, but otherwise kites are typically non territorial (Beissinger 1995). Bennetts and

Kitchens (2000) estimated the average probability of movement among wetland units (Figure 3-1) to be approximately 0.25 per month, which they associated with a nomadic type of behaviour. However, this probability was obtained without considering the complexity of the spatial configuration of the system.

We attempted to enhance our understanding of how kites perceive and move throughout the landscape by incorporating a detailed level of spatial complexity into a modelling approach at multiple spatial scales. First, we estimated movement within a group of **contiguous wetlands** (separated by small physical barriers, easily crossed by kites: such as a road). The distance between centroids of these contiguous wetlands varied between 16 and 110 km. Second, we estimated movement within a group of wetlands separated by a moderate extent of matrix (< 5 km): **moderately isolated wetlands**. Matrix areas generally consist of non-wetland areas (e.g., agricultural or urban areas). The distance between centroids of these moderately isolated wetlands varied between 10 and 44 km. Third, we estimated movement among wetlands or groups of wetlands isolated by extensive matrix (> 15 km): **isolated wetlands**. To be consistent with the classification of Bennetts et al. (1999a), we called these isolated wetlands: **regions**. Most regions used to be connected through the Kissimmee-Okeechobee-Everglades watershed, and became isolated as a result of habitat reduction (Davis and Ogden 1994; Light and Dineen 1994) (Figure 3-1). The distance between centroids of these regions varied between 69 and 232 km.

We also explored movement at two temporal scales. First, we examined movement at an annual scale. Because of the period of sampling (i.e., peak of breeding season), this informed us about patterns of breeding and natal philopatry of Snail Kites. Second, we examined movement patterns on a monthly scale. This period of sampling included the entire year (i.e., including

periods outside the breeding season). Thus this study also informed us about movement patterns that were independent of breeding activities (e.g., exploratory movement). Finally, we discussed the consequences of kite movement on survival.

To date, the assumption has been that during a drought, kites move from areas most affected by drought toward areas least affected by drought (Beissinger and Takekawa 1983; Bennetts and Kitchens 2000; Takekawa and Beissinger 1989); and that the impact of a drought on the kite population will depend on the spatial extent and intensity of the drought (Beissinger 1995; Bennetts and Kitchens 2000). However, all hypotheses regarding kite responses to drought are based on count data that do not consider detection probabilities. Therefore, these hypotheses have yet to be rigorously tested and quantified with appropriate statistical methodologies (Williams et al. 2002).

Hypotheses and Predictions

Prediction 1: Effect of fragmentation on movement

We predict that movement will covary positively with **connectivity** (i.e., amount of matrix between wetlands). Thus, movement among contiguous wetlands should be greater than among moderately isolated wetlands, and movement among moderately isolated wetlands should be greater than among isolated wetlands (i.e., regions). Prediction 1 implies that movement within regions will be greater than between regions, which could also be explained by a distance effect on movement. However, if movement among contiguous wetlands is greater than among moderately isolated wetlands, the effects of connectivity on movement can be separated from the effects of distance (between centroids), since distances between centroids of contiguous wetlands are greater than that of moderately isolated wetlands in the study area.

Prediction 2: Effect of patch configuration on movement

We expect patch size and distance between patch centroids to influence movement. Movement among patches (i.e., wetlands) should decrease with distance (Hanski 1999). Emigration should be higher from smaller patches (Hanski 2001; Schtickzelle and Baguette 2003), and immigration should be higher toward larger patches (Lomolino 1990; Hanski 2001).

Prediction 3: Patch configuration affects juvenile movement more than adult movement

Patch size and distance between patches are more likely to influence movement of birds that have never dispersed from their natal area (typically young individuals), than birds that are aware of wetlands outside their natal area. Because we expect the number of wetlands visited to increase with time, on average juveniles (≤ 1 year) should have visited fewer wetlands than adults. Therefore, movement of juveniles should be less influenced by habitat characteristics (e.g., habitat quality) of destination sites than movement of adults, whose movement may be partly influenced by their knowledge of the location of multiple wetlands (assuming that kites remember sites they have already visited). This prediction is derived from hypotheses developed by Bennetts and Kitchens (2000) and (Bell 1991), who suggested that many species learn from exploratory movements, and thus modify their movement patterns according to their experience with visited habitats. Thus we expect a stronger relationship between movement and geometric features of the landscapes for juveniles than for adults.

Prediction 4: Drought effect on movement

- a. During a drought, we predict that some birds will move from areas most affected to areas least affected by drought (e.g., Takekawa and Beissinger 1989).
- b. Because of their knowledge of alternative wetlands and the paths linking these wetlands, adult birds should be more successful than juveniles in moving refugia habitats.

Prediction 5: Drought effect on survival

- a. As predicted by Beissinger (1995) and Bennetts and Kitchens (2000), we expect survival to be lower during drought.
- b. Survival should be lower in regions most affected by drought.
- c. Because adults are more likely to move successfully to areas least affected by drought, we expect survival to decrease more for juveniles than for adults.

Methods

Study Area

This study was conducted throughout central and southern Florida, encompassing most of the habitats used by the Snail Kite. Thirteen wetlands were sampled (Figure 3-1). Given that kites can cross small physical barriers delimiting each wetland (e.g. road) with relative ease (Bennetts 1998), we further aggregated the units into five larger groups of wetlands (regions) (Figure 3-1). We used Bennetts (1998) and Bennetts et al. (1999a) definition of a region. Regions were separated from other regions by an extended matrix (>15 km). Water Conservation Areas (WCAs), Everglades National Park and Big Cypress National Preserve constituted a group of contiguous wetlands and were grouped into one region: the Everglades region (E). The Kissimmee Chain of Lakes region (K) included Lake Tohopekaliga, East Lake Tohopekaliga, Lake Kissimmee, and all the small lakes in the surrounding areas. Wetlands in the K region were isolated by moderate extent of matrix (< 5 km). Lake Okeechobee (O), St Johns Marsh (J), and Loxahatchee Slough (L), constituted their own regions. Areas of wetlands and distances between wetlands were estimated using a Geographic Information System (ArcView GIS 3.2; Xtools, DeLaune 2000).

Criteria for Determining the Regional Impact of the 2001 Drought

We used water-stage data (elevation of water surface measured in feet above the National Geodetic Datum of 1929) recorded daily in each of the major wetland units and made available

by the South Florida Water Management District (<http://www.sfwmd.gov/org/ema/dbhydro>) to develop an index of drought impact. We used the data corresponding to the period of study (1992 to 2003). Water stage was averaged by month for the entire time series. We calculated the mean of the monthly average stages for March through June of each year. This period is especially critical for apple snail breeding and availability to the kites (Darby 1998) and also includes the greater part of the seasonal dry season when water stages are at their annual minimum (i.e., when water levels are most likely to affect kite survival and movement).

We determined the mean stage for the period of record (1992-2003) for each major wetland unit and determined where drought-year water stage means fell in terms of standard deviations below this value. This method, proposed by Bennetts (1998), allows for comparisons of drought intensity among wetlands for the period of record. The 2001 drought occurred between January and August (Smith et al. 2003). Intensity of drought was maximal for the lowest drought score values (DSV). This analysis indicated that region E (WCA3B DSV = -2.32; Big Cypress DSV = -2.28; WCA1A DSV = -2.18; WCA3A DSV = -1.92; WC2B DSV = -1.41; WCA2A DSV = -1.20) and region O (DSV = -2.57) were the most-impacted, while region K (Lake Kissimmee DSV = -0.72; Lake Tohopekaliga DSV = -0.84; Lake East Toho DSV = -0.98) was the least affected. Region J was also affected (DSV = -1.92).

Statistical Models to Estimate Movement and Survival

Multistate capture-recapture models (Hestbeck, Nichols and Malecki 1991; Williams, Nichols and Conroy 2002) were used to estimate apparent survival (ϕ), movement probabilities (ψ) and detection probabilities (p) simultaneously. ϕ^u was defined as the probability for a kite alive in location u (i.e., wetland u) at time t to survive between time t and $t+1$; and p^u was the probability of detecting (sighting) a kite that was alive and associated with wetland u . We

defined ψ^{us} as the probability that a kite in wetland u at time t was in wetland s at time $t+1$, given that it was alive at $t+1$. Modelled parameters used notation from Senar, Conroy and Borrás (2002); time dependency was (t) and no time effect was (.). We assigned each bird to one of two age classes: juveniles (juv), 30 days to 1 year; and adults (ad), older than 1 year. Effects embedded in other factors are shown using parentheses. A multiplicative effect is shown by (*) and an additive effect is shown by (+). All computations of the movement and survival probabilities were carried out using program MARK V 4.1 (White and Burnham 1999).

Field Methods for the Study of Movement on a Monthly Scale

Between 1992 and 1995, 165 adult and 120 juvenile Snail Kites were equipped with radio transmitters with a battery life of approximately 9-18 months (Bennetts and Kitchens 2000). Between 1992 and 1995, aircraft radio-telemetry surveys were conducted on a weekly basis (two 4-5 hour flights every week) over a large portion of the entire range of the population in Florida. Previous analyses by Bennetts et al. (1999a) and Bennetts (1998) found no evidence of radio effects on survival or movement probabilities.

Statistical Methods to Estimate Movement on a Monthly Scale Using Radiotelemetry

Estimating monthly movement among regions

To estimate monthly movement probabilities (ψ) of radio-tagged individuals among regions, we used multistate models. Because monthly survival estimates were beyond the scope of our study, we removed individuals from the analysis after they were last observed and fixed survival parameters to 1. For this analysis, we included individuals for which the fate and location could be determined with certainty (i.e., detection probability equals 1). In addition, birds that temporarily disappeared and then reappeared in the sample were censored when they disappeared and were included again when they reappeared (Williams et al. 2002). This analysis included six states: the five regions described above (E, K, O, L, J) (Figure 3-1), and one state

containing peripheral habitats and matrix area (P, all locations outside the sampled areas). To compute the probability of movement out of a patch (wetland or region), we summed the transition probabilities out of that patch. To calculate the **average monthly probability** of movement out of any wetland within a region, we computed the average of the monthly movement probabilities out of every wetland in the region of interest.

We tested the effect of patch size (AR for the surface area of the receiving site, and AD for the surface area of the donor site), distance (d), region (r), age, and time on movement probabilities. The notations for age and time followed the ones common to all analyses. We also tested the effect of year ($year$), given that the radio-telemetry study was conducted between 1992 and 1995. A seasonal effect ($seas$) with respect to three 4-months seasons (January-April, May-August, September-December) (Bennetts and Kitchens 2000); and a breeding season effect ($breed$; breeding season: January-June; non-breeding season: July-December) were also included.

With known fate multistate data (for which the detection probability is 1), there is currently no appropriate **Goodness of Fit test (GOF)**. However, most analyses presented in our study included fairly general models.

Estimating monthly movement within regions using radio-telemetry

The same method was used for this analysis as for the among-regions analysis. Because two regions comprised several wetland units, we conducted two separate analyses. The analysis for the K region contained four moderately isolated wetlands (denoted: mw): Lake Tohopekaliga, Lake East Tohopekaliga, Lake Kissimmee, and a site containing all of the small lakes in the surrounding area (Figure 3-1). Analysis for the Everglades region contained five contiguous wetlands (denoted: cw): WCA3A, WCA3B, Everglades National Park, and Big Cypress (Figure 3-1). We also, aggregated three contiguous wetlands (WCA1, WCA2A and WCA2B), into one

site, as our data set would not have permitted a seven-site model. Patch size and distance were included as factors in the models of region E only. This analysis was not applicable for region K, because of the site that included all of the small lakes.

Field Methods for the Study of Movement and Survival on an Annual Scale

We used mark-resighting information collected during the peak of the breeding season (March 1-May 30), for a period of 13 years (1992 to 2004). Between 1992 and 2004, 1730 juveniles were marked just before fledging. Juveniles advance to the adult age class at the beginning of the next breeding season (Bennetts et al. 2002). In addition, between 1992 and 1995, 134 adults (i.e., older than 1 year) were banded. Bands were uniquely numbered anodised aluminium colour bands. Banded kites were identified from a distance, using a spotting scope. Each wetland was surveyed at least once using an airboat.

Statistical Methods to Estimate Annual Movement and Survival Using Banding Data

We used a multistate model to estimate annual movement and survival probabilities. We assigned the location of each bird to four regions (see STUDY AREA). We excluded region L from this analysis to maximize precision, as relatively few birds were recorded in this area.

Estimating survival

A set of biologically relevant models was developed that allowed ϕ and p to vary across time, or stay constant for each age class. Because our data set included kites banded as juveniles and as adults, age was modelled both as time since marking and as a group effect. We also created models that included drought effect on ϕ and p . We included a drought effect, which assumed different effects on apparent survival in 2000-2001 and 2001-2002 (denoted: D_{1-2}). We used this approach because the drought was likely to affect ϕ before and after the 2001 sampling occasion. ND indicated that ϕ was constant during the remaining non-drought years (denoted:

ND). For juveniles we designed models with additive effect of time and region ($t+r$) on ϕ , but because of the drought few juveniles were fledged in 2001 (32 juveniles were fledged in K, 3 in J and none in E and O). We thus constructed models with additive effect of time and region on ϕ , except during the interval 2001-2002, during which ϕ was assumed to be similar among regions (denoted: $\phi_{juv}(r+t_d)$). Consequently, during the interval 2001-2002 model $\phi_{juv}(r+t_d)$ reflected apparent survival for northern regions (K and J). Because we expect environmental conditions to be more similar among neighbouring regions than among regions that are far apart, we expect survival in regions close to each other, to be similar. Thus we developed models that assumed similar apparent survival probabilities in neighbouring regions. Due to the proximity of regions E and O in the south (separated by 30 km) and K and J in the north (separated by 25 km), (conversely, O and J were separated by 50 km; Figure 3-1), we developed models with a common survival parameter for each group of regions (denoted $\phi^{[E=O \neq K=J]}$; superscripts indicate regions the survival probabilities pertain to; “=” indicates that ϕ^E is the same as ϕ^O , similarly ϕ^K is the same as ϕ^J ; “ \neq ” indicates that ϕ^E and ϕ^O are different from ϕ^K and ϕ^J). Models assuming a different ϕ for each region were denoted ($\phi(r)$).

Because the drought intensity was strongest in E, O and J (lowest DSV), and weakest in K (highest DSV), some models assumed similar drought effects on ϕ in E, O, and J (denoted $\phi^{[E=O=J]}(D_{1-2})$); with no drought effect on ϕ in K ($\phi^K(\cdot)$).

Estimating annual movement probabilities among regions using banding data

Our multistate approach using the banding data (described above) provided annual estimates of movement probabilities (ψ), among four regions (E, O, K and J). We tested the effect of the drought on movement between 2000-2001(denoted D_1). We also estimated the

probability for a kite to be found in a particular region (u) at year $t+1$, given that it was present in that same region in year t (ψ^{uu}). These probability estimates were used to evaluate the level of philopatry at each site. These estimates were obtained as one minus the estimated probabilities of moving away from the area.

Goodness of fit

Previous survival analyses indicated a strong age effect on ϕ (Bennetts et al. 2002). Unfortunately, we are not aware of GOF test accounting for an age effect on ϕ for multistate model. However, it is possible to test the fit of adult data separately. We used program U-CARE version 2.02, which tests the fit of the “Jolly move” (JMV) and Arnason-Schwarz models (AS) (Pradel, Wintrebert and Gimenez 2003). We were only able to test model JMV, which fit the data satisfactorily when testing the fit of adult data separately ($\chi^2_{102} = 104.3, P = 0.42$). The fit of the JMV model could not be assessed on juveniles separately (Test M requires > 4 occasions). Thus, as suggested by Senar, et al. (2002) we computed a GOF accounting for an age effect (by summing Test 3.SM, Test 2.CT and Test 2.CL, available from program U-CARE, see Choquet *et. al.* 2003), for a site-specific Cormack-Jolly-Seber (CJS) model in lieu of a multistate model. The site-specific CJS model fitted the data satisfactorily ($\chi^2_{175} = 152.1, P = 0.89$). We concluded that there was no evidence of lack of fit of the multistate model used (i.e., models in Table 3-3 accounted for an age effect on ϕ ; Choquet et al. 2003).

Model Selection Procedure

For each mark-resight analysis, we first developed and fitted a set of biologically relevant models that corresponded to our best *a priori* hypotheses (referred as starting models). We then developed models whose relevance was linked to the need to evaluate the fit of each of the starting models (Cam, Oro and Jimenez 2004). We used AICc (Burnham and Anderson 2002) as

a criterion to select the model that provided the most parsimonious description of the variation in the data (i.e. model with the lowest AICc). The value of ΔAICc (the difference between the AICc of a particular model and that of the model with the lowest AICc) was presented in each set of model-selection results. We also used AICc weight (w) as a measure of relative support for each model (Burnham and Anderson 2002). We reported only the model whose w was greater than 0.01.

Effect of Patch Size and Distance on Movement

Movement probabilities were modelled as linear-logistic function of patch size and/or distance (Blums et al. 2003). For example, probabilities of moving from one patch to another in function of distance were modelled as:

$$\text{Logit}(\psi(d)) = \beta_i + \beta_d(d),$$

where β_i, β_d , are the parameters to be estimated. β_i is the intercept, β_d is the slope for distance between patch centroids (d). Probability of moving was predicted to decrease with increasing distance between patches ($\beta_d < 0$) (Blums et al. 2003). Whenever the 95%CI [$\hat{\beta}_d$] estimate did not overlap 0, the relation was considered statistically significant.

Effect Size

To measure the magnitude of the difference between estimates we computed estimates of “effect size” (\widehat{ES}) as the arithmetic difference between estimates. Whenever the 95%CI [\widehat{ES}] did not include 0 the difference was considered statistically significant (Cooch and White 2005).

Estimates of Precision

Variations for derived estimates in our study were computed using the delta method (Williams et al. 2002). Confidence intervals for estimates that were strictly positive (ϕ, ψ), were

computed using the method proposed by Burnham et al. (1987) based on the lognormal distribution (Appendix B-1 in Appendix B).

Estimates of effect size (not strictly positive), were approximated as follows: 95%CI [$\hat{\theta}$]=
 $\hat{\theta} \pm 1.96 * \widehat{SE} [\hat{\theta}]$.

Results

Monthly Movement Probabilities Among Regions

Effects of patch size and distance

The most parsimonious model (with lowest AICc; Table 3-1.a.), was a model that only included a site-specific effect of movement ($\psi(r)$). However, the model that assumed movement probabilities to be site-specific for adults, but included a patch-size and a distance-between-patches effect plus interaction of these factors for juveniles ($\psi_{ad}(r) \psi_{juv}(AR * d)$), also received some support ($\Delta AICc=1.7$; Table 3-1.a.). This model had considerably more support than the model that assumed movement probabilities to be solely site-specific for adult birds and juveniles ($\psi_{ad}(r) \psi_{juv}(r)$; $\Delta AICc = 15.2$; see also Table B-1.a. in Appendix B).

When the analysis is conducted on juveniles only, the model $\psi_{juv}(AR * d)$ is considerably better than $\psi_{juv}(r)$ ($\Delta AICc = 14$; Table 3-1.b; see also Table B-1.b. in Appendix B), indicating that patch size and distance may be important in determining the movement probabilities of juveniles. Model $\psi_{juv}(AR * d)$ indicates that the probability of moving between two locations decreased with distance between these locations ($\hat{\beta}_d = -0.020$, 95 %CI = -0.032 to -0.007). Conversely, we could not show any relationship between the receiving site area and movement with this model ($\hat{\beta}_{AR} = -0.020$, 95 % CI = -0.247 to 0.207). The interaction for this model was positive, but not very strong ($\hat{\beta}_{AR*d} = 0.002$, 95 %CI = 0.0001 to 0.003). We also tried a model

with an additive effect of distance and patch size of the receiving sites, $\psi_{ad}(r) \psi_{juv}(AR + d)$. That model did not reach numerical convergence with program MARK when the data set included both juvenile and adult birds; we consequently ran this model on a data set that only comprised juvenile birds ($\psi_{juv}(AR + d)$; Table 3-1b). Although this model was less parsimonious than one that incorporated an interaction effect ($\Delta AICc = 3$; Table 3-1.b), it was considerably better than the site-specific model ($\Delta AICc = 14$; see also Table B-1.b. in Appendix B). Model $\psi_{juv}(AR + d)$ supported the hypothesis of a negative relationship between movement probabilities and distance ($\hat{\beta}_d = -0.011$, 95 %CI = -0.020 to -0.0030). This model also supported the hypothesis of a positive relationship between movement and size of the receiving sites ($\hat{\beta}_{AR} = 0.205$, 95 %CI = 0.120 to 0.289). The models that included the size effect of the donor patch on juvenile movement $\psi_{juv}(AD)$ received little support ($\Delta AICc = 6.5$; Table 3-1.b), but the β parameter for AD supported the hypothesis that emigration was lower out of larger patches ($\hat{\beta}_{AD} = -0.191$, 95%CI = -0.298 to -0.084).

There was no evidence of any patch size or distance effect on adult movement (Table 3-1.a and Table 3-1.c). Models that included effects of time, year, or season received no support ($w \sim 0$).

Monthly Movement Probabilities Within Regions

Movement within the Everglades region

The most parsimonious model for this analysis was $\psi(seas * cw)$ ($w \sim 1$; Table 3-2.a), which assumed movement probabilities to vary by season and to be site-specific.

Movement within the K region

The most parsimonious model for this analysis assumed movement to vary by season ($\psi(seas)$; $w = 0.67$; Table 3-2.b).

Comparison Among and Within Regions

The probability that a Snail Kite in any of the five wetlands in region E moved to another unit in that same region within the next month (**average monthly movement probability** among contiguous wetlands), using model $\psi(seas * cw)$ for the Everglades region (Table 3-2.a), was 0.29 (95%CI = 0.24 to 0.35). By contrast, the monthly movement probabilities from E to the four other regions was only 0.04 (95%CI = 0.03 to 0.05), using model $\psi(r)$ (Table 3-1.a). The same pattern was observed in region K where kites moved extensively among the moderately isolated wetlands in this region, using model $\psi(seas)$ (Table 3-2.b) we found the average monthly probability $\hat{\psi} = 0.15$ (95%CI = 0.13 to 0.17); with only a 0.09 (95%CI = 0.06 to 0.12) monthly movement probability from this region to the four other regions, using model $\psi(r)$ (Table 3-1.a).

The probability that kites in any of the five regions moved to another region within the next month (average monthly movement among isolated wetlands), using model $\psi(r)$ (Table 3-1.a) was 0.10 (95%CI = 0.08 to 0.12).

Average monthly movement among contiguous wetlands was significantly greater than among moderately isolated wetlands ($\widehat{ES} = 0.14$, 95%CI = 0.08 to 0.20). Average monthly movement among moderately isolated wetland was significantly greater than among isolated wetlands ($\widehat{ES} = 0.05$, 95%CI = 0.02 to 0.07); and average monthly movement among contiguous wetlands was significantly greater than among isolated wetlands ($\widehat{ES} = 0.19$, 95%CI = 0.13 to 0.25).

Interannual Survival Estimates

The most parsimonious model

$(\phi_{ad}^{[E=O \neq K=J]}(ND)\phi_{ad}^K(\cdot)\phi_{ad}^{[E=O=J]}(D_{1-2})\phi_{juv}(r+t_d)p(r*t)\psi(r*D_1)$, received overwhelming support from the data ($w = 0.96$; Table 3-3). This model had region specific apparent survival for adults, which did not vary over time but differed significantly between drought and non-drought years (Figure 3-2). There was an additive effect of region and time for estimates of apparent survival of juveniles, except for the interval 2001-2002, during which ϕ was assumed to be time dependent only. Sighting probabilities were region and time specific. Movement probabilities were region specific and were affected by the drought. Apparent survival estimates for adults kites located in neighbouring regions during non-drought were similar (i.e., $\hat{\phi}^E = \hat{\phi}^O$ and $\hat{\phi}^J = \hat{\phi}^K$). During non-drought years $\hat{\phi}^E$ was greater than $\hat{\phi}^K$ ($\widehat{ES} = 0.08$, 95%CI= 0.03 to 0.13; Figure 3-2). This model also assumed no significant effect of drought on adult apparent survival in K (the region with the highest DSV > -1), but assumed a similar effect of drought on adult apparent survival in E, O and J (which all had lower DSV < -1) (see Figure 3-2 for estimates).

Average estimates of juvenile apparent survival during non-drought years were higher in southern regions ($\hat{\phi}^E = 0.520$, 95%CI = 0.460 to 0.588; $\hat{\phi}^O = 0.471$, 95%CI = 0.372 to 0.597) than in northern regions ($\hat{\phi}^K = 0.355$, 95%CI = 0.233 to 0.541; $\hat{\phi}^J = 0.412$, 95%CI = 0.295 to 0.575), but confidence intervals overlapped. During drought years confidence intervals of region specific juvenile apparent survival overlapped widely ($\hat{\phi}^E = 0.07$, 95%CI = 0.014 to 0.349; $\hat{\phi}^O = 0.0647$, 95%CI = 0.010 to 0.427; $\hat{\phi}^K = 0.054$, 95%CI = 0.007 to 0.405; $\hat{\phi}^J = 0.058$, 95%CI = 0.004 to 0.837). Because no juveniles were marked in 2001 in E and only 4 were

marked in K in 2000, we could not test the hypothesis of a lower effect of the drought on apparent survival of juveniles in K. Given that juvenile apparent survival estimates were not significantly different from one another we averaged these estimates across regions (Figure 3-2).

Estimates of adult apparent survival averaged across regions remained fairly high and constant over time ($\hat{\phi} = 0.86$; Figure 3-2), but dropped substantially during drought years between 2000 and 2002 (average apparent survival between 2000 and 2002 was $\hat{\phi} = 0.72$; Figure 3-2). This represented a relative decrease of 16% in apparent survival during the years that were affected by the drought when compared to non-drought years, but the decrease was only significant between 2001 and 2002 ($\widehat{ES} = 0.39$, 95%CI= 0.24 to 0.53; Figure 3-2). Juvenile apparent survival varied widely over time, but reached a record low between 2000 and 2002 (average $\hat{\phi}$ between 2000-2002 was $\hat{\phi} = 0.06$; Figure 3-2). Juvenile apparent survival decreased by 86% in 2000 and 2002 (relative decrease) when compared to its average over the non-drought years (average $\hat{\phi}$ during 1992-1999 and 2002-2003 was $\hat{\phi} = 0.44$).

Inter-Annual Movement Among Regions and Drought Effect on Movement

The most parsimonious model (described above; Table 3-3), had site-specific annual transition (movement) probabilities that were constant over time, except during the drought (Table 3-3). This model was substantially better supported than the same model without a drought effect ($\Delta AICc = 7$; Table 3-3). Using the most parsimonious model, we found that during the 2001 drought, movement estimates were higher from the areas with the lowest DSV (i.e., most impacted regions: O and E) toward areas with highest DSV (i.e., least impacted region: K), $\hat{\psi}^{OK} = 0.33$ (95%CI = 0.146 to 0.580), $\hat{\psi}^{EK} = 0.030$ (95%CI = 0.014 to 0.066), than during non-drought years $\hat{\psi}^{OK} = 0.044$ (95%CI = 0.024 to 0.080), $\hat{\psi}^{EK} = 0.015$ (95%CI = 0.010

to 0.022). However, the difference was only statistically significant for birds moving from O to K ($\widehat{ES} = 0.28$, 95%CI= 0.05 to 0.52). Estimated movement probabilities toward the most-impacted region (i.e., E and O) during the drought approached 0. This contrasted with non-drought years during which movement probabilities toward E and O were typically much higher than 0 (ranged from 0.02 to 0.16; Table B-4 in Appendix B). Surprisingly the probability of moving from J to K during the drought approached 0, while during non-drought years this probability was $\widehat{\psi}^{JK} = 0.06$ (95%CI = 0.03 to 0.11).

Models including an age effect as well as a drought effect on movement did not reach numerical convergence; however, we did not detect any movement of juvenile bird from the most to the least impacted regions between 2000 and 2001. Models including an age effect on movement but no drought effect were not supported ($w < 0.01$; Table B-3 in Appendix B).

We used the most parsimonious model to estimate the probability of staying in each region from one year to another. The probability of staying in E was $\widehat{\psi}^{EE} = 0.95$ (95%CI = 0.94 to 0.96), the probability of staying in O was $\widehat{\psi}^{OO} = 0.76$ (95%CI = 0.71 to 0.82), the probability of staying in K was $\widehat{\psi}^{KK} = 0.72$ (95%CI = 0.66 to 0.79), and the probability of staying in J was $\widehat{\psi}^{JJ} = 0.75$ (95%CI = 0.69 to 0.82).

Discussion

Monthly Movement Among Contiguous and Isolated Wetlands

We found that kites moved extensively over large areas of contiguous wetlands (average monthly movement probability: 0.29). However, our study also showed much less movement among isolated wetlands (average monthly movement probability: 0.10). As expected average monthly movement probability among moderately isolated wetlands was intermediate: 0.15. Differences between these estimates were all statistically significant. These results agree with

Prediction 1, that loss of connectivity reduces movement of kites. However, as stated in *Prediction 1*, only by comparing movement among contiguous wetlands and among moderately isolated wetlands could the effect of connectivity and distance be separated. Indeed, despite the fact that distances between the centroids of contiguous wetlands (E) were greater than between the centroids of moderately isolated wetlands (K), movement among wetlands in E were greater than in K. The results also suggest that seasonality influenced movement within, but not among regions. One possible explanation is the pronounced wet-dry seasonality resulting in spatio-temporally variable habitat conditions at both the local and regional levels (Davis and Ogden 1994; Bennetts and Kitchens 2000). The fact that this seasonal pattern was not observed for movements among regions may be due to the higher costs (i.e., mortality) associated with moving among regions than when moving within the regions.

Patch Size and Distance Between Patches as Factors Driving Movement

Our modelling approach provided supportive evidence that patch size and interpatch distance constitute important factors influencing movement of juveniles at the regional scale. The support for this hypothesis was weak when movement was modelled for juveniles and adults simultaneously (Table 3-1.a). However this hypothesis received substantially more support when juvenile movement was modelled separately (Table 3-1.b. and Table 3-1.c.). Our results are thus consistent with *Prediction 2*, which predicts that movement probabilities between regions on a monthly scale decrease with distance. The hypothesis that immigration should be higher toward larger patches because of more frequent encounters with patch boundaries (*see Prediction 2*; Lomolino, 1990; Hanksi, 2001) received some limited support. Indeed, model $\psi_{juv}(AR+d)$ (Table 3-1.b), which supported the hypothesis of a positive relationship between movement and the size of the receiving site had a w of 0.17 (Table 3-1.b). Although the model that assumed

higher emigration out of smaller areas for juveniles ($\psi_{juv}(AD)$) was not parsimonious (Table 3-1.b), examination of the β parameter for this model supported this hypothesis.

The fact that we only found evidence of a patch size and distance effect on the monthly movement probabilities of the juveniles at the regional scale is consistent with *Prediction 3*. However, we can only infer that juveniles may respond to distance and size of the destination site, whereas adults do not (Table 3-1.c.), possibly indicating that adults are responding to other factors (e.g., habitat quality). Only by including a measure of habitat quality (currently unavailable) in our models could we test the hypothesis that adult movements are more likely to be determined by the acquired knowledge of the quality of the available habitats than by the patch boundary effect. The fact that we found no influence of patch size and distance on monthly movement among contiguous or moderately isolated wetlands can be explained by the fact that movements among these wetlands are so frequent that the effect of patch size effect and distance may be diluted over time (i.e., after a few months birds may not search wetlands blindly anymore).

If patch size and distance affect movement patterns among patches, one can see how habitat loss and fragmentation may affect dispersal, particularly for juvenile birds. It is particularly likely to increase the search cost when animals move to locate new suitable wetlands.

Inter-annual Pattern of Movement

Despite relatively high average monthly movement probabilities out of regions (e.g., average movement probabilities out of E and K were 0.04 and 0.09, respectively), kites exhibited strong philopatric tendencies to particular regions at an annual scale (e.g., annual estimates of site tenacity for regions E and K were 0.95 and 0.72, respectively).

This extent of site tenacity is surprising given the high environmental variability that characterizes the kite's range in Florida (Beissinger, 1986; DeAngelis and White 1994). Indeed many species that use environments where food resources vary strongly in space and time are often nomadic (e.g., DeAngelis and White 1994). However movement out of familiar areas may incur important search costs (starvation, predation). Kites may also benefit from staying in or returning to familiar regions, as it could contribute to maximizing their breeding output and chance of survival (e.g. predation avoidance) (Stamps 2001).

In summary, kites movement in this fragmented system varies from site tenacity (between breeding season and at the regional scale) to nomadism (within region on a monthly scale), depending on the spatio-temporal scale of observation and hence on the activities of primary relevance at different times and places. In particular, one may want to distinguish between breeding (or natal) philopatry and exploratory movements, as the factors governing these processes may be different. Additionally, our results indicate that Snail Kites move substantially less between regions that have been isolated by human-induced fragmentation than within these regions. Thus, many kites may have little familiarity with wetlands located outside their natal region. A regional disturbance could therefore have significant demographic consequences. Kites that are familiar with many landscapes within the population's range may survive a regional drought by moving to other less-affected regions, while survival of birds without knowledge of alternative wetlands could be dramatically reduced. The drought that occurred in Florida in 2001 provided an opportunity to evaluate the effects of this type of natural disturbance on kites.

Regional Survival and Resistance of the Population to Natural Disturbance

The analysis of annual movement indicates that kite movement was affected by the 2001 drought. As expected, a proportion of birds moved from the most to the least-impacted regions, which is consistent with *Prediction 4.a.* (but the drought effect was only significant for kites

moving from O to K). Although models including an age effect on annual movement were not supported (possibly because of low sample size), no juveniles that had fledged one year prior to the drought were found to have moved toward refugia (i.e., only adult birds were observed moving to region K in 2001). This latter observation is not based on any robust estimation procedure and therefore should be interpreted with caution. However, it is worth pointing it out as it supports *Prediction 4.b*, which states that because adults are more familiar with the surrounding landscapes they are more likely to reach refugia habitats than juveniles.

Despite the fact that a proportion of kites moved from the most to the least-impacted regions, most birds did not appear to successfully reach refugia habitats and overall, this regional drought had a substantial demographic effect on the population (Figure 3-2), which is consistent with *Prediction 5.a*. The survival analysis conducted over the last 13 years, at the scale of the whole population, also indicates that apparent survival varied among regions. During non-drought, adult survival was lower in northern regions (K and J) than in southern regions (E and O), possibly because of lower apple snail availability in the northern regions (Cattau unpublished). Juvenile apparent survival was also lower in northern regions than in southern regions during non-drought years, but differences were not statistically significant. Our results supported *Prediction 5.b*, which predicted that survival should be lower in areas most impacted by the drought than in areas least impacted. Adult apparent survival in regions E, O and J (lowest DSV), decreased significantly during the drought, while survival in K (highest DSV) did not decrease (Figure 3-2). *Prediction 5.b* could not be tested for juveniles because of low sample size. When averaging survival over all the regions apparent survival of adults decreased by 16% during the drought while juvenile apparent survival dropped by more than 86% during the drought (Figure 3-2). Thus, the drought had a larger effect on juvenile apparent survival than on

adult apparent survival, which is consistent with *Prediction 5.c*. Interestingly, adult apparent survival only decreased significantly between 2001 and 2002, while juvenile apparent survival had already decreased significantly between 2000 and 2001, indicating that juveniles were also more susceptible to early effects of the drought. A declining trend in juvenile apparent survival is also evident in Figure 3-2. However, we had no good *a priori* reason to expect this trend. It could be due to stochastic variation or unrecognised variations in wetland conditions. Additionally, we should note that out of 65 juveniles equipped in 2003 with radio transmitters, 36 were observed alive between March and May 2004 (Martin et al. unpublished data). Therefore, juvenile survival between 2003 and 2004 rebounded since the drought to at least 0.55 (detection probability was not accounted for this estimate).

The dry-down effects of the drought began in mid January 2001; most of the birds that fledged during the previous breeding season (from the 2000 cohort) were approximately 9 months. Because juveniles are somewhat proficient at capturing snails after only 2 months (Beissinger 1988), by 9 months these birds should be equally efficient at capturing and extracting snails. Field observations of kite interactions indicate no dominance of adults over juveniles that are 4 months or older (Martin et al. unpublished data). The only major difference in foraging abilities between young and older birds, that we are aware of, would be their respective familiarity with the landscapes. Adults would potentially have explored more wetlands than juveniles (Bennetts et al. 2002). This may thus explain the weaker effect of the drought on adults (see *Prediction 5.c*).

We note that the survival estimates presented in this study are apparent survival estimates, indicating that the complement of these estimates includes both mortality and permanent emigration from the study system. Thus, lower survival during drought could be due to both

permanent movement out of the system and lower true survival due to the drought. It is possible that some kites moved temporarily to peripheral habitats (typically highly disturbed habitats: agricultural areas, large canal) during drought. Although these habitats will typically retain more water than major kite habitats during drought, they are unlikely to be suitable for breeding activity; thus, when conditions improve, most birds should move back to major wetlands. Hence, because the Snail Kite population in Florida is assumed to be an isolated population (Bennetts et al. 1999a) and because the geographic scope of our study encompasses the major kite habitats, it is unlikely that many kites remained outside the sampled areas for three consecutive sampling seasons after the drought. Even if substantial temporary emigration into unsampled areas occurred during drought it would not have biased survival if it was followed by movement back into the study system when conditions improved.

Conclusions and Conservation Implications

Reducing habitat fragmentation has now become almost a rubber-stamp recommendation for maintaining populations of many species of terrestrial mammals, insects, and even birds with reduced dispersal abilities. However, the benefits may be less obvious when dealing with species able to cover several hundred kilometres in one day and whose daily dispersal abilities exceed the distance separating patches that have been isolated through fragmentation. As suggested by previous theoretical studies (e.g., Doak, Marino and Kareiva 1992), we found that considering scale issues was critical to understanding movement of kites in fragmented landscapes. The case study of the Snail Kite in Florida also provides an example of how fragmentation could indirectly affect the persistence of species with great dispersal abilities. As suggested by Bennetts and Kitchens (2000) and Bell (1991), exploratory behaviours may be important for many animals to resist periodic low food availability events (such as droughts). Thus, if fragmentation reduces exploratory movements of kites, it could also reduce resistance of the kite

population to disturbance events. Further work to support this hypothesis may be particularly critical to conserve this endangered species, but may also be relevant to other avian nomads (e.g., waterbirds in Australia, see Roshier et al. 2001).

Table 3-1. Multistate models (with survival and detection probabilities equal to 1) of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) Snail Kites among the five major regions (E, O, K, L, J) and P (peripheral and matrix areas), based on radio-telemetry data. These models evaluate the effect of patch size, distance and regional identity alone on movement probabilities.

Model	$\Delta AICc$	w	K
a-Movement among regions of juvenile and adult modelled simultaneously			
$\psi(r)$	0	0.69	30
$\psi ad(r) \psi juv(AR*d)$	1.7	0.30	43
$\psi ad(r) \psi juv(AD)$	8.2	0.01	40
b-Movement among regions modelled using data from juvenile only			
$\psi juv(AR*d)$	0	0.79	13
$\psi juv(AR+d)$	3.0	0.17	12
$\psi juv(AD)$	6.5	0.03	10
$\psi juv(AR)$	8.8	0.01	11
c-Movement among regions modelled using data from adult only			
$\psi ad(r)$	0	1.00	30

Notes: AICc is the Akaike's Information Criterion. $\Delta AICc$ for the *i*th model is computed as $AICc_i - \min(AICc)$. w refers to AICc weight. K refers to the number of parameters. Only models with $w > 0.01$ are presented (see Table B-1 in Appendix B, for models with $w < 0.01$). "*r*": region (includes 6 states: E, O, K, J, L and P (peripheral and matrix); "*AR*": Area of the receiving site; "*AD*": Area of the donor site; "*d*": distance.

Table 3-2. Multistate (with survival and detection probabilities equal to 1) models of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) Snail Kites among wetlands in the E and K region based on radio-telemetry data. These models evaluate the effect of patch size, distance, season, wetland identity alone on movement probabilities.

Model	ΔAICc	w	K
a-Movement within the E region of adult and juvenile Snail Kites			
ψ (<i>seas</i> * <i>cw</i>)	0	1	20
b-Movement within the K region of adult and juvenile Snail Kites			
ψ (<i>seas</i>)	0	0.67	3
ψ <i>ad</i> (<i>seas</i>) ψ <i>juv</i> (<i>seas</i>)	2.6	0.18	6
ψ (.)	5.4	0.04	1
ψ <i>ad</i> (.) ψ <i>juv</i> (.)	6.5	0.03	2
ψ (<i>mw</i>)	6.5	0.03	12
ψ (<i>breed</i>)	7	0.02	2
ψ (<i>years</i> * <i>seas</i>)	8	0.01	10

Notes: Only models with $w > 0.01$ are presented (see Table B-2 in Appendix B, for models with $w < 0.01$). “*cw*”: contiguous wetland; “*mw*”: moderately isolated wetland; “*seas*”: season; “*breed*”: breeding season. For other notations see Table 3-1.

Table 3-3. Multistate models of annual apparent survival (ϕ), sighting (p), and movement probabilities (ψ) of adults (ad) and juveniles (juv) Snail Kites based on banding data. The drought effect on ϕ during 2000-2002 was denoted D_{1-2} . The drought effect on ψ in 2001 was denoted D_1 . Constant ϕ during non-drought years (1992-2000 and 2002-2004) was denoted ND . Because all models included in Table 3 had region and time dependent sighting probabilities ($p(r*t)$), Table 3-3 only includes model structures for ϕ and ψ .

Model	$\Delta AICc$	w	K
$\phi_{ad}^{[E=O \neq K=J]}(ND)\phi_{ad}^K(.)\phi_{ad}^{[E=O=J]}(D_{1-2})\phi_{juv}(r+td)\psi(r*D_1)$	0	0.96	85
$\phi_{ad}^{[E=O \neq K=J]}(ND)\phi_{ad}^K(.)\phi_{ad}^{[E=O=J]}(D_{1-2})\phi_{juv}(r+td)\psi(r)$	7	0.03	78

Notes: Only models with $w > 0.01$ are presented (see Table B-4 in Appendix B, for models with $w < 0.01$). “ t ”: time (years); “ $r+td$ ”: additive effect of region and time on ϕ , except during 2001-2002, during which ϕ was time dependent only; “.”: ϕ is constant during 1992-2004. Superscript indicate region specific ϕ ; “=”: regions have identical ϕ ; “ \neq ”: regions have different ϕ . For other notations see Table 3-1.

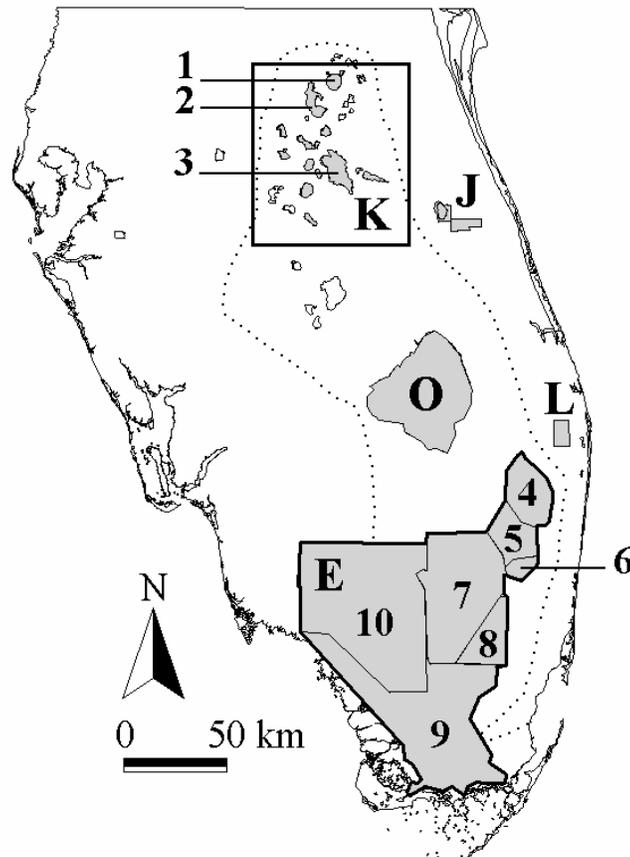


Figure 3-1. Major wetlands used by the Snail Kite in Florida. Regions: Kissimmee Chain of Lakes (K), Everglades (E), Lake Okeechobee (O), Saint Johns Marsh (J), and Loxahatchee Slough (L). Moderately isolated wetlands included in K are: East Lake Tohopekaliga (1), Lake Tohopekaliga (2), Lake Kissimmee (3), as well as the small lakes coloured in grey within the rectangle. Contiguous wetlands included in E: Water Conservation Areas 1A (4), 2A (5), 2B (6), 3A (7), 3B (8), Everglades National Park (9), and Big Cypress National Preserve (10). The grey colouring of the wetlands indicates the area of the wetlands that were included in this study. The thick contour lines delimit regions that include several wetlands. The dotted line indicates the historic Kissimmee-Okeechobee-Everglades watershed which constituted a network of well connected wetlands (Davis and Ogden 1994; Light and Dineen 1994).

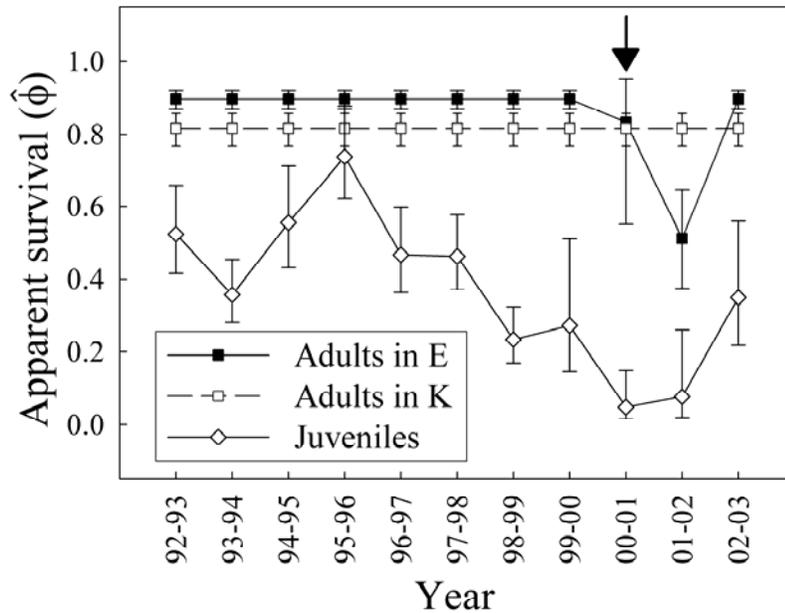


Figure 3-2. Apparent survival ($\hat{\phi}$) between 1992 and 2003 of adult and juvenile Snail Kites, obtained using the most parsimonious model in Table 3. Error bars correspond to 95% confidence intervals. During non-drought years (1992-2000 and 2002-2003), $\hat{\phi}$ of adults were similar in E and O; and in K and J. During drought (2000-2002), $\hat{\phi}$ of adults were similar in E, O and J, but different in K. For readability, only $\hat{\phi}$ in E and K are presented for adults. $\hat{\phi}$ of juveniles were averaged across regions. Arrow indicates the beginning of the drought that started in January 2001. Estimates between 1992 and 1999 were consistent with Bennetts et al. (2002).

CHAPTER 4
NATAL LOCATION INFLUENCES MOVEMENT AND SURVIVAL OF THE SNAIL KITE

Introduction

In heterogeneous environments, the place of birth (or natal location) is likely to be critical to the growth, survival, and future reproduction of organisms. Indeed, resource availability and other factors (e.g., parasitism) that can affect vital rates (e.g., survival and reproduction) often vary in space and time (Latham and Poulin 2003; Pettorelli et al. 2003). Moreover, it has been shown that environmental conditions during prenatal and early post-natal stages can have long term consequences on key life history traits (e.g., lifespan and age of first reproduction) (Metcalf and Monaghan 2001). Natal location, by shaping the habitat preferences of many animals, may also affect their movement and settling decisions during the course of their lifetimes (Stamps 2001; Davis and Stamps 2004). Thus, natal location may influence the ecological dynamics of wild populations through its effects on movement, habitat selection and survival (Stamps 2001; Blums et al. 2003; Davis and Stamps 2004).

Despite the importance of better understanding how natal location affects movement decisions and survival, rigorous analyses to estimate movement and survival in relation to the place of birth are lacking (Blums et al. 2003). Most past studies used *ad hoc* methods to estimate site fidelity (e.g., return rates, reviewed in Doherty et al. 2002). These *ad hoc* measures can be severely biased, because they are also functions of resighting and survival probabilities (Doherty et al. 2002). Modern analytical techniques, such as multistate models provide more robust estimates of movement and survival (Doherty et al. 2002). Although a few studies have now successfully used multistate models to estimate site fidelity (typically to breeding sites) (Hestbeck et al. 1991; Lindberg et al. 1998), only a handful of studies have used these models to estimate philopatry to the natal site (Lindberg et al. 1998). In fact, we are not aware of any study

that used robust estimators of movement to compare fidelity to the natal site (at the adult stage) with fidelity to non-natal sites. Nonetheless, the fact that some animals may exhibit a particular attraction toward their natal site at the adult stage could be critical to the dynamics of many wild populations. Indeed, attraction by individuals to the natal site could influence habitat selection, patterns of patch occupancy, reproduction, and survival (see Schjørring 2002).

We studied patterns and consequences of movement related to the natal site in a geographically isolated and spatially structured population of Snail Kites (*Rostrhamus sociabilis*) in Florida. The Snail Kite is a highly specialized raptor that feeds almost exclusively on freshwater snails (Beissinger 1988). Because of this food specialization, Snail Kites are confined to the remaining wetlands in Central and South Florida (Takekawa and Beissinger 1989). The environment occupied by the Snail Kite in Florida is highly variable spatially and temporally (Beissinger 1986). Animals such as Snail Kites that occupy habitats whose food abundance is unpredictable in space and time are generally expected to be nomadic (Bennetts and Kitchens 2000; Wiens 1976). By modeling movement rates among wetlands used by this bird, Bennetts and Kitchens (2000) measured the extent of nomadism. However, Martin et al. (2006) found that despite frequent exploratory movement, Snail Kites showed strong site tenacity on an annual scale during the breeding season. Bennetts and Kitchens (2000) hypothesized that exploratory movement may familiarize kites with their landscapes. It has been recognized that exploring unfamiliar habitats is energetically costly (Schjørring 2002). However, if the exploration phase occurs at times when search costs are minimal (i.e., when food is most abundant), the familiarity with alternative locations gained by birds during exploration may greatly outweigh exploration costs by reducing the risk of mortality during a subsequent disturbance, such as a regional

drought, which dramatically decrease snail availability to kites (Beissinger 1995; Bennetts and Kitchens 2000; Martin et al. 2006).

On the other hand, benefits of staying in or returning to a familiar area range from increased competitive ability to enhanced predator avoidance (Stamps 2001). Thus staying in or returning to a familiar habitat may also, in some circumstances, increase an animal's probability of surviving and/or of breeding successfully. Although Martin et al. (2006) found that kites exhibit site fidelity (i.e., philopatry) to certain regions during the breeding season, these authors did not specifically examine the level of site tenacity relative to the natal site. Nonetheless, distinguishing between site fidelity specific to the natal site as opposed to site fidelity to non-natal sites, and examining consequences on survival, may be essential to disentangle the ecological dynamics of many vertebrates.

Hypotheses and Predictions

Prediction 1

If kites prefer their place of birth when compared to any post-dispersal sites they may have explored in the course of their lifetimes, we expect: (1) movement from post-dispersal sites toward birds' natal site to be greater than movement from post-dispersal sites toward non-natal sites; (2) we expect greater movement toward the natal site than away from the natal site; (3) finally, we predict that philopatry to the natal site should be greater than philopatry to non-natal sites. Here, we define philopatry as the probability for a kite to be found in a particular region at year $t+1$, given that it was present in that same region in year t (Martin et al. 2006). Thus, philopatry to the natal site (or natal philopatry) corresponds to the probability for a kite to be found in its natal region at year $t+1$, given that it was present in its natal region in year t .

Prediction 2

Wetland conditions affect survival (Beissinger 1995; Bennetts and Kitchens 2000; Martin et al. 2006) and movement (Takekawa and Beissinger 1989; Bennetts and Kitchens 2000; Martin et al. 2006) of Snail Kites. During a regional drought a proportion of Snail Kites is likely to move to the least disturbed areas (Takekawa and Beissinger 1989; Bennetts and Kitchens 2000; Martin et al. 2006). Consequently, we expect the level of natal philopatry to vary according to wetland conditions. Kites should be less philopatric to their natal site when it is affected by a drought. Conversely, during a drought, natal philopatry of birds whose natal areas are located in **refugia habitats** (areas least affected by droughts) should be greater than during non-drought years. Because of their greater familiarity with the paths linking post-dispersal habitats to their natal habitat, birds hatched in a refugia habitat should also have higher probabilities of moving to that refugia during a drought.

Prediction 3

If natal location influences adult survival, we expect adult survival to vary substantially among groups of kites that were hatched in different regions.

Prediction 4

Because we expect kites to be more likely to stay in or return to their natal location (see *Prediction 1*), we predict that during a drought, kites whose natal site is located in refugia habitats should be less impacted by a drought (i.e, their survival should decrease less) than birds whose natal site is located outside of a refugia habitat.

Study Area

We sampled four major wetland complexes that encompass a very large proportion of all the landscapes used by the Snail Kite in Florida (Figure 4-1). Most of these wetland complexes (hereafter referred to as regions) consist of several wetlands that were separated by small physical barriers (e.g., road, levee or limited extent of non-wetland areas) easily crossed by Snail

Kites (Bennetts 1998). On the other hand, each region was isolated from the others by extensive areas mostly unsuitable for breeding or foraging (i.e., matrix), and not easily crossed by kites. We used the same four primary regions as Bennetts et al. (1999a): Everglades “E”; Kissimmee Chain of Lakes “K”; Lake Okeechobee “L”; Saint Johns “J” (Figure 4-1).

Material And Methods

Field Methods

Capture-mark-recapture

The Snail Kite population in Florida has been monitored since 1992 using capture-mark-recapture methods (Bennetts et al. 1999a). Because our study focused on movement and survival related to the natal region of Snail Kites, we only included birds banded as juveniles (before fledging, at approximately 30 days), whose natal regions we knew (sample size: 1722 birds). Those birds were captured and marked directly at the nest during the peak of the breeding season between 1992 and 2004. Birds were then resighted during annual surveys (which also took place during the peak of breeding season: March through June). Each region was surveyed at least once using an airboat, and bands were identified using a spotting scope.

Data Analysis

Multistate modeling

Multistate models (Hestbeck et al. 1991; Williams et al. 2002) simultaneously estimate transition probabilities among geographic states “ ψ ”, sighting probabilities “ p ”, and apparent survival probabilities “ ϕ ” (hereafter simply referred to as survival). We defined “ ψ^{QS} ” as the probability that an animal in region “Q” at time t is in region “S” at time $t+1$, given that it is alive at $t+1$. In this example, regions “Q” and “S” are geographic states. We defined “ p^Q ” as the probability that an individual alive in region “Q” in year t is sighted (Williams et al., 2002). We

defined “ ϕ^Q ” as the probability of surviving (and not permanently emigrating from the study system) over the interval $[t, t+1]$ for a kite alive in year t in region “Q” (Williams et al., 2002). Modeled parameters used notation from Martin et al. (2006); time dependency was “t” and no time effect was “.”. We assigned each bird to one of two age classes: juveniles (denoted “J”), 30 days to one year in age; and adults (denoted “AD”), older than one year. Effects embedded in parameters (i.e., “ ϕ ”, “ ψ ” and “p”) were shown using parentheses. A multiplicative effect was denoted “*”. Additional effects included: (1) a drought effect; (2) an age effect denoted “age”; (3) a natal region effect denoted “nr”; and (4) a regional effect denoted “r”. The regional effect “r” allowed parameters of interest (i.e., “ ϕ ”, “ ψ ” or “p”) to vary among regions. Regions included both natal and non-natal regions. We used multistate models with four groups (each group included birds hatched in the same natal region: “E”, “L”, “K” or “J”); and four geographic states (each state corresponded to a region: “E”, “L”, “K” or “J”) to estimate movement and survival of Snail Kites. It is important to recognize the distinction between groups and geographic states. A particular kite can belong to only one group (which corresponds to its natal region). In contrast, a kite can move from one geographic state to another. A geographic state corresponds to a region occupied by a kite at some point in time.

Movement

First, we used a classic parameterization of multistate models which ignored any effects of natal regions (e.g., Hestbeck et al. 1991, Blums et al. 2003, Martin et al. 2006). For instance, model “ $\psi_{(r)}$ ” allowed transitions to vary among regions (i.e., geographic states) but assumed no natal region effect. We used an alternative parameterization (hereafter referred as parameterization “NOA”) that allowed us to develop models that estimated three types of transition probabilities for each group of kites hatched in the same region (each group was

exclusively comprised of birds from the same natal region). The first two types of probabilities were transitions between the natal region (denoted “N”, for “natal”) and post-dispersal regions (denoted “O”, for “other”). Post-dispersal region “O” potentially included any of the four major regions used by kites except for their natal region. The notation “ ψ^{NO} ” corresponded to transition probability from region “N” to “O”, while “ ψ^{ON} ” corresponded to transition probability from region “O” to “N”. In addition to “ ψ^{ON} ” and “ ψ^{NO} ”, we were able to estimate transition “ ψ^{OA} ”: transition from region “O” (occupied at time t) toward any post-dispersal region “A” (at time $t+1$). “A” included any regions except for the natal region and the post-dispersal region occupied at t while in region “O”. Next, we provide an example of the constraints that were used to estimate “ ψ^{ON} ”, “ ψ^{NO} ”, and “ ψ^{OA} ”. For example, for all kites that were hatched in region “E”, we developed models that assumed: (1) “ $\psi_E^{EL} = \psi_E^{EK} = \psi_E^{EJ} = \psi_E^{NO}$ ” (subscripts indicate the natal region; in this example all transitions probabilities pertain to kites that were hatched in region “E”); (2) “ $\psi_E^{LK} = \psi_E^{LJ} = \psi_E^{KL} = \psi_E^{KJ} = \psi_E^{JL} = \psi_E^{JK} = \psi_E^{OA}$ ”; and (3) “ $\psi_E^{LE} = \psi_E^{KE} = \psi_E^{JE} = \psi_E^{ON}$ ”. We used similar constraints to model movement of kites hatched in the other three regions. These constraints were imposed in order to compare models that formalised our *a priori* hypotheses (see HYPOTHESES AND PREDICTIONS). We developed four different types of models using the parameterization “NOA”: (1) “ $\psi^{[NO \neq ON \neq OA]}(nr)$ ” (which assumes “ ψ^{NO} ”, “ ψ^{ON} ” and “ ψ^{OA} ” to be different and to vary among natal regions); (2) “ $\psi^{[NO=OA \neq ON]}(nr)$ ”; (3) “ $\psi^{[NO=ON \neq OA]}(nr)$ ”; and (4) “ $\psi^{[NO=ON=OA]}(nr)$ ”. These four types of models were developed to evaluate whether “ ψ^{NO} ”, “ ψ^{ON} ” and “ ψ^{OA} ” differed substantially within each natal region. In addition, we developed a model that included an interaction between a natal region effect (“nr”) and a region effect (“r”) on movement. This model was denoted “ $\psi(r * nr)$ ”. Finally, because a drought occurred between

January and August 2001, we evaluated models that included a drought effect on “ ψ ” between 2000 and 2001 (see also Martin et al. 2006). This effect was denoted “ D_m ”. We developed a model which assumed that “ ψ^{NO} ”, “ ψ^{ON} ”, and “ ψ^{OA} ” differed among groups of birds hatched in different natal regions but also differed during drought and non-drought years. This model was denoted “ $\psi^{[NO \neq ON \neq OA]}(nr * D_m)$ ”. We also considered a model that included an interaction between “nr”, “r” and “ D_m ”. This model was denoted “ $\psi(r * nr * D_m)$ ”.

Based on model averaged estimates (see “MODEL SELECTION”) of movement parameters of all models described above, we derived natal philopatry (denoted “ ψ^{NN} ”, the probability for a kite to be found in region “N” at time $t+1$, given that it was present in “N” at time t); and philopatry to non-natal site (denoted “ ψ^{OO} ”, the probability for a kite to be found in region “O” at time $t+1$, given that it was present in “O” at time t ; in other words “ ψ^{OO} ” is the probability that a kite located in a particular non-natal region at time t will be found in that same non-natal region at time $t+1$). These estimates of philopatry were obtained as one minus the estimated rates of moving away from the area of interest, and the associated variance of these derived estimates was computed using the delta method (see also Hestbeck et al. 1991; Williams et al. 2002).

Survival

We developed models that allowed “ ϕ ” and “p” to vary across time or remain constant for each age class. Given that environmental conditions are similar among certain groups of regions as a result of spatial proximity, similar topography, similar latitude or management (see Bennetts 1998), we developed models that assumed similar apparent survival probabilities across groups of regions. Thus, we developed models based on proximity (see Figure 4-1) that evaluated the similarity of survival in the northern regions “K” and “J”. Even though the boundaries of “E”

and “L” are closer together than “L” and “J”, the distance between the centers of “E” and “L” is greater than the distance between the centers of “L” and “J” (Figure 4-1). Therefore, we considered models allowing survival in “L” to be different from “K”, “J” and “E”. An analysis of hydrological data by Bennetts (1998) showed that wetland conditions in “E” and “L” were the most positively correlated among all the regions. We therefore developed a model that assumed apparent survival to be similar in these two regions. To illustrate our notation system we chose a model with a common survival parameter for two groups of natal regions: “ $\phi^{nr[E=L \neq K=J]}$ ”. The superscript “nr” indicates that “ ϕ ” is “natal region specific”. In models with the superscript “nr”, survival was allowed to vary among natal regions (i.e., groups) but it was constrained to be equal among regions occupied (i.e., geographic states). The superscripts on the right of model “ $\phi^{nr[E=L \neq K=J]}$ ” indicate regions to which the survival probabilities pertain (“=” indicates that “ ϕ^E ” is the same as “ ϕ^L ”; similarly “ ϕ^K ” is the same as “ ϕ^J ”; “ \neq ” indicates that “ ϕ^E ” and “ ϕ^L ” are different from “ ϕ^K ” and “ ϕ^J ”). We also constructed models in which adult survival varied among regions; we referred to these survival rates as “region specific” survival. In models that estimated “region specific” survival, survival parameters were allowed to vary among regions occupied (i.e., geographic states), but were constrained to be equal among natal regions (i.e., groups). “Region specific” survival estimates were obtained using the same parameterization as Martin et al. (2006) and were denoted by a superscript “r” instead of “nr” (e.g., “ $\phi^{r[E=L \neq K=J]}$ ”). In age structured models, adult survival was denoted “ ϕ_{AD} ” and juvenile survival was denoted “ ϕ_j ”. We also created models that included a drought effect on “ ϕ ”. As in Martin et al. (2006), the drought effect on survival was modeled as a two years effect and was denoted “D”. Conversely, a no drought effect on “ ϕ ” was denoted “ND”. We used this approach

because the drought was likely to affect “ ϕ ” before and after the 2001 sampling occasion. We used subscripts on the right of “ ϕ ” to indicate whether the model structure of a particular component of “ ϕ ” pertained to drought years (subscript d reflected survival during the interval 2000-2002) or non-drought years (subscript nd reflected survival during the interval 1992-2000 and 2002-2004). For example, the first part of model “ $\phi_{AD,nd}^{[E \neq L \neq K \neq J]}(\cdot) \phi_{AD,d}^K(ND) \phi_{AD,d}^{[E \neq L \neq J]}(D)$ ” indicates that during non-drought years “ ϕ_{AD}^E ”, “ ϕ_{AD}^L ”, “ ϕ_{AD}^K ” and “ ϕ_{AD}^J ” differed substantially while remaining constant over time. The second part of this model (i.e., “ $\phi_{AD,d}^K(ND)$ ”) indicates that during the period that corresponded to drought years (2000-2002) there was no drought effect on “ ϕ_{AD}^K ”. The third part of the model (i.e., “ $\phi_{AD,d}^{[E \neq L \neq J]}(D)$ ”) indicates that during drought years there was an effect of the drought on “ ϕ_{AD}^E ”, “ ϕ_{AD}^L ”, and “ ϕ_{AD}^J ”. The symbol “ \neq ” between “E”, “L” and “J” indicates that “ ϕ_{AD}^E ”, “ ϕ_{AD}^L ” and “ ϕ_{AD}^J ” were different during the drought. Because the drought intensity was strongest in “E”, “L” and “J”, and weakest in “K” (see “WETLAND CONDITIONS”), some models assumed similar drought effects on “ ϕ ” in “E”, “L”, and “J” (e.g., “ $\phi_{AD,d}^{[E=L=J]}(D)$ ”) with no drought effect on “ ϕ ” in K (e.g., “ $\phi_{AD,d}^K(ND)$ ”) (see also Martin et al. 2006). The absence of subscript “ nd ” or “ d ” indicated that the survival term reflected the entire period of study (1992-2004). For example model “ $\phi_{AD}(r * nr)$ ” assumed a multiplicative effect between “ r ” and “ nr ” on adult survival for the entire period of study (1992-2004). This model did not assume any drought effect on adult survival. Model “ $\phi_{AD}(r * nr * D)$ ”, on the other hand, assumed a multiplicative effect between “ r ”, “ nr ” and “ D ”.

Model Selection, Goodness of Fit and Program Used

We developed a set of models that corresponded to our best *a priori* hypotheses. Next we used Akaike information criterion adjusted for small sample size (AICc) (Burnham and Anderson, 2002) as a criterion to select the model that provided the most parsimonious description of the variation in the data (i.e., model with the lowest AICc). Models with a value of ΔAICc (the difference between the AICc of a particular model and that of the model with the lowest AICc) less than two were considered to receive a substantial level of empirical support (Burnham and Anderson 2002). We also used the AICc weight (w) as a measure of relative support for each model (Burnham and Anderson, 2002). Values of w range from 0 to 1 (with 0 indicating no support; and 1 indicating maximum support). The sum of weights of all models including a particular effect was denoted (w_i). As recommended by Burnham and Anderson (2002), we used model averaging to compute estimates of movement and survival. All computations of the movement and survival rates were carried out using program MARK V 4.1 (White and Burnham 1999). We used the sin link function available from program MARK. Estimates of standard error (\widehat{SE}) and 95% confidence intervals (95%CI) were obtained directly from program MARK. We used the delta method to compute estimates of precision for derived parameters (Burnham and Anderson 2002). All the confidence intervals for the derived estimates “ $\hat{\theta}$ ” in our study were approximated as follows: $95\%CI [\hat{\theta}] = \hat{\theta} \pm 1.96 * \widehat{SE} [\hat{\theta}]$. Goodness of fit (GOF) tests of multistate models were computed using program U-CARE version V2.22 (Pradel et al. 2003; Choquet et al. 2005). Program U-CARE test the fit of the fully time dependent “Jolly Move” model (JMV) to the data. To our knowledge there is currently no rigorous test that directly assesses the fit of the Arnason-Schwarz (AS) model that accounts for an age effect on survival (“ $\phi(\text{age} * r * t)\psi(r * t)p(r * t)$ ”). However, program U-CARE tests the fit

of the “Jolly-move model” (JMV) that accounts for an age effect on “ ϕ ” (hereafter referred as model JMVA) (Choquet et al. 2005). This test is also generally valid for the AS model that accounts for an age effect on survival (Cooch and White 2006). Indeed, in practice the JMV model is unlikely to show significantly better fit to the data than the AS model (Cooch and White 2006). The JMV model differs from the AS model in that it allows the capture probability for time $t+1$ to depend on the state at periods t and $t+1$, whereas the AS model only allows the encounter probability to depend on the current state and time. However, the dependence of the capture probability at time $t+1$ on the state at periods t and $t+1$ is unlikely to be often observed in practice (Cooch and White 2006). The test for the JMVA model requires the summation of the component WBWA, 3G.Sm, M.ITEC, M.LTEC (see Choquet et al. 2005, for a detailed description of the procedure). If the test is significant (i.e., $P < 0.05$), Choquet et al. (2005) recommend a correction for overdispersion.

Effect Size

We estimated the magnitude of the difference between two estimates of movement (or survival) by computing the arithmetic difference between these estimates (hereafter referred as “effect size” denoted “ \widehat{ES} ”). Whenever the 95%CI[\widehat{ES}] did not overlap 0, we considered the difference to be statistically significant (Cooch and White 2006). We note that estimates of 95%CI[\widehat{ES}] take into consideration covariances between estimated movement and survival rates. Therefore, differences between estimates may be statistically significant based on 95%CI[\widehat{ES}], even though 95%CI of the estimates to be compared overlap.

Notes Concerning Regional Specific Survival

We note that the parameterizations used in the present study to estimate “region specific” survival were similar to the ones described in Martin et al. (2006). Therefore estimates of “region

specific” survival should theoretically not differ substantially between the two studies. Any differences between these estimates should primarily be due to the fact that the data set used in the present study included exclusively kites whose natal locations were known. In contrast, all models assessing the influence of natal location on movement and survival used parameterizations that differed substantially from any models presented in Martin et al. (2006). We emphasize that comparing estimates of “region specific” survival (parameterizations used by Hestbeck et al. 1991; Martin et al. 2006 and other authors) with estimates of “natal region specific” survival (parameterization specific to this paper), was necessary to fully evaluate the importance of natal location on regional survival of adult birds. It was also important to make these comparisons using a common data set that only included individuals whose natal locations were known (as opposed to using the data set analyzed by Martin et al. 2006). Model averaged estimates of “region specific” survival were obtained by model averaging estimates from models that assumed survival to be “region specific” whereas model averaged estimates of “natal region specific” survival were obtained by model averaging estimates of models that assumed survival to be “natal region specific”.

Wetland Conditions

Martin et al. (2006) determined wetland conditions during drought using hydrological data. Their results suggest that “E”, “L” and “J” were the regions most affected by a drought that occurred between January and August 2001 and “K” was the least affected. Martin et al. (2007a) and Bennetts (1998) found high levels of spatio-temporal variation in wetland conditions. Not surprisingly they found a positive correlation in water levels among wetlands that were located nearby. The coefficient of correlation decreased as distance increased. Martin et al. (2007a.) also found that during most multiregional droughts that affected region “E” (e.g., 1981, 1985, 1989,

1990, 1991, 1992 and 2001) at least one of the wetlands within region “K” was wetter (based on hydrological indicators) than any other wetland within the region “E” (Martin et al. 2007a).

Results

GOF Tests

The GOF test indicated that model JMVA fit the data satisfactorily ($\chi^2_{137} = 82, P > 0.99$).

This test is also generally valid for the most general model in our model set (i.e., “ $\phi(\text{age} * r * t)\psi(r * t)p(r * t)$ ”). Therefore, there was no need to correct for overdispersion.

Movement

The two most parsimonious models included the component “ $\psi^{[NO \neq ON \neq OA]}(nr)$ ” ($w_t = 0.54$, Table 1). These models assumed movement probabilities between “N” and “O” (“ ψ^{NO} ”); between “O” and “N” (“ ψ^{ON} ”); and between “O” and “A” (“ ψ^{OA} ”) to be different for each natal region. Model averaged movement estimates “ $\hat{\psi}^{ON}$ ” were greater than either “ $\hat{\psi}^{NO}$ ” or “ $\hat{\psi}^{OA}$ ”. This was true for all natal regions (Figure 4-2). Differences between “ $\hat{\psi}^{ON}$ ” and “ $\hat{\psi}^{OA}$ ” were statistically significant for regions “E” ($\widehat{ES} = 0.45, 95\%CI = 0.27 \text{ to } 0.62$), “K” ($\widehat{ES} = 0.14, 95\%CI = 0.04 \text{ to } 0.25$), and “J” ($\widehat{ES} = 0.21, 95\%CI = 0.05 \text{ to } 0.38$), but not for region “L” ($\widehat{ES} = 0.05, 95\%CI = -0.09 \text{ to } 0.18$). Differences between “ $\hat{\psi}^{ON}$ ” and “ $\hat{\psi}^{NO}$ ” were statistically significant for regions “E” ($\widehat{ES} = 0.46, 95\%CI = 0.29 \text{ to } 0.63$), “K” ($\widehat{ES} = 0.10, 95\%CI = 0.01 \text{ to } 0.19$), and “J” ($\widehat{ES} = 0.17, 95\%CI = 0.02 \text{ to } 0.33$), but not for region “L” ($\widehat{ES} = 0.09, 95\%CI = -0.02 \text{ to } 0.19$).

Models “ $\psi^{[NO \neq OA \neq ON]}(nr * D_m)$ ” received less support from the data than model “ $\psi^{[NO \neq OA \neq ON]}(nr)$ ” ($\Delta AICc = 14.2$; see also Appendix C). Similarly models “ $\psi^{[NO = OA \neq ON]}(nr * D_m)$ ” received less support from the data than model “ $\psi^{[NO = OA \neq ON]}(nr)$ ” (difference in AICc between

these two models was 6.8, Table 1). Therefore the hypothesis of a drought effect on movement received little support from our data. Models “ $\psi^{[NO=ON=OA]}(nr)$ ”, “ $\psi^{[NO=ON\neq OA]}(nr)$ ”, “ $\psi^{[NO=ON=OA]}(nr)$ ”, “ $\psi(r)$ ”, “ $\psi(t)$ ” and “ $\psi(.)$ ” received considerably less support based on AICc weights ($w \sim 0$) (see also Appendix C). Models “ $\psi^{[NO=ON\neq OA]}(nr * age)$ ”, “ $\psi(nr * r)$ ”, and “ $\psi(nr * r * D_m)$ ” did not reach numerical convergence when optimizing the likelihood.

Comparison of Natal Philopatry and Philopatry to Non-Natal Site

Estimates of natal philopatry were greater than estimates of philopatry to non-natal regions (Figure 4-3). The differences between these estimates were statistically significant for regions “E” ($\widehat{ES} = 0.49$, 95%CI = 0.31 to 0.66) and “L” ($\widehat{ES} = 0.16$, 95%CI = 0.02 to 0.31), but not for regions “K” ($\widehat{ES} = 0.01$, 95%CI = -0.12 to 0.13), and “J” ($\widehat{ES} = 0.10$, 95%CI = -0.07 to 0.26).

Survival

Adults

Models that measured “region specific” survival received more support than models that measured “natal region specific” survival ($\Delta AICc \geq 8.4$, Table 1). Models that assumed “region specific” survival to be similar for regions “K” and “J” in the north and “E” and “L” in the south during non-drought years (e.g., “ $\Gamma \phi_{AD,nd}^{[E=L\neq J=K]}(.)$ ”) were among the most parsimonious models ($w = 0.74$, Table 1). Models that assumed no drought effect on region “K” were well supported ($w \sim 1$, Table 1), as were models that assumed similar drought effect for regions “E” and “L” ($w \sim 0.99$, Table 1). Figure 4-4 shows a substantial decrease in survival in regions “E” and “L”. On the other hand, the effect of the drought on region “J” was not clear. Indeed, the $\Delta AICc$ was only 1.7 between the most parsimonious model (i.e., “ $\Gamma \phi_{AD,nd}^{[E=L\neq J=K]}(.) \Gamma \phi_{AD,d}^{[K=J]}(ND) \Gamma \phi_{AD,d}^{[E=L]}(D)$ ”), which assumed no drought effect on “J” and the second most parsimonious model which assumed a

drought effect on “J” (i.e., “ $r_{\phi_{AD,nd}^{[E=L=J=K]}(\cdot)} r_{\phi_{AD,d}^K(ND)} r_{\phi_{AD,d}^{[E=L=J]}(D)}$ ”, Table 1). Models “ $\phi_{AD}(r * nr)$ ”,

“ $\phi_{AD}(r * nr * D)$ ”, “ $r_{\phi_{AD}^{[E=L=J=K]}(t)}$ ”, “ $r_{\phi_{AD,nd}^{[E=L=J=K]}(\cdot)} r_{\phi_{AD,d}^{[E=L=J=K]}(ND)}$ ”, “ $r_{\phi_{AD,nd}^{[E=L=J=K]}(\cdot)} r_{\phi_{AD,d}^{[E=L=J=K]}(ND)}$ ”

received almost no support based on AICc weights ($w \sim 0$) (see also Appendix C). Among models that estimated “natal region specific” survival, model

“ $nr_{\phi_{AD,nd}^{[E=L=J=K]}(\cdot)} nr_{\phi_{AD,d}^{[K=J]}(ND)} nr_{\phi_{AD,d}^{[E=L]}(D)}$ ” was the most parsimonious, and model

“ $nr_{\phi_{AD,nd}^{[E=L=J=K]}(\cdot)} nr_{\phi_{AD,d}^{[K=J]}(ND)} nr_{\phi_{AD,d}^{[E=L]}(D)}$ ” was the second most parsimonious (difference in AICc

between these two models was 2.5, see Table 1).

As pointed out earlier, models that assumed “region specific” survival were better supported than models that assumed “natal region specific” survival. However, model averaged survival estimates for these two types of models were similar ($\widehat{ES} \leq 0.06$, Figure 4-4), except for region “J” ($\widehat{ES} = 0.14$, but the difference was not statistically significant 95%CI = -0.02 to 0.30, Figure 4-4). Estimates of “natal region specific” survival varied significantly among groups of kites hatched in different regions (Figure 4-4). During non-drought periods “natal region specific” survival estimates were not significantly greater in “E” than in “L” ($\widehat{ES} = 0.031$, 95%CI = 0 to 0.06, Figure 4-4). “Natal region specific” survival estimates were greater in “L” than in “K” ($\widehat{ES} = 0.08$, 95%CI = 0.04 to 0.12, Figure 4-4); and were greater in “L” than in “J” ($\widehat{ES} = 0.08$, 95%CI = 0.04 to 0.12, Figure 4-4). Overall, during non-drought years, “natal region specific” survival estimates were significantly greater in the southern regions (“E” and “L”) than in the northern regions (“K” and “J”) ($\widehat{ES} = 0.11$, 95%CI = 0.05 to 0.16, Figure 4-4). During the time interval when the drought most severely impacted adult survival (2001-2002), “natal region specific” survival in the southern regions (“E” and “L”) was significantly lower than in northern

region “K” ($\widehat{ES} = 0.35$, 95%CI = 0.23 to 0.48, Figure 4-4); it was also lower than in northern region “J” ($\widehat{ES} = 0.35$, 95%CI = 0.19 to 0.52, Figure 4-4).

Juveniles

Models that assumed juvenile survival to be time dependent (i.e., “ $\phi_J(t)$ ”) received the most support ($w_t \sim 1$, Table 4-1). Models “ $\phi_J(nr * t)$ ”, “ $\phi_J(nr * D)$ ” and “ $\phi_J(.)$ ” received almost no support ($w \sim 0$, see also Appendix C).

We do not present juvenile survival estimates because they were not the focus of the current analysis. Furthermore these estimates were almost identical to the ones published in Martin et al. (2006).

Detection Probabilities

Models that assumed a multiplicative effect of region and time on detection (i.e., “ $p(r*t)$ ”) received the most support ($w_t \sim 1$, Table 4-1). Models “ $p(t)$ ”; “ $p(\text{age}*t)$ ”; “ $p(\text{age}*r*t)$ ”; “ $p(r)$ ”, “ $p(.)$ ” received almost no support ($w_t \sim 0$, see also Appendix C).

Discussion

Effect of Natal Region on Movement

This study, which focuses on movement and survival related to the place of birth, shows that Snail Kites, in addition to exhibiting some high level of site tenacity to most regions during the breeding season (Martin et al. 2006), also exhibit a particular attraction for their natal region. Indeed, using multistate models with four geographic states we found that estimates of movement from post-dispersal regions toward birds’ natal region were greater than movement from post-dispersal regions toward non-natal regions (differences were statistically significant for regions “E”, “K” and “J”, Figure 4-2). We also found that estimates of natal philopatry were greater than estimates of philopatry to non-natal regions (differences were statistically significant

for regions “E” and “L”, Figure 4-3). Finally, we found that estimates of movement were greater toward the natal region than away from the natal region (differences were statistically significant for regions “E”, “J” and “K”). These findings provide evidence supporting *Prediction 1*. The extent of affinity to the natal region appeared to depend on the region (Figure 4-2 and Figure 4-3). Interestingly, our results show that it may be worthwhile to compute simultaneously the three estimates of natal attraction described in this study. The fact that the effect of natal location on movement was not statistically significant for all regions when using all estimators may be due to lack of statistical power (e.g., due to small sample size). Alternatively, one should note that even if movements toward natal sites are substantially greater than toward non-natal sites, when movements from post-dispersal sites toward non-natal sites are small, estimates of natal philopatry may not differ from estimates of philopatry to non-natal sites (Figure 4-2 and Figure 4-3).

Fidelity to the natal region may benefit kites in numerous ways including reducing the risks associated with movement. Movement often incurs costs (Baker and Rao 2004), it is energetically costly (Schjørring 2002) and it can increase the risks of predation (Stamps 2001). Furthermore, familiarity with a particular region may potentially increase the fitness of kites if performance of activities related to foraging or reproduction can be improved through training and learning of habitat features specific to a particular region (Stamps 2001).

On the other hand, exploring habitats away from the natal region may be critical to the survival of most kites, given the unpredictability of the system used by kites (Beissinger 1986; Bennetts and Kitchens 2000; Martin et al. 2006). A combination of exploratory movement during the non-breeding period when search costs are relatively low, and a natal-philopatric type

of behavior when birds begin reproductive activities, is an appealing hypothesis to explain the movement of kites in Florida, but this hypothesis remains to be tested.

Models that included a drought effect on movement were not well supported based on AICc, and therefore, did not support *Prediction 2*. This contrasts with a previous study by Martin et al. (2006) that indicated evidence of a drought effect on movement. The discrepancy between the two studies may be due to a difference in sample size. In the present study we used only data on kites for which the natal location was known, which significantly reduced our sample size, and therefore, our ability to detect drought effect on movement. Given previous findings that most droughts affect regions differentially, and given the fact that the probability of staying or returning to a particular region is greatly dependent on the region of birth, we can expect great influences of the natal region on kite survival. Next we examine effects of the natal region on kite survival.

Influence of Natal Region on Survival

We found that estimates of adult survival varied substantially among groups of kites that were hatched in different regions (see “natal region specific” survival, Figure 4-4). This result is consistent with *Prediction 3*. When comparing models that assumed “natal region specific” survival with models that assumed “region specific” survival, “region specific” models received more support from the data. However, estimates of “region specific” and “natal region specific” survival were very similar (Figure 4-4). Thus, our results suggest that kites experience survival rates that are characteristic of the region occupied (i.e., geographic state) when survival is measured, but because kites have a tendency to stay in or return to their natal region more than to any other regions, as a consequence adult survival is ultimately influenced by the natal region.

Interestingly, during most years, adult survival rates of birds hatched in the southern regions (i.e., “E”, “L”) were higher than for birds hatched in the northern regions (i.e., “K” and

“J” regions). The difference in survival rates between birds hatched in various regions may be explained by varying quality among habitats. For instance, snail availability to kites appear to be lower in the northern regions during non-drought conditions (Cattau unpublished data, also reviewed in Martin et al. 2006).

During the drought that occurred in 2001, adult birds hatched in “E” and “L” suffered high mortality rates, while birds hatched in “K” were substantially less affected (Figure 4-4). This finding is consistent with *Prediction 4*. Martin et al. (2006) found that during a drought kites moved from regions most affected by the drought toward regions least impacted by the drought. In the current study, we did not find any evidence of a drought effect on movement (possibly because of low sample size). Nonetheless, we found that kites exhibit a particular attraction to their natal region (Figure 4-2 and Figure 4-3). Therefore, at any one time, kites are likely to be found in their natal region. Thus, many of the birds hatched in “K” may have survived the drought by staying in region “K”, or by moving back to natal region “K” (which as reflected by the hydrological indicator was the region least impacted by the 2001 drought). Indeed, we expect birds that were hatched in “K” to be more likely to reach that region than birds hatched in other regions because of their potentially greater experience with the path linking region “K” to their post-dispersal regions. The impact of the drought on “J” remains unclear. On one hand, model averaged estimates of “natal region specific” survival estimates did not indicate any substantial decrease during the drought for region “J” (Figure 4-4). On the other hand “region specific” survival indicated a decrease during the drought although not as great as in regions “E” and “L” and this decrease was not statistically significant (Figure 4-4).

Interestingly, during most multiregional droughts for which kite distribution data were available (1981-1982, 1985 and 2000-2001), many kites appeared to use region “K” as a refugia

habitat (Martin et al. 2006; Takekawa and Beissinger 1989), suggesting that this region is generally less impacted than the major southern regions (i.e., “E” and “L”). This is also confirmed by hydrological data for the last 30 years (Martin et al. 2007a). Indeed, during most multiregional droughts which affected region “E” (e.g., 1981, 1985, 1989, 1990, 1991, 1992 and 2001), at least one of the wetlands within region “K” was wetter (based on hydrological indicators) than any other wetland within the region “E” (Martin et al. 2007a).

Thus, birds hatched in region “K” may have lower survival and reproduction rates for many years, but may be more resistant to multiregional disturbance events, which are believed to be a major cause of mortality among Snail Kites (Beissinger 1995; Bennetts and Kitchens 2000; Martin et al. 2006).

Conclusions and conservation implications

Most ecologists would probably recognize that the effect of natal location on movement and survival may have important conservation implications for species which are notorious for their high degree of natal philopatry (e.g. albatross species, Bekkum et al. 2006). In contrast, conservation implications may be less obvious when dealing with vertebrate species which exhibit more subtle patterns of natal philopatry. The Snail Kite which has been described as a nomad (e.g. Bennetts and Kitchens 2000), may be one of such species. Indeed, we found that natal region is critical in influencing movement and survival of Snail Kites in Florida and that large variations in these vital rates may occur among habitats, in part because of temporal variation in habitat conditions. Thus, one should be cautious when evaluating the conservation value of habitats (see also Holt and Gomulkiewicz 2004; Jonze' et al. 2004). In particular, this study and that of Martin et al. (2006) show that regions in which survival is low for many years may be critical during disturbance events, such as droughts, by serving as refuges during drought and possibly by providing the entire population with a pool of individuals (i.e., kites hatched in

refugia habitats) with greater ability to resist such disturbance (see also Holt and Gomulkiewicz 2004).

Aside from its practical implications for conservation, our study highlights the importance of considering natal location as a potentially important factor affecting the ecological dynamics of spatially structured populations of animals, which, like Snail Kites, inhabit heterogeneous environments and use experience to base their settling decisions.

Table 4-1. Multistate models of apparent survival (“ ϕ_{AD} ”: survival of adults; “ ϕ_J ”: survival of juveniles) and annual transition probabilities (“ ψ ”) among the four major wetland complexes used by Snail Kites in Florida between 1992 to 2004. Factors incorporated in the models included: age, region, natal region; and a drought effect on movement and survival.

Model	$\Delta AICc$	w	K	DEV
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^{[K=J]}}(ND) \Gamma_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	0.0	0.38	76	2591.2
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^K}(ND) \Gamma_{\phi_{AD,d}^{[E=L=J]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	1.7	0.16	76	2592.9
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^{[K=J]}}(ND) \Gamma_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO=OA \neq ON]}(nr) p(r * t)$	2.0	0.14	72	2601.7
$\Gamma_{\phi_{AD,nd}^{[E \neq L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^{[K=J]}}(ND) \Gamma_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	2.0	0.14	77	2591.1
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^K}(ND) \Gamma_{\phi_{AD,d}^{[E=L=J]}}(D) \phi_J(t) \psi^{[NO=OA \neq ON]}(nr) p(r * t)$	3.7	0.06	72	2603.3
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^K}(ND) \Gamma_{\phi_{AD,d}^{[E=L=J]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	3.8	0.06	77	2592.8
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^K}(ND) \Gamma_{\phi_{AD,d}^{[E=L \neq J]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	5.1	0.03	79	2589.9
$\Gamma_{\phi_{AD,nd}^{[E \neq L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^K}(ND) \Gamma_{\phi_{AD,d}^{[E=L \neq J]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	7.1	0.01	80	2589.8
$\Gamma_{\phi_{AD,nd}^{[E \neq L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^K}(ND) \Gamma_{\phi_{AD,d}^{[E \neq L \neq J]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	8.1	0.01	82	2586.6
$nr_{\phi_{AD,nd}^{[E \neq L \neq J=K]}}(\cdot) nr_{\phi_{AD,d}^{[K=J]}}(ND) nr_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	8.4	0.01	77	2597.4
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) \Gamma_{\phi_{AD,d}^{[K=J]}}(ND) \Gamma_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO=OA \neq ON]}(nr * D_m) p(r * t)$	8.8	0.00	80	2591.5
$nr_{\phi_{AD,nd}^{[E=L \neq J=K]}}(\cdot) nr_{\phi_{AD,d}^{[K=J]}}(ND) nr_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	10.9	0.00	76	2602.1

Notes: AICc: Akaike information criterion. $\Delta AICc$ for the *i*th model is computed as $AICc_i - \min(AICc)$. w : AICc weight. K: number of parameters. DEV: deviance as given by program MARK. “nr”: natal region; “r”: region; “t”: time; “.”: no time effect; “age”: age effect; “*”: multiplicative effect. Superscripts on the right of “ ϕ ” indicate the natal region survival pertain to (e.g., “ ϕ^E ”: survival in region “E”; there were 4 regions: Everglades “E”; Lake Okeechobee “L”; St Johns “J”; Kissimmee “K”). Superscripts on the left of “ ϕ ” indicate whether survival is natal-region-specific (denoted “ $^{nr} \phi$ ”) or simply region-specific (denoted “ $^r \phi$ ”). “ \neq ”: regions have different “ ϕ ”; “=”: regions have similar “ ϕ ” (e.g., “ $\phi^{[E=L \neq J]}$ ”, survival rates are similar in “E” and “L” but different in “J”). Subscript “*nd*”: survival term reflects non-drought years (1992-2000 and 2002-2004). Subscript “*d*”: survival term reflects drought years (2000-2002). “ND”: no drought effect on “ ϕ ” during the interval 2000-2002. “D”: drought effect on “ ϕ ” during the interval 2000-2002. Superscripts on the right of “ ψ ” indicate the direction of movement between two regions (“ ψ^{NO} ”: transition from “N” to “O”; and “ ψ^{OA} ” transition from “O” to “A”). “N”: natal region; “O” is a post-dispersal region (“O” includes all regions except for the natal region); “A” is a post-dispersal region (“A” includes all regions except for the natal region and the post-dispersal region “O” occupied in the previous year); “ \neq ”: regions have different transitions probabilities (e.g., “ $\psi^{[NO \neq ON \neq OA]}$ ”, “ ψ^{NO} ”, “ ψ^{ON} ” and “ ψ^{OA} ” are different). “ D_m ”: drought effect on “ ψ ” between 2000 and 2001. “p”: sighting probability. Only models with $\Delta AICc < 11$ are presented (see supplementary materials for models with $\Delta AICc \geq 11$).

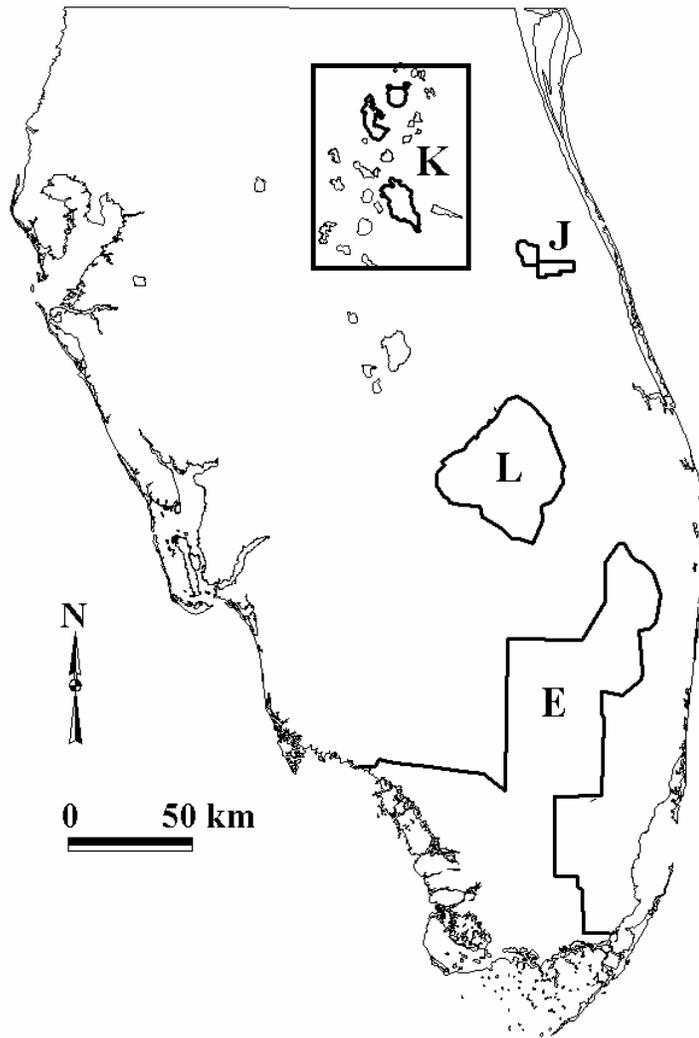


Figure 4-1. Major wetland complexes (i.e., regions) used by the Snail Kite in Florida. Kissimmee Chain of Lakes (K), Everglades (E), Lake Okeechobee (L), and Saint Johns Marsh (J).

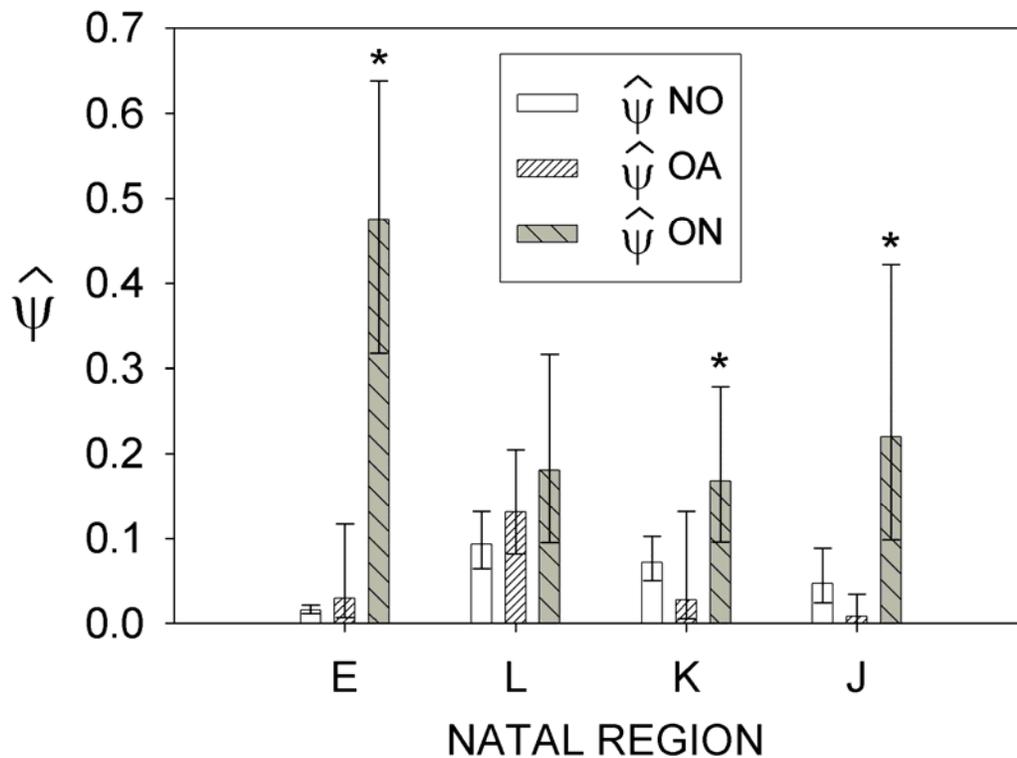


Figure 4-2. Movement probabilities ($\hat{\psi}$) between natal region “N”; post-dispersal region “O” (potentially includes all regions except for the natal region); and post-dispersal region “A” (potentially includes all regions except for the natal region and the post-dispersal region “O” occupied in the year prior to moving to “A”) for Snail Kites hatched in four regions. Model averaged estimates of movement between “N” and “O” ($\hat{\psi}^{NO}$); between “O” and “N” ($\hat{\psi}^{ON}$); and between “O” and “A” ($\hat{\psi}^{OA}$) are presented. Error bars: 95%CI. Asterisks indicate that differences between $\hat{\psi}^{ON}$ and $\hat{\psi}^{OA}$ were statistically significant (i.e., 95%CI[\hat{ES}] do not include 0).

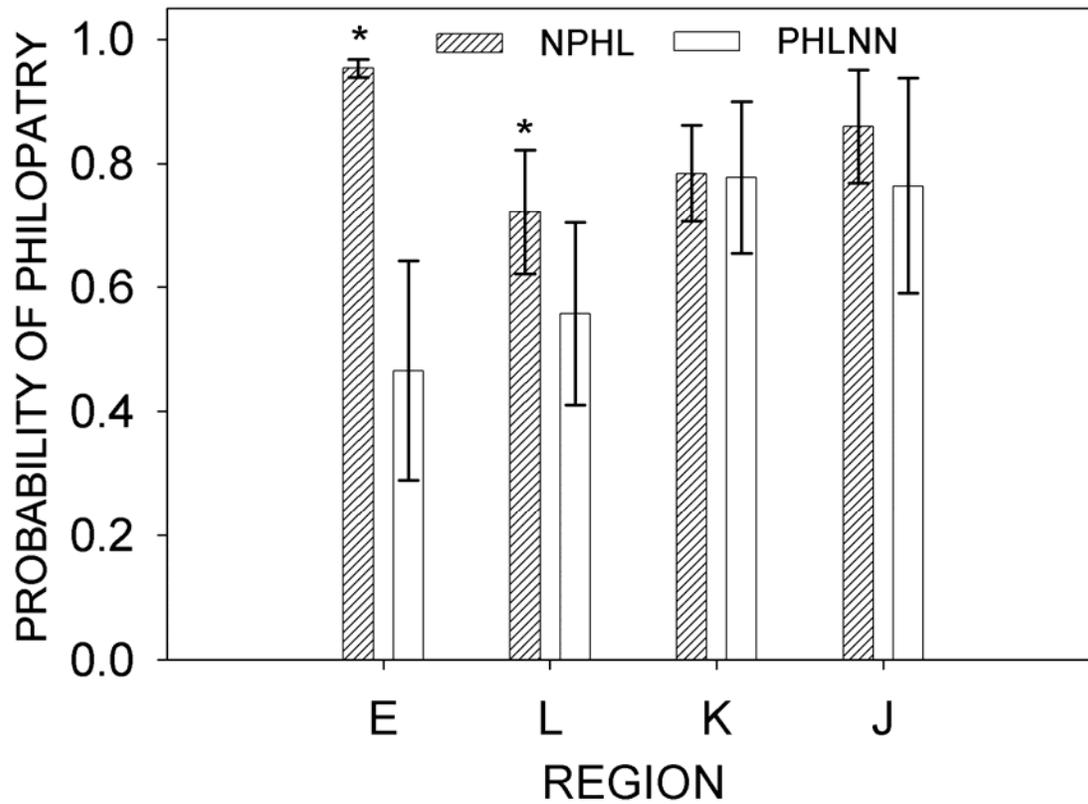


Figure 4-3. Model averaged estimates of natal philopatry (NPHL) and philopatry to non-natal region (PHLNN). Error bars: 95%CI. Asterisks indicate that differences between estimates of NPHL and PHLNN were statistically significant (i.e., 95%CI[$\hat{E}S$] do not include 0).

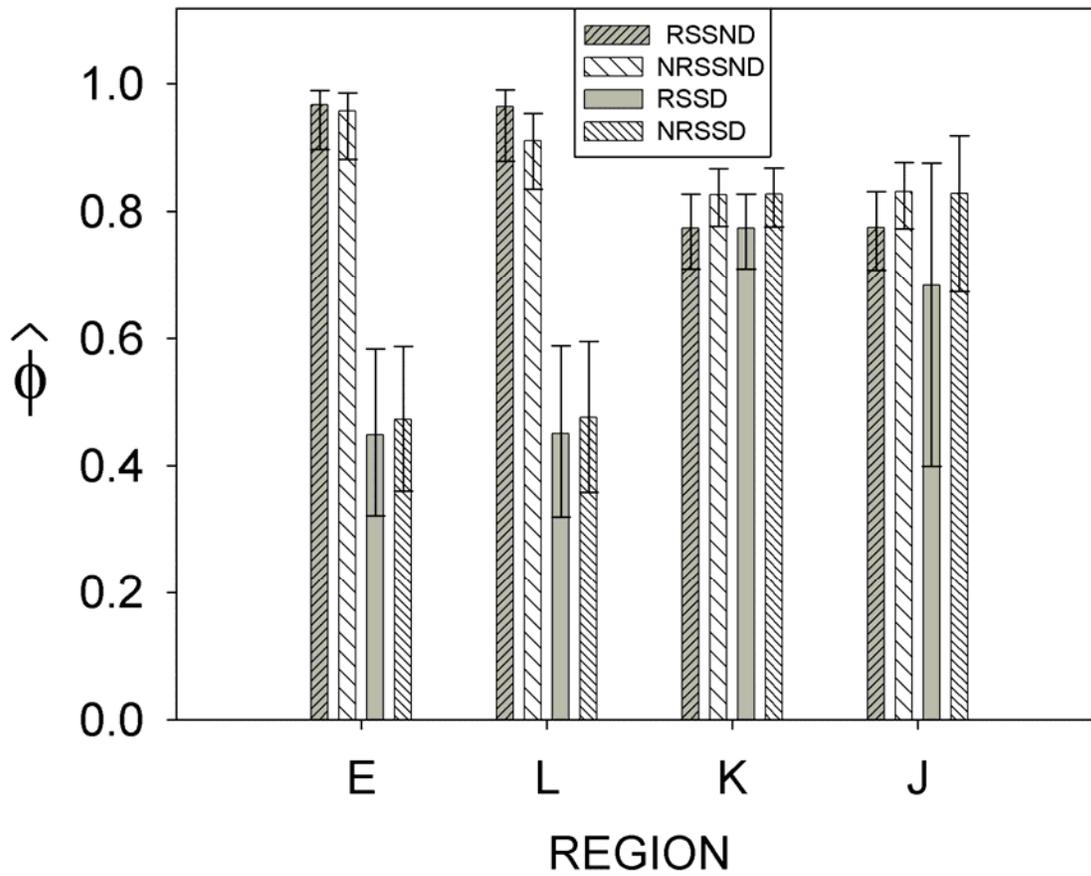


Figure 4-4. Model averaged estimates of “region specific” and “natal region specific” survival ($\hat{\phi}$) of Snail Kites in four regions. “Region specific” survival is denoted “RSSND” during non-drought, and “RSSD” during drought (time interval 2001-2002). “Natal region specific” survival is denoted “NRSSND” during non-drought, and “NRSSD” during drought (time interval 2001-2002). Error bars: 95%CI.

CHAPTER 5
EXPLORING THE EFFECTS OF NATURAL DISTURBANCES AND HABITAT
DEGRADATION ON THE VIABILITY OF THE SNAIL KITE

Introduction

Natural disturbances and habitat degradation have major influences on the dynamics of many wild populations. Natural disturbances are environmental events that generally induce temporary changes in the system state (Reeves, Benda et al. 1995). Habitat degradation disturbances are typically caused by human activities and often lead to more permanent changes in the system state (Reeves, Benda et al. 1995). Natural disturbances are often perceived as “catastrophes” (e.g., flood, droughts) that impose large numerical responses on wild populations (Casagrandi and Gatto 2002). However, natural disturbances may also play a role in organizing ecosystems (DeAngelis and White 1994). In the long term, natural disturbances may be crucial to the persistence of wild populations (DeAngelis and White 1994). In some instances, degradation of natural habitats by human activities may have altered the organizing role of disturbances, and as a consequence, may have changed the short and long term response of populations to these naturally occurring events. Because most wildlife studies are conducted in the short term and at relatively small spatial scales, most studies investigating the effects of natural disturbances on natural populations have focused on the negative effects of disturbances (White and Pickett 1985). Studies that clearly show beneficial effects of disturbances remain scarce. A troubling fact is that suppressing the natural effects of natural disturbances can actually cause the degradation of natural habitats with long term consequences for populations inhabiting these systems (e.g., Reeves et al. 1995). Better understanding the role of natural disturbances on populations, both in the short term and in the long term, is an important challenge in order to uncover the ecological dynamics of

many natural systems in a changing world. This challenge is also of particular interest to management and conservation because management actions that benefit certain threatened species in the short term, may be detrimental to the long term restoration of the systems.

We examined three hypotheses related to the effect of natural disturbances and habitat degradations on Snail Kite dynamics and viability. The Snail Kite is a wetland specialist whose diet consists almost exclusively of freshwater snails (Beissinger 1988). Vital rates of Snail Kites are finely tuned to the hydrology of its habitat. Drying events reduce availability of snails to kites, and therefore can dramatically increase mortality (Beissinger and Takekawa 1983; Takekawa and Beissinger 1989; Martin et al. 2006). The impact of drying events on kites depends on the intensity, spatial extent and duration of these disturbances (Kitchens et al. 2002; Mooij et al. 2007). Drying events often occur naturally, but in some instances can be induced by management (e.g., managed draw downs). When natural disturbances occur adult Snail Kites are better able than juvenile birds to resist disturbances by moving to refugia habitats (Martin et al. 2006). As pointed out by Kitchens et al. (2002), droughts are natural disturbances that are an organizing force of Florida ecosystems, and suppressing them may cause habitat conversion. In addition, prolonged hydroperiods and excessive flooding intensity and frequency may also shift the vegetation communities toward communities less suitable for foraging and nesting activities of Snail Kites (Kitchens et al. 2002; Darby et al. 2005). During the period 1993 to 2005 most primary kite habitats experienced a high frequency of flooding events and unusually prolonged hydroperiods during the Fall, and a single extensive drought was reported between 1993 and 2005 (Martin et al. 2007a). The increase in

flooding frequency resulted from an increase in precipitation but also from the regulation of pumping stations, particularly in WCA3 and Lake Okeechobee. In this study we consider habitat conversion caused by water management as a type of habitat degradation. Several authors have argued that these changes in hydro patterns have degraded kites' habitat (Kitchens et al. 2002). Martin et al. (2007b) noted that the number of juveniles appeared to decrease dramatically after 1998. The 2001 drought had a large effect on kite survival and the population decreased substantially after 2001; however, the kite population has not recovered since (Martin et al. 2007b). Adult survival does not appear to have been reduced substantially, except during the drought that occurred in 2001 (Martin et al. 2006). Survival of juveniles appears to have decreased since 1999, but the pattern is not absolutely clear and could be due to stochastic variation (Martin et al. 2006). Based on these observations, we defined two periods: a pre-1998 period (which included 1998) and a post-1998 period (which did not include 1998). The pre-1998 period reflected a pre-decline environment (i.e., before the number of young produced decreased, see Martin et al. 2007b). Based on past research on Snail Kites (e.g., Kitchens et al. 2002; Darby et al. 2005; Mooij et al. 2007; and Martin et al. 2007a), we considered three primary hypotheses to explain lack of recovery of the kite population after the 2001 drought. First, we considered the habitat degradation hypothesis, which assumes that an increase in frequency of flooding events (during the period August to January, hereafter referred as the Fall) has led to a deterioration of foraging and nesting habitats of Snail Kites (*Hypothesis 1*). Second, we considered the hypothesis that an increase in moderate drying events during the Spring-Summer (i.e., during the breeding season, period March to June) is limiting recovery (*Hypothesis 2*). Indeed, Martin et al. (2007a) found that after

1998 there was an increase in moderate drying events in WCA3A during the Spring-Summer (which includes the peak of the breeding season). As explained in the section *Hydrological Conditions*, moderate drying events are more moderate disturbances than droughts. Finally, we considered *Hypothesis 3* which assumes that both habitat degradation and an increase in moderate drying events are limiting population growth rate of kites.

It is important to recognize that analyses associated with the examination of *Hypothesis 1, 2 and 3* are exploratory. The goal of our exercise was not to demonstrate the effect of specific factors (e.g., habitat degradation) on population growth rate. Instead, our objective was to measure the potential impact of selected factors in the context of each of the three hypotheses. For example, in the context of *Hypothesis 1* our question was, “what would be the effect of habitat degradation on population growth rate of kites if in fact *Hypothesis 1* was true?” We applied the same reasoning for *Hypotheses 2 and 3*.

We selected these three hypotheses because they are the most relevant to current management of kite habitats and are also among the hypotheses best supported by the existing literature.

Objectives

Beissinger (1995) used matrix population models to examine the viability of kites in relation to drought frequency. In this paper we used a similar matrix population approach to address seven primary objectives. *Objective 1*: based on the most current estimates of vital rates we provided several measures of Snail Kite viability under the current state of the system (deterministic population growth rate, stochastic population growth rate, and probability of quasi-extinction). *Objective 2*: we determined the key vital rates that governed the population growth of the kite population (based on sensitivity

analyses). *Objective 3:* We compared deterministic population growth rates (λ_1) before and after 1998. *Objective 4:* Based on deterministic one way Life Table Response Experiment (LTRE, Caswell 2001), we estimated how differences in vital rates between the pre and post-1998 environments have contributed to changes in population growth rates. *Objective 5:* We estimated stochastic population growth rates for pre and post-1998 environment and varied the frequency of drought. This analysis allowed us to evaluate the relative importance of an increase in drought frequency as opposed to the “before versus after 1998” effect on population growth rate (e.g., due to habitat conversion under *Hypothesis 1*). *Objective 6:* we examined the hypothesis that the primary factor for kite decline was related to an increase in moderate drying events and not to habitat degradation (*Hypothesis 2*). *Objective 7:* we evaluated a hypothesis that assumed that both an increase in moderate drying events frequency and the “before versus after” effect (e.g., due to habitat conversion) were responsible for lack of recovery of kites (*Hypothesis 3*). In the final section of our presentation we discuss the conservation implications of our findings.

Methods

Study Area

Our study encompassed the entire population of Snail Kites located in Florida; see Dreitz et al. (2002) for a detailed map of the sampled areas.

Life Cycle

All population matrix models in this paper assumed a pre-breeding census and considered only the female part of the population (Caswell 2001). We assumed a 50:50 sex ratio (Beissinger 1995).

As in Beissinger (1995) we considered three stage classes: juveniles (35 days to < 1 year old); subadults (1 to < 2 years old); adults (≥ 2 years). However, because we assumed a pre-breeding census, the youngest birds during the census are the individuals that were produced during the previous breeding event, and these individuals will be subadults by the time of the birth pulse (Morris and Doak 2002). If subadults survive (survival probability P_s) to the next census they will become adults. If adults survive (survival probability: P_a), they will remain adults. To contribute to age class 1 at the next census a reproductive female will have to generate a number of juvenile females (referred herein as fecundity of females: m_a ; m_s , is the fecundity of subadult females), and these juvenile females will have to survive until the next census (with survival probability of juvenile: P_j) (Morris and Doak 2002). Thus, as explained in Caswell (2001) adult fertility (F_a) is:

$$F_a = P_j \times m_a \quad (\text{Eq. 5.1})$$

and subadult fertility (F_s) is:

$$F_s = P_j \times m_s \quad (\text{Eq. 5.2})$$

Hydrological Conditions

We performed an agglomerative hierarchical clustering analysis in order to establish three groups of years characterized by contrasted hydrological conditions. The three categories of years were: wet years (1993 to 1998, 2003 and 2005), moderately dry years (1999 to 2000, 2002 and 2004), and drought years (1992 and 2001; [see appendix D for details]). Droughts were characterized by the greatest intensity (e.g., lowest water levels during the dry season), the longest duration and the greatest spatial extent (e.g., proportion of wetlands affected by dry conditions).

All but one hydrological variable (spatial extent) were measured in Everglades Water Conservation Area 3A (WCA3A). There were two primary reasons for focusing on hydrological conditions in WCA3A; (1) WCA3A has been identified as the single most important wetland unit currently occupied by kites (Martin et al. 2007a); (2) hydrological conditions in WCA3A are highly correlated with conditions in all the WCAs, Everglades National Park and Lake Okeechobee which, by far constitute the largest extent of wetlands occupied by kites (Martin et al. 2007a).

Data Source and Estimates of Vital Rates

Survival rates

Because apparent survival was estimated and modeled for the entire Florida population of Snail Kites, data from all regions were combined into a single analysis. Cormack-Jolly-Seber model (CJS) (Lebreton *et al.*, 1992) were used to produce estimates of ϕ (probability of surviving and not permanently emigrating to an area not sampled between year t and $t+1$) and estimates of p (probability of sighting an individual in year t , given that it was present and alive in the sampling area). Modeled parameters used notation from Lebreton *et al.* (1992); time dependency was (t) and no time effect was ($.$). We assigned each bird to one of two age classes: juveniles (denoted by subscript “J”), which were 30 days to 1 year old; and adults (denoted by subscript “AD”), older than 1 year. Effects embedded in other factors are shown using parentheses. A multiplicative effect is shown by (*) and an additive effect is shown by (+).

Because previous survival analyses (Bennetts, Kitchens & Dreitz, 2002) indicated an age effect on ϕ , we computed a Goodness Of Fit test (GOF) accounting for an age effect by summing Test 3.SM, Test 2.CT and Test 2.CL (available from program U-

CARE), yet the model still fit the data poorly ($\chi^2_{120} = 197.18, P < 0.0001$) indicating excess variation (Choquet et al., 2003). We thus calculated a variance inflation factor, \hat{c} , which shows the amount of extra-binomial variation present in the data (Burnham & Anderson, 1998). We computed this variance inflation factor as $\hat{c} = (\text{Test 3.SM} + \text{Test 2.CT} + \text{Test 2.CL}) / (\text{df 3.SM} + \text{df 2.CT} + \text{df 2.CL})$, and obtained 1.64 (Choquet et al. 2003). This value was well below 3, above which the model structure is frequently considered to be inadequate (Burnham & Anderson, 1998). We used the \hat{c} value in the program MARK to estimate variance of $\hat{\phi}$ and \hat{p} and for model-selection procedures (Burnham & Anderson, 1998; White & Burnham, 1999).

A set of biologically relevant models was developed that allowed ϕ and p to vary across time (denoted “ t ”), or stay constant (denoted “.”) for each age class (i.e., adults: subscript “AD”, and juveniles: subscript “J”). Age was modeled both as time since marking and as a group effect. We also created models that included drought effect on ϕ and p . We included three types of drought effects. “D1”: “ ϕ ” was assumed to be constant except during the drought period 00-02, (“ ϕ ” during 00-01, was assumed to be different from 01-02, see also Martin et al. 2006). “D2”: same as “D1” except that 92-93 was also considered a drought period (see section *Hydrological Conditions*). Under “D2”, the drought effect on survival was assumed to be the same in 92-93 and 01-02. “D3”: same as “D2” except that the drought effect in 92-93 was assumed to be different from 01-02 (see also Martin et al. 2006 for additional information on drought effect on Snail Kite survival). In the section *Hydrological Conditions*, we identified three categories of years: wet, moderately dry and drought. Hence, we designed models with the effect “WMD1”: “ ϕ ” was associated with 3 years categories, wet (93 to 98), moderately dry (99 to 01, 02-

03, 04-05), and drought (92-93, 01-02, but in these models the drought effect on survival is assumed to be the same in 92-93 and 01-02). We also constructed models with the effect: “WMD2” (same as “WMD1” except that the drought effect on survival was assumed different in 92-93 and 01-02). “D1”: “ ϕ ” was constant except during the drought period 00-02, (during 00-01, “ ϕ ” was assumed to be different from 01-02).

In addition, we included some trend models (see Cooch and White 2005). In these models, survival probabilities were modeled as linear-logistic function of a covariate: TCOV (where COV is a covariate). TAVGJD was a trend model with annual mean water levels for the period January to December (of year t) as a covariate. TAVGMJ was a trend model with annual mean water levels for the period March to June (of year t) as a covariate. TMWL was a trend model with minimum annual water levels as a covariate. TSPAT was a trend model with spatial extent of drying (i.e., proportion of regions with index of dryness less than 1) event as a covariate. TTIME was a trend model with time as a covariate. Some trend models included a drought effect (i.e., survival was modeled as a function of a covariate for most years except during drought years of 2000-2002). These models were denoted ϕ_J (D4/TCOV) (for juvenile survival) and ϕ_{AD} (D5/TCOV) (for adult survival). Because in 1992 most juveniles were fledged outside the WCAs (i.e., in areas not affected by the 1992 drying event, see Hydrological conditions), we built models that were similar to ϕ_J (D4/TCOV), but did not include the interval 92-93 as part of the trend (i.e., the survival estimate for this time period was estimated independently from the trend). These models were denoted ϕ_J (D6/TCOV). We also designed models similar to ϕ_{AD} (D5/TCOV), but which assumed identical effects of the drought on adult survival during the period 1992-1993 and 2001-2002 (in these models adult survival

during the interval 2000-2001 was not included in the trend, and was assumed to be different than during the intervals 1992-1993 and 2001-2002), these models were denoted ϕ_{AD} (D7/TCOV). For each trend model we made a priori predictions about the direction of the relationship (i.e., positive or negative relationship). Because past research suggests that survival should be greater during wet years and lower during dry years, we predicted a positive relationship between survival and the slope of TAVGJD, TAVGMJ, and TMWL. Based on work from Bennetts and Kitchens (2000), we predicted that survival would decrease as the spatial extent of drying events increased. If juvenile and adult survival declined over time the slope of TTIME should be negative for juveniles and adults. We used QAICc (see Chapter 3 and 4) as a criterion to select the model that provided the most parsimonious description of the variation in the data (i.e., model with the lowest QAICc). Survival rates were obtained by model averaging (see Chapter 4).

Fecundity rates

In order to be able to construct population projection models, we need to be able to estimate m_a (fecundity of adults) and m_s (fecundity of subadults):

$$\hat{m}_a(t) = \frac{\hat{N}_{f,j}(t)}{\hat{N}_{f,a}(t) + \frac{\hat{N}_{f,s}(t)}{q(t)}} \quad (\text{Eq. 5.3})$$

Where $\hat{N}_{f,a}(t)$ is the estimated number of adult females and $\hat{N}_{f,j}(t)$ the estimated number of juvenile females in the population. $\hat{q}(t)$ is the estimated ratio of fecundity rates:

$$\hat{q}(t) = \frac{\hat{m}_a}{\hat{m}_s} \quad (\text{Eq. 5.4})$$

Hence,

$$\hat{m}_s = \frac{\hat{m}_a}{\hat{q}(t)} \quad (\text{Eq. 5.5})$$

In 2004 and 2005 we directly estimated the number of juveniles in the population (see Martin et al. 2007b for methodology). The number of juvenile females was obtained by dividing these superpopulation estimates for juveniles by two (assuming a sex ratio of 50:50). For the period 1992 to 2003 we did not have estimates of the number of juveniles, but counts were available. For these years $\hat{N}_{f,j}(t)$ can be obtained using:

$$\hat{N}_{f,j}(t) = \frac{C_{f,j}(t)}{\hat{\beta}(t)} \quad (\text{Eq. 5.6})$$

Where $C_{f,j}(t)$ is a count of the number of juvenile females at time t and $\hat{\beta}(t)$ is the fraction of juveniles counted from the overall population of juveniles at time t (i.e., hereafter referred as detection of juveniles (see Martin et al. 2007b).

$$\hat{N}_{f,a}(t) = \hat{N}_{f,SUP}(t) - \hat{N}_{f,s}(t) \quad (\text{Eq. 5.7})$$

Where $\hat{N}_{f,SUP}(t)$ is the estimate of superpopulation size of females at time t (Estimates of $\hat{N}_{f,SUP}(t)$ are obtained by dividing superpopulation size estimates by two, assuming a 50:50 sex ratio; estimates of superpopulation size are available in (Martin et al. 2007)). $\hat{N}_{f,s}(t)$ in Eq. 5.7, corresponds to the number of subadult females at time t , which was computed as:

$$\hat{N}_{f,s}(t) = \hat{N}_{f,j}(t) \times \hat{P}_j(t) \quad (\text{Eq. 5.8})$$

We computed $\hat{q}(t)$ based on estimates obtained from Bennetts (1998). We obtained $\hat{q}(t) = 4.2$ (see Appendix E for more details). Varying $q(t)$ from 4 to 8.5 had little effect on population growth rates and other relevant measures.

Detection of juveniles

Estimates of detection of juveniles ($\hat{\beta}(t)$) were needed to compute fecundity rates.

We used a range of values of $\hat{\beta}(t)$ to evaluate the robustness of our results (see electronic supplementary materials for details on how $\hat{\beta}(t)$ was derived). First, we assumed that $\hat{\beta}(t)$ was constant over time and was equal to 0.16 (this estimate was the lowest of our empirical estimates and probably underestimated the “true” detection for most years, Appendix F). Second, we assumed that $\hat{\beta}(t)$ was constant over time but was equal to 0.70 (this estimate probably greatly overestimated the “true” detection, we picked this value because it was twice the value of our greatest estimate of detection, see Appendix F for more details). Third, we assumed that $\hat{\beta}(t)$ varied from 0.16 to 0.35 (see Appendix F for additional details).

Matrix Analyses

λ_1 , damping ratio, sensitivity and elasticity analysis (Objectives 1 and 2)

All matrix population models were based on the demographic life cycle described earlier. We constructed a matrix based on the most current estimates of vital rates; this included 9 years of data from (1997 to 2005). Hereafter, we refer to this matrix as the FULL1 matrix. Survival rates in the FULL1 matrix were computed as the average survival rates for the period 1997-2005. Fertilities were estimated as the product of the average fecundity and the average survival rate for juveniles. We computed the dominant eigenvalue (λ_1) for this matrix, which corresponds to the asymptotic population growth rate (Caswell 2001). We followed procedures described by Caswell (2001) to compute sensitivities and elasticities. Sensitivity measures how absolute changes in individual

vital rates influence λ_1 (Caswell 2001). Elasticity measures the proportional change in λ_1 resulting from a proportional change in individual vital rates (Morris and Doak 2002; Caswell 2001). Elasticities are more readily comparable among vital rates than sensitivities (Horvitz and Schemske 1995).

The damping ratio was computed by dividing the largest eigenvalue by the absolute number of the second largest eigenvalue. This ratio is indicative of the rate of convergence to the stable age structure (Caswell 2001).

Before versus after effect on λ_1 and Life Table Response Experiment (Objectives 3 and 4)

We applied a deterministic, fixed design one-way Life Table Response Experiment described by Caswell (2001), to assess how differences in vital rates before and after 1998 contributed to changes in λ_1 . Matrix “BEF” summarized the environment before 1998. Survival rates included in “BEF” were computed as the average annual survival for the interval 1993 to 1998, excluding estimates for 1992 identified by Martin et al (2007a) as a drought year. Fertilities were computed as the product of the average juvenile survival rates (for 1993 to 1998) and the average fecundity for the interval 1997 to 1998. Matrix “AFT” summarized the environment after 1998. Survival and fertility rates for this matrix included estimates from 1999 to 2005, excluding estimates of survival and fertilities affected by the 2001 drought and the 2004 drying event (both drying events had large effects on juvenile survival). Therefore, estimates of juvenile survival did not include estimates for the interval 2000 to 2002. Estimates of fecundity did not include estimates for 2001 and 2004. For this analysis we used matrix “BEF” as the “reference” matrix, and “AFT” matrix as the “treatment level” (Caswell 2001).

Stochastic population growth rate (objectives 1, 4, 5 and 6)

We computed the stochastic population growth rate (λ_s) and 95%CI of λ_s , by using the simulation method described by Caswell (2001, p.396). $\widehat{\log \lambda_s} = \frac{1}{T} \sum_{t=0}^{T-1} r_t$, and an approximate 95%CI: $\widehat{\log \lambda_s} \pm 1.96 \sqrt{\frac{V(r)}{T}}$, where T is the simulation time,

$r_t = \log \frac{(N_f(t+1))}{(N_f(t))}$, where $N_f(t)$ is the population size of females at t , $V(r)$ is the variance

of r_t . T was set to 10,000 time steps (i.e., 10,000 years). The initial population size and population structure were set based on the observed values in 2005 (Martin et al. 2007b).

The simulations assumed independent and identically distributed sequences (iid): at each time step t , a matrix (which corresponded to a particular environmental state) was drawn from a fixed distribution (Caswell 2001). For all the stochastic analysis (i.e., λ_s and

probability of quasi-extinction (PQE)) we incorporated the variance associated with each vital rate (which included both process and sampling variance), as well as the within year correlation among vital rates using the approach described by Morris and Doak (2002:

284-285). The correlation matrix was computed based on fecundity and survival rates for the period 1997 to 2004 (estimates of fecundity were available for the period 1997 to

2005 but estimates of survival were only available for the period 1992 to 2004). As suggested by Morris and Doak (2002), we used the *Stretched-Beta* distribution to

simulate random variation in fecundity and fertility rates, whereas we used the *Beta* distribution to simulate random variation in survival rates. The variance for each

parameter (e.g., survival and fecundities) was computed as: $\text{var}(\hat{\theta}) = \frac{\sum (\theta_i - \hat{\theta})^2}{n-1}$. These

estimates of variance included both sampling and process variance. In instances where only one estimate was available (e.g. drought year of 2001), we used the sampling variance. Variances for derived parameters were computed using the delta method (Williams et al. 2002).

We estimated λ_s for 11 sets of environmental conditions (denoted by *Conditions* (x), with $x = 1$ to 11) that addressed *Objectives 1, 5, 6 and 7*:

Viability of Snail Kites under current conditions (Objective 1)

- *Condition (1)*: we computed λ_s for the time series 1997 to 2005. For this simulation we could have used matrix FULL1. However, because the 2001 drought was considered an extreme event, we followed the suggestion of Morris and Doak (2002, p. 272) and used three matrices for this simulation: (a) matrix FULL2 (means and variances were estimated for the period 1997 to 2005, but excluded data for the period 2000-2001 which corresponded to the drought); (b) matrix DRO1 (based on the data for 2000); (c) matrix DRO2 (based on the data for 2001). These matrices were drawn at random with the observed frequencies for the period 1997 to 2005: frequency for FULL2 was: 7/9 and frequencies for DRO1 and DRO2 were 1/9.

Evaluation of Hypothesis 1: Reduction of λ_s after 1998 (Objective 5)

- *Conditions (2) and (3)*: we computed λ_s for the environmental state that corresponded to the period before 1998. This simulation was based on two matrices. (a) One matrix summarized the conditions before 1998 (i.e., means and variances were obtained for the period 1993 to 1998). (b) One matrix summarized the drought conditions DRO (see section *Hydrological conditions*). We estimated two values of λ_s : one assuming a drought frequency of 0.111 (i.e., drought occurred on average every 9 years: *Condition (2)*) and another assuming a drought frequency of 0.25 (i.e., one drought every four years: *Condition (3)*).
- *Conditions (4)*: same as *Condition (2)*, but for the environmental state that corresponded to the period after 1998.
- *Conditions (5)*: same as *Condition (3)*, but for the environmental state that corresponded to the period after 1998.

Hypothesis 1 assumes that habitat degradation has caused a reduction in λ_s after 1998. The logical prediction for this hypothesis is *Prediction 1*: λ_s under *Condition (2)* > λ_s under *Condition (4)*; and λ_s under *Condition (3)* > λ_s under *Condition (5)*.

Evaluation of Hypothesis 2: Increase in drying event frequency reduces λ_s (Objective 6)

Hypothesis 2 assumes that an increase in moderate drying events frequency has caused a reduction in λ_s after 1998. In the section *Hydrological conditions* we explained that the frequency in moderate drying event was greater after 1998 than before 1998.

- *Condition (6)*: we computed λ_s by simulating an environment with three environmental states: WET₁, MOD and DRO (see *Hydrological conditions*). This simulation ignored the effect of habitat degradation. The matrix summarizing wet years was based on means and average of all years that were identified as wet years for the period 1992 to 2005 (i.e., for ma and ms: 1993 to 1998, 2003 and 2005; for Pa and Py 1993 to 1998 and 2003). The matrix summarizing moderately dry years was based on means and averages of all years that were identified as dry years for the period 1992 to 2005 (i.e., for ma and ms: 1999 to 2000, 2002 and 2004; for Pa and Py 1999, 2002 and 2004). The matrix summarizing drought years is described in *Hydrological conditions*. For condition (6) we applied observed frequencies for each environmental state for the first seven years of the study (i.e., 1992 to 1998; we refer to this environment as Low Frequency of Moderate Drying event: LFMD). During this time period: 1 drought year was observed (frequency: 1/7); no moderately dry years were observed (frequency: 0/7); and 6 wet years were observed (frequency: 6/7).
- *Condition (7)*, same as condition (6), except that we used frequencies observed for the last 7 years (i.e., 1999 to 2005, High Frequency of Moderate Drying event (HFMD), 1 drought: 1/7; 5 moderately dry years: 4/7; and two wet years: 2/7).

Under *Hypothesis 2* we predict *Prediction 2*: λ_s under *Condition (6)* > λ_s under *Condition (7)*.

Evaluation of Hypothesis 3: Increase in frequency of drying events and “before versus after” effect (Objective 7)

- *Conditions (8)*, we computed λ_s by simulating an environment with three environmental states: WET₂, MOD and DRO. The matrix summarizing the wet years was estimated based on means and variances of parameters estimated prior to 1998. Ideally, we would also have computed matrices for MOD and DRO based on parameters estimated prior to 1998. Unfortunately, there were no data available for moderately dry years prior to 1998, and in *Hydrological conditions* we explained why we did not use parameters estimated from 1992. Thus, matrices MOD and DRO were based on data collected after 1998, and were the same matrices used for *Condition (6)*. For condition (8) we applied the observed frequency for each environmental state for the first 7 years of the study (LFMD, see *Condition (6)*).

- Condition (9), same as condition (8), except that we used frequencies observed for the last 7 years (HFMD: 1 drought: 1/7; 5 moderately dry years: 4/7; and two wet years: 2/7).
- Condition (10) same as condition (8) except that the matrix summarizing the wet years was based on parameters estimated after 1998. We refer to this matrix as WET₃. For Condition (10) we applied the observed frequency for each environmental state for the first 7 years of the study (LFMD, see Conditions (6 and 8)).
- Condition (11) same as Condition (10) but we applied the observed frequency for each environmental state for the last 7 years of the study (HFMD, see Conditions (7 and 9)).

Hypothesis 3 assumes that both an increase in moderate drying events and the “before versus after” effects have contributed to a decrease in λ_s after 1998. Under this hypothesis we predict *Prediction 3a*: λ_s under *Condition (8)* > λ_s under *Condition (9)*; and λ_s under *Condition (10)* > λ_s under *Condition (11)*. We also predict *Prediction 3b*: λ_s under *Condition (8)* > λ_s under *Condition (10)*; and λ_s under *Condition (9)* > λ_s under *Condition (11)*.

Probability of Quasi-Extinction (Objective 1)

We calculated the probability of reaching a quasi-extinction state for a set time. We chose a quasi-extinction threshold of 50 females. This number appeared to be a reasonable compromise to deal with concerns about demographic stochasticity, yet would be low enough to make the population at this level immediately imperiled (Morris and Doak 2002). We estimated the PQE at a projected time of 150 years. We calculated the cumulative distribution for quasi-extinction time by simulation (100 runs) by computing the proportion of trajectories that fell below 50 kites during and until a projected time of 150 years. We repeated this procedure 100 times. From the distribution of PQE at each time step we determined the lower and upper 95% percentiles for each analysis. We used these latter values as estimates of 95%CI of the estimate of PQE. We used the mean of

the distribution as an estimate of PQE. The initial population size and age structure used in the simulation were based on average estimates of population size obtained in 2005 (Martin et al. 2006). We generated the same stochastic environmental conditions as for the computation of λ_s .

Validation

We repeated all the analyses to estimate λ_1 , λ_s and PQE assuming (1) constant detection of juveniles $\hat{\beta}(t) = 0.16$; (2) detection varying between $\hat{\beta}(t) = 0.16$ and 0.35; and (3) constant detection of juveniles $\hat{\beta}(t) = 0.70$ (see *Detection of Juveniles* and Appendix F). Analyses assuming constant $\hat{\beta}(t) = 0.16$ resulted in the most optimistic scenarios (i.e., lowest PQE, greatest λ_s); whereas, analyses assuming constant $\hat{\beta}(t) = 0.70$ resulted in the most pessimistic scenarios. Analyses that assumed that $\hat{\beta}(t)$ varied between 0.16 to 0.35 were probably the most reasonable (see Appendix F for more details).

All matrix analyses were conducted using MATLAB (Mathworks 2005).

Results

Survival estimates

The most parsimonious model $\phi_{AD}(\text{WMDI})\phi_j(t)p(t)$, was marginally better supported by the data than the next 4 most parsimonious models ($w = 0.234$; Table 5-1). The ΔQAICc among the five most parsimonious models were less than 1, which indicate that these models received very similar support from the data. Models that assumed a time effect on juvenile survival and detection probabilities were well supported by the data ($w = 1$; Table 5-1). Model averaged estimates indicated that adult survival was significantly

lower during the periods 92-93 and 00-02 (Figure 5-1). However adult survival was exceptionally low during the interval 01-02 (Figure 5-1; see also Martin et al. 2006). Models that assumed a “wet-moderately dry-drought” effect on survival (e.g., WMD1) received some support, in fact the most parsimonious model was: $\phi_{AD}(WMD1)\phi_J(t)p(t)$. However, the differences in adult survival (model averaged estimates) during these three year-categories were not substantially different (Figure 5-1). Although models assuming a WMD1 or WMD2 effect on juvenile survival were not well supported by the data based on QAICc (when compared to the time dependent model), we found that there was a substantial differences in juvenile survival during wet, moderately dry and drought years. As expected Juvenile survival was highest during wet years ($\hat{\phi}_J = 0.557$; 95%CI = 0.498 to 0.617), lowest during the 2001 drought ($\hat{\phi}_J = 0.074$; 95%CI = 0.012 to 0.339), and intermediate during moderately dry years ($\hat{\phi}_J = 0.255$; 95%CI = 0.194 to 0.316) (see also Figure 5-1). Interestingly, juvenile survival in 92-93 was high even though this period was categorized as a drought period based on the Hydrological Analysis. This is probably explained by the fact that, most birds were fledged in areas located outside of the WCAs: Lake Okeechobee, St Johns Marsh and KCL, all these areas were not affected dryer than average in 1992 (see Hydrological Conditions, Table 7-1 and 7-2).

The trend models received almost no support based on QAICc weights ($wt \sim 0$, Table 5-1). However, the slope parameters for most trend models indicated a significant relationship between the covariates and survival of juveniles. The slope parameter β_{TAVJD} from model $\phi_{AD}(D2)\phi_J(D6/T_{AVGJD})p(t)$ (Table 5-1) indicated a positive relationship between average water levels for the period January to December and survival of

juveniles ($\beta_{TAVJD} = 2.13$; 95%CI = 1.22 to 3.05). The slope parameter β_{TAVMJ} from model $\phi_{AD}(D2) \phi_J(D6/T_{AVGMJ}) p(t)$ (Table 5-1) indicated a positive relationship between average water levels for the period March to June and survival of juveniles ($\beta_{TAVMJ} = 1.23$; 95%CI = 0.475 to 1.98). The slope parameter β_{TMWL} from model $\phi_{AD}(D2) \phi_J(D6/T_{MWL}) p(t)$ (Table 5-1) indicated a positive relationship between annual minimum water levels and survival of juveniles ($\beta_{TMWL} = 1.93$; 95%CI = 1.37 to 2.48, see Figure 5-1). The slope parameter β_{TDUR} from model $\phi_{AD}(D2) \phi_J(D6/T_{DUR}) p(t)$ (Table 5-1) indicated a negative relationship between duration of drying event and survival of juveniles ($\beta_{TDUR} = -0.04$; 95%CI = -0.06 to -0.03). The slope parameter β_{TSPAT} from model $\phi_{AD}(D2) \phi_J(D6/T_{SPAT}) p(t)$ (Table 5-1) indicated a negative relationship between spatial extent of drought and survival of juveniles ($\beta_{TSPAT} = -6.95$; 95%CI = -10.75 to -3.16). The slope parameter β_{TTIME} from model $\phi_{AD}(D2) \phi_J(D6/T_{TIME}) p(t)$ (Table 5-1) indicated a negative relationship between time and survival of juveniles (slope for juveniles: $\beta_{TTIME} = -0.14$; 95%CI = -0.22 to -0.06). This estimate suggested that juvenile survival decreased significantly over time. In contrast the slope parameter from β_{TTIME} from model $\phi_{AD}(D7/T_{TIME}) \phi_J(D6/T_{TIME}) p(t)$, did not support the hypothesis of a significant decrease of adult survival over time (slope for adults: $\beta_{TTIME} = 0.04$; 95%CI = -0.09 to 0.16).. Model averaged estimates for adult and juvenile survival are presented in Figure 5-1.

Probability of Quasi-extinction (Objective 1)

PQE increased dramatically as detection of juveniles increased (Figure 5-2). PQE at 50 years was 0.65 (95%CI = 0.59 to 0.70) when $\hat{\beta}(t) = 0.16$, and it was 0.975 (95%CI = 0.96 to 1) when $\hat{\beta}(t) = 0.16$ to 0.35.

λ_1 , sensitivity and Elasticity analysis (Objectives 1 and 2)

The deterministic lambda: λ_1 for the last nine years were 0.92 (with $\hat{\beta}(t) = 0.16$), 0.89 (with $\hat{\beta}(t) = 0.16$ to 0.35), and 0.85 (with $\hat{\beta}(t) = 0.70$). The damping ratios were: 13.7 (for $\hat{\beta}(t) = 0.16$), 19.2 ($\hat{\beta}(t) = 0.16$ to 0.35) and 56.7 (for $\hat{\beta}(t) = 0.70$). These values were large and indicated rapid convergence to the stable population structure following perturbations (Caswell 2001).

Sensitivity analysis of matrix “FULL”, indicated that λ_1 was most sensitive to changes in adult survival and adult fertility (note that sensitivities were slightly higher for changes in adult survival, Figure 5-3.a). Sensitivity of λ_1 to changes in other vital rates (F_s and P_s) was considerably lower (Figure 5-3a). Elasticity analyses indicated that λ_1 was most sensitive to proportional changes in P_a (Figure 5-3.b). Elasticity of λ_1 to changes in F_a and P_s were considerably lower (< 0.1). Elasticity of λ_1 to change in F_s was almost 0, and this was true independently of the detection of juveniles assumed (Figure 5-3.b).

Life Table Response Experiment (Objective 3)

The deterministic lambda: λ_1 for matrix “BEF” was 1.2 (with $\hat{\beta}(t) = 0.16$), 1.13 (with $\hat{\beta}(t) = 0.16$ to 0.35), and 0.95 (with $\hat{\beta}(t) = 0.70$). The deterministic lambda: λ_1 for

matrix “AFT” was 0.97 (with $\hat{\beta}(t) = 0.16$), 0.92 (with $\hat{\beta}(t) = 0.16$ to 0.35), and 0.89 (with $\hat{\beta}(t) = 0.70$).

There was a large difference in F_a between matrix “BEF” and matrix “AFT” when detection of juveniles was assumed to be 0.16 or varied from 0.16 to 0.35 (Figure 5-4). The reduction in F_a was considerably lower when detection of juveniles was assumed to be large ($\hat{\beta}(t) = 0.70$). Reduction in other vital rates was less than 0.05 (Figure 5-4). When $\hat{\beta}(t) = 0.16$ and $\hat{\beta}(t) = 0.16$ to 0.35, was assumed F_a contributed the most to the reduction in λ_1 between “BEF” and “AFT” (contribution > 90%), whereas P_a , P_s and F_s contributed less than 4% each (Figure 5-4). When $\hat{\beta}(t) = 0.70$ was assumed, F_a still contributed the most (84%), but the contribution of P_a was also greater (14%). In all cases, there were close correspondences between the sum of LTRE contributions and observed differences in λ_1 (differences < 0.22%), which suggest that the first order approximation used was sufficient (Caswell 2001).

Stochastic population growth rate λ_s

Viability of Snail Kites under current conditions (Objective 1)

Condition (1): When assuming $\hat{\beta}(t) = 0.16$, λ_s for the last 9 years was 0.940 (95%CI = 0.936 to 0.944). When assuming $\hat{\beta}(t) = 0.16$ to 0.35, λ_s for the last 9 years was 0.9033 (95%CI = 0.8998 to 0.9069). When assuming $\hat{\beta}(t) = 0.7$, λ_s for the last 9 years was 0.853 (95%CI = 0.8509 to 0.8561).

Evaluation of Hypothesis 1: Reduction of λ_s after 1998 (Objective 5)

Conditions (2) to (5): There was an additive effect of drought frequency and the “before versus after 1998” effect. The additive effect was due to the fact that we assumed

the drought effect to be the same in the before and after 1998 environment. Increasing drought frequency from 0.11 to 0.25 caused a large decrease in λ_s (Figure 5-5). There was evidence of a large reduction in λ_s when comparing the before versus after 1998 environments. λ_s estimated from vital rates obtained prior to 1998 was substantially greater than λ_s based on vital rates obtained after 1998. This was true no matter what detection of juveniles was assumed. However, the magnitude of the difference decreased as detection of juveniles increased (Figure 5-5). The magnitude of the difference in λ_s due to the change in conditions before and after 1998 was greater than the effect of an increase in drought frequency (from 0.11 to 0.25) when $\hat{\beta}(t) = 0.16$ and $\hat{\beta}(t) = 0.16$ to 0.35 was assumed. When $\hat{\beta}(t) = 0.70$ was assumed, the reduction in λ_s due to an increase in drought frequency was greater than the effect of the change in conditions before and after 1998 (Figure 5-5).

**Evaluation of Hypothesis 2: Increase in drying event frequency reduces λ_s
(Objective 6)**

Conditions (6) and (7): λ_s was greater when we simulated environmental states at the frequency observed during the first seven years of our study (LFMD, Figure 5-6). This pattern was apparent no matter what detection of juveniles was assumed (Figure 5-6). However, the magnitude of the difference was greater when detection of juveniles was assumed to be high (Figure 5-6). The reduction in λ_s , was due to the fact that the frequency of moderate drying events increased during the last seven years (or alternatively, the frequency of wet years decreased). The frequency of droughts remained the same under these two environments, thus droughts did not contribute to the reduction in λ_s when comparing these two environments.

Evaluation of Hypothesis 3: Increase in frequency of drying events and “before versus after” effect (Objective 7)

Conditions (8) to (11): λ_s was greater when we simulated environmental states at the frequency observed for the first seven years (HFMD) than for the last seven years (LFMD). This pattern was observed no matter what detection of juveniles was assumed. However, the magnitude of the difference decreased as $\hat{\beta}(t)$ increased. In addition, in most cases λ_s was greater when the simulations were based on parameters estimated with data collected prior to 1998. This was true when the frequency of the wet, dry and drought mimicked the frequency observed for the first seven years (LFMD, Figure 5-7). The magnitude of the difference was considerably smaller when the frequency of wet, dry and drought mimicked the frequency observed for the last seven years (HFMD, Figure 5-7). The magnitude of the difference also decreased considerably as $\hat{\beta}(t)$ increased over time (Figure 5-7). The principal explanation for the stronger effect of the “before versus after 1998” effect under the LFMD scenario is related to the higher frequency of wet years under the LFMD. Indeed, only the wet matrix differed when comparing the before and after 1998 environment. Therefore, the difference in λ_s caused by the difference in wet years was amplified as the frequency of wet years increased.

Discussion

Snail Kite Viability and Key Vital Rates

Our results indicate that if the environmental conditions observed between 1997 and 2005 are representative of future conditions there is a high likelihood of a rapid extinction of the Snail Kite population in Florida. This finding addressed *Objective 1*. The deterministic population growth rate for the “FULL1” matrix was low ($\lambda_1 = 0.919$), even when the detection probability for juveniles was assumed to be low (i.e., $\hat{\beta}(t) =$

0.16 to 0.35). When incorporating variation and correlation among vital rates we obtained values of λ_s that were slightly greater than λ_1 . The probability of quasi-extinction (PQE) was high even when assuming a low detection probability for juveniles (Figure 5-2). PQE increased dramatically when detection probabilities $\hat{\beta}(t) = 0.70$ were assumed. Although one could infer the time to extinction based on Figure 5-1, several authors have warned against interpreting time to extinction literally (e.g., Reed et al. [2002]). Instead, our analyses should be viewed as supportive evidence that Snail Kites are facing high risks of extinction. Caswell (2001) suggests that population projection models are particularly useful for evaluating the importance of demographic or environmental factors in influencing population dynamics. This latter idea motivated the sensitivity analyses as well as the exploratory analyses discussed in the remaining part of our presentation.

We determined the sensitivity of λ_1 to absolute changes (i.e., sensitivities) and relative changes (elasticities) in vital rates. These analyses addressed *Objective 2*. Elasticity of λ_1 to changes in adult survival was by far the greatest (Figure 5-3), which indicates that a proportional change in adult survival would cause the largest proportional change on λ_1 . This pattern is typical of the patterns observed for other long-lived species (Stahl and Oli 2006). Regarding sensitivity patterns, λ_1 was most sensitive to absolute changes in adult survival. Despite the greater elasticity of λ_1 to changes in adult survival, we found that adult fertility was particularly critical in influencing λ_1 (Figure 5-3). Asymptotic population growth rate based on vital rates estimated for the period prior to 1998 was greater than λ_1 estimated from vital rates obtained for the period 1999 to 2005. The difference in λ_1 was substantial even after removing the effects of the 2001 and 2004 drying events. We performed a LTRE analysis that indicated that the observed reduction

in λ_1 for the two periods was largely due to a reduction in adult fertilities between these two periods (Figure 5-4). This finding held true for the three levels of detection of juveniles that we considered. Thus, even though the dramatic reduction in adult survival during the 2001 drought contributed to a large decrease in population size (Martin et al. 2006; Martin et al. 2007b), other factors associated with a reduction in adult fertilities are responsible for the reduction in population growth.

Next, we examined the three primary hypotheses explaining reduction in Snail Kite population growth during the most recent years.

Hypothesis 1: “Before versus After 1998” Effect (Objective 4)

Habitat conversion in the wetlands of south Florida, resulting from frequent and prolonged floods, has concerned many ecologists (Gunderson and Loftus 1994; Bennetts et al. 1998; Kitchens et al. 2002). Habitat conversion is believed to reduce apple snail densities (Darby et al. 2005) and could also reduce the availability of suitable nesting habitats for Snail Kites (Bennetts et al. 1998). Although other factors may have contributed to the decrease in population growth rate after 1998, habitat conversion, especially in the WCAs, appears to be well documented and should receive particular attention.

As explained earlier, λ_1 was greater in the pre than in the post 1998 environment even when removing the effects of the drying events of 2001 and 2004. The same pattern was observed for λ_s (Figure 5-5). The magnitude of the difference decreased when detection of juveniles was assumed to be high. But in all instances the difference was substantial, indicating that some changes in the environment may have caused a decrease in population growth. This result supported *Prediction 1*. We were able to examine the relative effects of drought frequency and “the before versus after 1998” effect on λ_s .

Thus, if we are ready to assume that the reduction in population growth was entirely due to habitat conversion, our stochastic analyses suggest that the effect of habitat conversion was greater (except when $\hat{\beta}(t) = 0.70$) than a substantial increase in drought frequency (from 1 drought every nine years to 1 drought every 4 years) (Figure 5-5). This prospect is particularly alarming given the slow dynamic of habitat conversion. Under this scenario, the positive effects of adequate habitat restoration plans on kite population growth would only be perceptible at the timescale of multiple years (i.e., multiple years are needed to convert vegetation communities back to suitable kite habitats). However, as explained in the next section, it is unlikely that habitat conversion was solely responsible for the observed reduction in population growth.

Hypothesis 2: Increase in Frequency of Moderate Drying Events (Objective 6)

In the previous section we considered the effects of habitat conversion and increase in drought frequency on kite population growth. Under *Hypothesis 2*, we ignored the effect of habitat degradation, but still considered the effect of drought frequency. In addition to droughts with a large spatial and temporal extent (e.g., 2001 drought), we also considered drying events with a more moderate spatial and temporal extent. In fact, based on hydrological criteria developed by (Bennetts 1998) these moderate drying events would not have been considered as a threat to kites persistence because it was believed that kites could readily escape drying conditions by moving to less affected wetlands. Interestingly, we found that even if we ignored the effect of habitat degradation, an increase in moderate drying event frequency could reduce λ_s substantially. We found that the increase in moderate drying events frequency observed during the last 7 years of our study could explain some of the observed variation in λ_s between the pre and post 1998

environments (Figure 5-6). This result supported Prediction 2. There are several reasons that can explain the impact of moderate drying events on kite population growth. First, even though a proportion of adults may be able to move to wetlands less affected by a drying event, fledglings, on the other hand, are less likely to be aware of refugia habitats and therefore are more likely to die during a drying event (Martin et al 2006). This hypothesis is consistent with the fact that adult survival is remarkably stable (except during extensive droughts). However, juvenile survival is strongly affected by drying events, even when they are moderate (Figure 5-1).

Hypothesis 3: Increase in Moderate Drying Events and “Before versus After 1998” effect (Objective 7)

We believe that both habitat conversion and an increase in frequency of moderate drying events are highly relevant to our study system. Therefore, we examined λ_s under *Hypothesis 3* which considered both factors. Although we only had data to estimate vital rates during wet years in the pre and post 1998 environment, we found evidence of an effect of both factors on λ_s (Figure 5-7). This result supports *Prediction 3a* and *3b*. If we had used the 1992 data to construct the drought matrix for the pre 1998 environment, the differences in λ_s due to the “before versus after 1998” effect would have appeared to be even greater. It is in fact, possible that long term habitat degradation has reduced the resistance of kite to droughts; however, given the uncertainty associated with 1992 (see *Hydrological Conditions*) we preferred not to include 1992 into our analyses.

Limits of the Models

First, because estimates of detection of juveniles were only available for 2004 and 2005, we had to find ways to account for detection for the period 1997 to 2003 (see *Methods*). Although, estimates of detection of juveniles were not directly estimated 1997

to 2003, it is probably safe to assume that the “true” values of $\hat{\beta}(t)$ were in fact between 0.16 and 0.70. Therefore, by including analyses that assumed constant $\hat{\beta}(t) = 0.16$ and $\hat{\beta}(t) = 0.70$ we evaluated the robustness of our analyses to large changes in $\hat{\beta}(t)$. An alternative to compute fecundity rates would have been to derive this rate from: the proportion of birds attempting to breed (α_i), the proportion of successful breeding attempts (S_i), the number of breeding attempts per year (δ_i), the number of juveniles per successful nest (Y_i), and the sex ratio (assumed to be 50:50) (Bennetts 1998). The reason we did not use this approach is that we currently do not have good estimates of α_i and θ_i under varying environmental conditions.

Second, we ignored density dependence because at this point there is no evidence of density dependence in this population of Snail Kite (i.e., correlating vital rates with population size do not indicate any relation reflecting density dependence, Martin unpublished data). As pointed out by Beissinger (1995) the setting of an upper boundary would have been arbitrary, and therefore, should be avoided. Ignoring density dependence in our simulation models allowed population size to grow to levels unlikely to occur in Florida (Beissinger 1995). Thus, we expect estimates of population growth to be positively biased and PQE to be negatively biased (i.e., underestimated). Although we did not directly include the effect of demographic stochasticity in our PVAs, we followed Morris and Doak’s (2002) suggestion and picked a quasi-extinction threshold of 50, which obviates the need to directly simulate demographic stochasticity (Morris and Doak 2002). On the other hand, concerns about genetic stochasticity were not included. At this point the Snail Kite population is assumed to be demographically isolated. However,

additional studies are needed to evaluate the genetic structure of the Snail Kite population in Florida, as well as possible gene flows with other populations (e.g., Snail Kite population in Cuba). If the Snail Kite population in Florida is completely isolated, genetic stochasticity could further increase the risk of extinction of the Florida population.

Another shortcoming of our study is that we ignored temporal correlation. For instance, some ecologists have hypothesized that foraging conditions for kites should be lower than average one year after a drought (Beissinger 1995). This is certainly a reasonable assumption. We did not include this effect for two reasons. First, fecundity and survival were lower than average for the year after the 2001 drought, but this could be because 2002 was a moderately dry year. In fact, if we compare vital rates of 2002 with vital rates after 1998, the rates are not lower than average. So including a lag effect based on our data would not have addressed concerns about lag effect. Thus, rather than imposing arbitrary reduction in vital rates we preferred to ignore this effect. If lag effects have major influences on kites, our estimates of stochastic population growth rates would be overestimated.

Another limitation of our approach is that we did not account for the spatial structure of the kite population. Taking spatial structure into consideration would add an important element of realism. We believe that extending our work to spatially explicit models would be an important next step (Mooij and DeAngelis 2003). Nonetheless, we think that our approach is a useful one because it is based on robust parameter estimates (e.g., survival rates were based on Cormack-Jolly-Seber model) and provides a good starting point for further modeling efforts. Moreover, even though the Snail Kite population is spatially structured, there is enough movement among habitats for the

population to be considered a single population as opposed to a strict metapopulation (Bennetts and Kitchens 2000; Martin et al. 2006). Finally, our work focused on a limited number of factors. Other disturbances or catastrophes such as diseases, fire, etc. were ignored. All these factors are likely to increase PQE.

Management Implications

Our results were based on recent demographic information on Snail Kites in Florida. They were consistent with the hypothesized critical importance of considering drought frequency when evaluating kite's persistence (Beissinger 1995). However, our results also emphasized the potential importance of more moderate drying events that appear to primarily affect reproduction and juvenile survival. These moderate drying events had not previously been considered critical to kite persistence (Bennetts 1998). However, under the current system, adult fertility appears to be crucial, and factors likely to have large effects on adult reproduction and juvenile survival should receive more attention. Thus, our results suggest that water management plans should focus on reducing the frequency of moderate drying events. As discussed earlier, the effect of habitat conversion on kite dynamics should also receive attention, as it has the potential to have a large impact on kite population growth. As suggested by recent studies, the repeated flooding of the wetlands during the Fall in south Florida is likely to be responsible for habitat conversion deemed detrimental to kites (Gunderson and Loftus 1994; Bennetts et al. 1998; Kitchens et al. 2002). Therefore, water management plans aimed at improving kite persistence should also focus on reducing water levels in the WCAs during the Fall. Reducing flood duration and frequency should help restore vegetation communities favorable to foraging kite habitats. We note that the positive effect of this restoration effort on kite population growth is likely to only be perceptible

after multiple years of implementation. In contrast, during the spring-summer, managers should attempt to reduce the frequency of moderate drying events. Nevertheless, as discussed earlier droughts may play a critical organizing role in the system occupied by kites, therefore managers should probably not attempt to systematically prevent drying events to occur. Ideally, when a drought occurs, managers should accommodate kites by storing some water in refugia habitats contiguous or near the wetlands affected by the drought (see Martin et al. 2006 and Martin et al. 2007c). Some managers are concerned that lowering water levels during the Fall and raising water levels during the Spring and Summer would reduce the amplitude of water level fluctuations to a degree that could be detrimental to the system. In fact it has been proposed to decrease the highs during the Fall, but also decrease the lows during the spring-summer. Although this management plan could contribute to restoring suitable foraging habitat for some time during the year, the frequency of moderate drying events and possibly drought would also be increased, which would further reduce reproduction and survival. This management strategy would likely increase the probability of extinction. An alternative to this management strategy would be to maintain water levels at higher levels during the spring-summer (i.e., > than during the years that were identified as dry years), but occasionally allow the area to dry down to lower levels than during most moderate drying event. We believe that there is a minimum threshold for each wetland unit below which kites have to leave or die (Mooij et al. 2007). Habitat conversion may in fact have raised this threshold in WCA3A by shifting suitable foraging kite habitats to higher elevations, which are more prone to frequent and prolonged drying periods (Mooij et al. 2007). Once water levels fall below this threshold, it probably does not matter any more from the kite perspective whether

water levels are 1 cm below the threshold or 20 cm below the threshold; kites will have to move or die in both cases. Therefore, management plans that favor infrequent moderate drying events (e.g. 1 moderate drying event every 7 years), yet allow occasional droughts (e.g., water levels that fall 20 cm below the threshold but occur lets say every 7 years), may be better for kites than management plans that would favor more frequent drying events (water levels falls 5 cm below the threshold but occur with frequency: 6/7 years) even if no drought ever occurred. Indeed, when assuming a high frequency of moderate drying events (drought frequency: 0/7; moderately dry years frequency: 6/7; wet years: 1/7; with $\hat{\beta}(t) = 0.16$ to 0.35) λ_s was 0.92; whereas when assuming a low frequency of moderate drying events and droughts (drought frequency: 1/7; moderately dry years frequency: 1/7; wet years: 5/7; with $\hat{\beta}(t) = 0.16$ to 0.35) λ_s was 0.95. However, the issue is complicated by the fact that lower water levels may also be more likely to be followed by longer drying events. Drought duration is known to be critical to the survival and recruitment of snails (Darby 1998), and thus will adversely affect kites (Mooij et al. 2007). Therefore, managers should also consider this factor when setting their management actions.

In summary, current management practices of kites' habitats appear to be detrimental in two ways: (1) they promote habitat degradation by favoring prolonged hydroperiod and by increasing flooding frequency during the period September to February; (2) they increase the propensity of drying events occurring during the dry season (April to June).

More generally, our results support the argument that it is critical to carefully consider the organizing role of natural disturbances when modeling the dynamics of

populations of organisms. Indeed, focusing exclusively on their “catastrophic” effects without considering their organizing role in the ecosystems may be misleading to both our understanding of the ecological dynamics of the system and to management (Reeves et al. 1995).

Table 5-1. Cormack-Jolly-Seber models (CJS) of apparent survival (“ ϕ_{AD} ”: survival of adults; “ ϕ_J ”: survival of juveniles) and annual transition probabilities (“ ψ ”) among the four major wetland complexes used by snail kites in Florida between 1992 to 2004. Factors incorporated in the models included: age, region, natal region; and a drought effect on movement and survival.

Modelbis	QAICc	Δ AICc	w	K
ϕ_{AD} (WMD1) ϕ_J (t) p(t)	5597.542	0	0.234	31
ϕ_{AD} (D1) ϕ_J (t) p(t)	5597.546	0	0.233	31
ϕ_{AD} (D2) ϕ_J (t) p(t)	5597.75	0.21	0.211	31
ϕ_{AD} (WMD2) ϕ_J (t) p(t)	5598.286	0.74	0.161	32
ϕ_{AD} (D3) ϕ_J (t) p(t)	5598.367	0.82	0.155	32
ϕ (age * t) p(t)	5604.666	7.12	0.007	41
ϕ (age + t) p(t)	5610.439	12.9	0.004	28
ϕ_{AD} (D2) ϕ_J (D6/T _{AVGJD}) p(t)	5615.359	17.82	0.00003	21
ϕ_{AD} (D2) ϕ_J (D6/T _{DUR}) p(t)	5616.193	18.65	0.00002	21
ϕ_{AD} (D3) ϕ_J (D6/T _{AVGJD}) p(t)	5616.22	18.68	0.00002	22
ϕ_{AD} (D2) ϕ_J (D6/T _{MWL}) p(t)	5618.59	21.05	0.00001	21
ϕ_{AD} (WMD1) ϕ_J WMD1) p(t)	5622.894	25.35	0	22
ϕ_{AD} (.) ϕ_J (t) p(t)	5623.019	25.48	0	29
ϕ_{AD} (D2) ϕ_J (D4/T _{AVGJD}) p(t)	5625.349	27.81	0	20
ϕ_{AD} (D2) ϕ_J (T _{MWL}) p(t)	5265.47	27.92	0	20
ϕ_{AD} (D3) ϕ_J (D4/T _{AVGJD}) p(t)	5626.502	28.96	0	21

Notes: AICc: Akaike information criterion. Δ AICc for the *i*th model is computed as AICc_{*i*} - min(AICc). w: AICc weight. K: number of parameters. “ ϕ ”: apparent survival. “p”: detection probability. “t”: time; “.”: no time effect; “age”: age effect; “*”: multiplicative effect; “+”: additive effect. “WMD1”: “ ϕ ” is associated with 3 years categories, wet (93 to 98), moderately dry (99 to 01, 02-03, 04-05), and drought (92-93, 01-02, but in these models the drought effect on survival is assumed to be the same in 92-93 and 01-02). “WMD2”: same as “WMD1” except that the drought effect on survival is assumed different in 92-93 and 01-02. “D1”: “ ϕ ” is constant except during the drought period 00-02, (“ ϕ ” during 00-01, is assumed different from 01-02). “D2”: same as “D2” except that 92-93 is also considered a drought, the drought effect on survival is assumed to be the same in 92-93 and 01-02. “D3”: same as “D2” except that the drought effect in 92-93 is assumed to be different from 01-02. T_{AVGJD}: trend model with annual mean water levels for the period Jan-Dec as a covariate. T_{AVGMI}: trend model with annual mean water levels for the period Mar-Jun as a covariate. T_{AVGJD}: trend model with annual mean water levels for the period Jan-Dec as a covariate. T_{SPAT}: trend model with spatial extent of drying event as a covariate. T_{DUR}: trend model with drying event duration as a covariate. T_{MWL}: trend model with annual minimum water levels as a covariate. T_{TIME}: trend model with time as a covariate. See text for additional details.

Table 5-1. (continued) CJS models of apparent survival

Model	QAICc	ΔAICc	K
$\phi_{AD}(D7/T_{AVGJD}) \phi_J(D4/T_{AVGJD}) p(t)$	5626.76	29.21	21
$\phi_{AD}(WMD2) \phi_J(WMD2) p(t)$	5626.912	29.37	23
$\phi_{AD}(D5/T_{AVGJD}) \phi_J(D4/T_{AVGJD}) p(t)$	5627.374	29.83	20
$\phi_{AD}(D1) \phi_J(D4/T_{AVGJD}) p(t)$	5627.504	29.96	20
$\phi_{AD}(D2) \phi_J(D6/T_{TIME}) p(t)$	5635.93	38.39	21
$\phi_{AD}(D2) \phi_J(D6/T_{SPAT}) p(t)$	5636.68	39.14	21
$\phi_{AD}(D2) \phi_J(D4/T_{DUR}) p(t)$	5637.064	39.52	20
$\phi_{AD}(D2) \phi_J(D4/T_{MWL}) p(t)$	5637.214	39.67	20
$\phi_{AD}(D7/T_{TIME}) \phi_J(D6/T_{TIME}) p(t)$	5637.64	40.1	22
$\phi_{AD}(D2) \phi_J(D6/T_{AVGMJ}) p(t)$	5639.25	41.71	21
$[\phi_{AD}(T_{AVGJD}) + \phi_J(T_{AVGJD})] p(t)$	5641.983	44.44	17
$\phi_{AD}(T_{AVGJD}) \phi_J(T_{AVGJD}) p(t)$	5642.593	45.05	18
$\phi_{AD}(D2) \phi_J(D4/T_{AVGMJ}) p(t)$	5644.897	47.35	20
$\phi_{AD}(D2) \phi_J(D4/T_{SPAT}) p(t)$	5647.766	50.22	20
$\phi_{AD}(D1) \phi_J(D1) p(t)$	5649.877	52.33	20
$\phi_{AD}(WMD1) \phi_J(WMD2) p(t)$	5652.142	54.6	22
$[\phi_{AD}(T_{DUR}) + \phi_J(T_{DUR})] p(t)$	5657.333	59.79	17
$\phi_{AD}(D2) \phi_J(T_{MWL}) p(t)$	5657.839	60.3	19
$[\phi_{AD}(T_{MWL}) + \phi_J(T_{MWL})] p(t)$	5663.667	66.12	17
$\phi_{AD}(T_{MWL}) \phi_J(T_{MWL}) p(t)$	5664.292	66.75	18
$\phi_{AD}(T_{AVGMJ}) \phi_J(T_{AVGMJ}) p(t)$	5670.601	73.06	18
$[\phi_{AD}(T_{AVGMJ}) + \phi_J(T_{AVGMJ})] p(t)$	5672.816	75.27	17
$\phi_{AD}(D2) \phi_J(T_{SPAT}) p(t)$	5680.487	82.94	19
$\phi_{AD}(D1) \phi_J(.) p(t)$	5682.229	84.69	18
$\phi_{AD}(.) \phi_J(.) p(t)$	5729.546	132	16

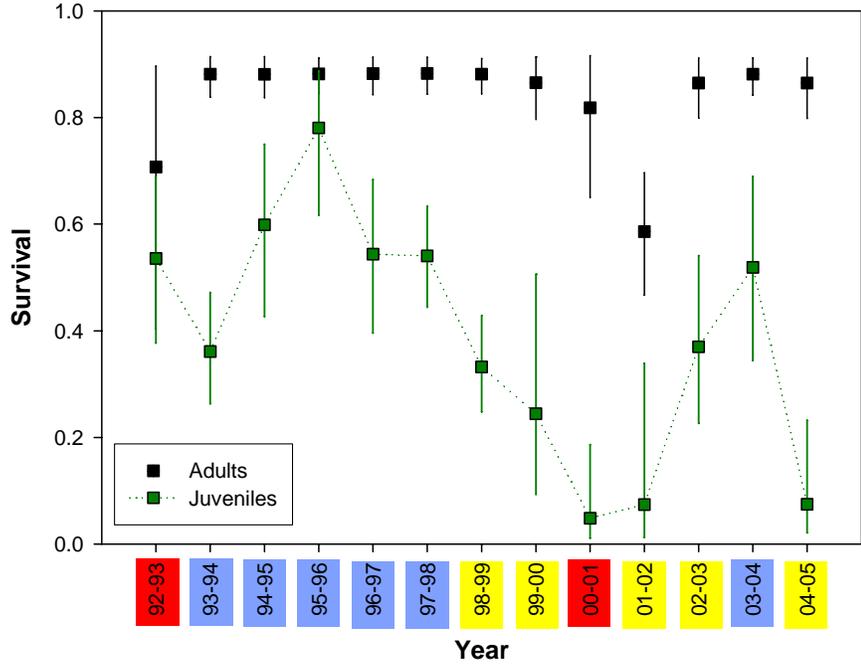


Figure 5-1. Model averaged estimates of adult and juvenile survival between 1992 and 2005. The colors correspond to the hydrological conditions: red indicate drought years, yellow indicates moderately dry years and blue indicate wet years (see Appendix D for details about how the categorization was established).

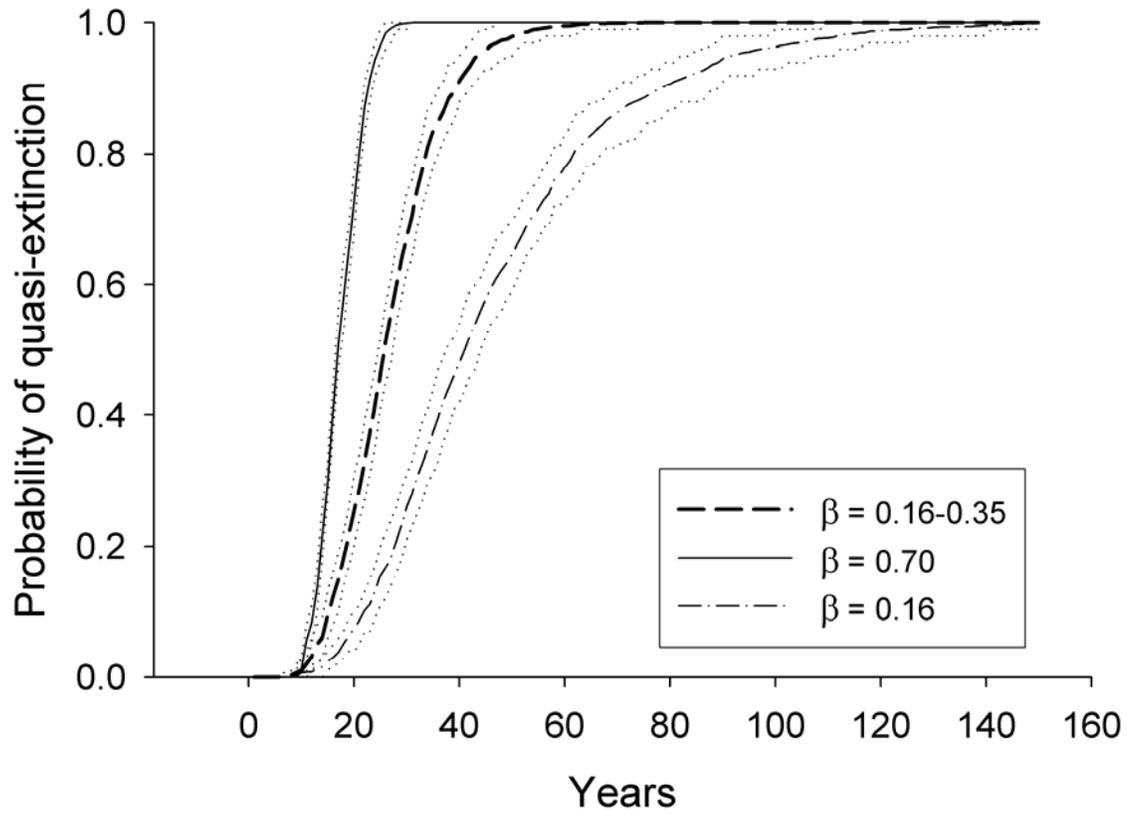


Figure 5-2. Estimates of probability of quasi-extinction (quasi-extinction threshold was fixed at 50 females) assuming three separate detections of juveniles: $\hat{\beta}(t) = 0.16$, $\hat{\beta}(t) = 0.7$ and $\hat{\beta}(t) = 0.16$ to 0.35. Error bars correspond to 95% confidence intervals.

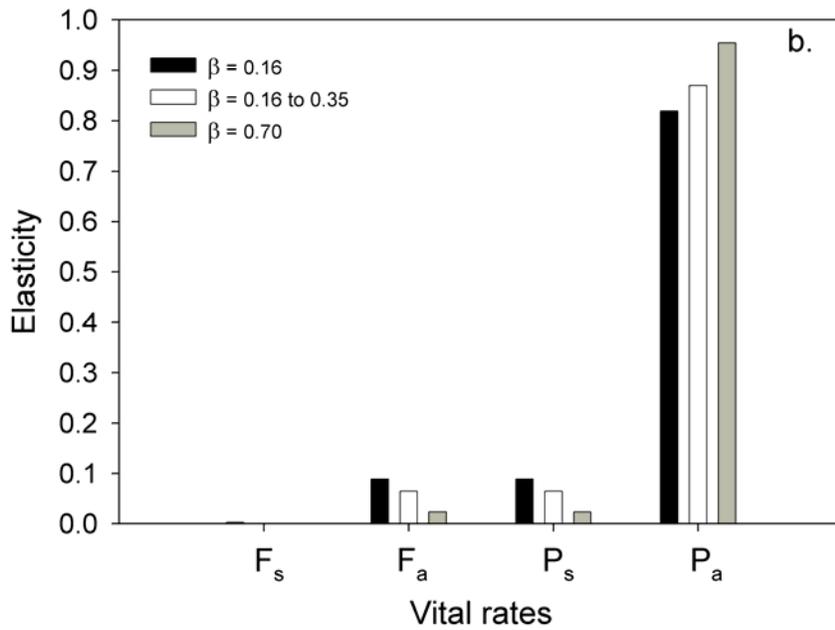
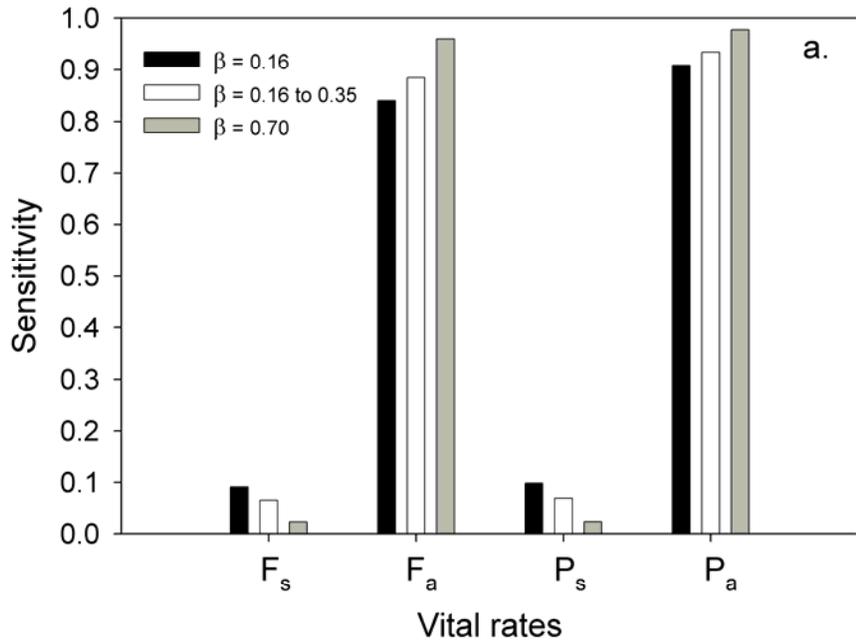


Figure 5-3. Sensitivity (a) and elasticity (b) of λ_1 to changes in age-specific vital rates (F corresponds to fertility rates, and P to survival, subscripts indicate the age classes, subscript “s” indicates the subadults and subscript “a” refers to the adults)..

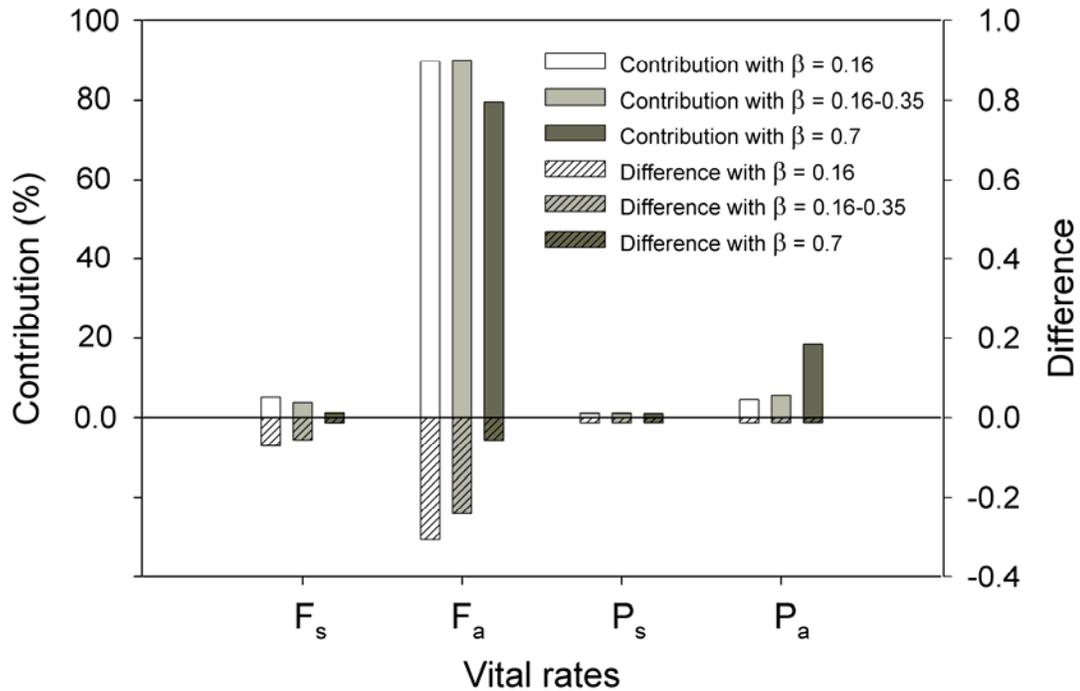


Figure 5-4. (Negative bars) The difference in age-specific vital rates (F , corresponds to fertility rates and P , to survival, subscripts indicate the age classes, “a”: adults, “s”: subadults) between the matrix BEF and matrix AFT. (Positive bars) The contributions (in %) of those differences to the effect of changes in the environment on λ_1 . Differences and contribution were computed for three detection of juveniles ($\hat{\beta}(t) = 0.16$, $\hat{\beta}(t) = 0.16$ to 0.35 and $\hat{\beta}(t) = 0.7$).

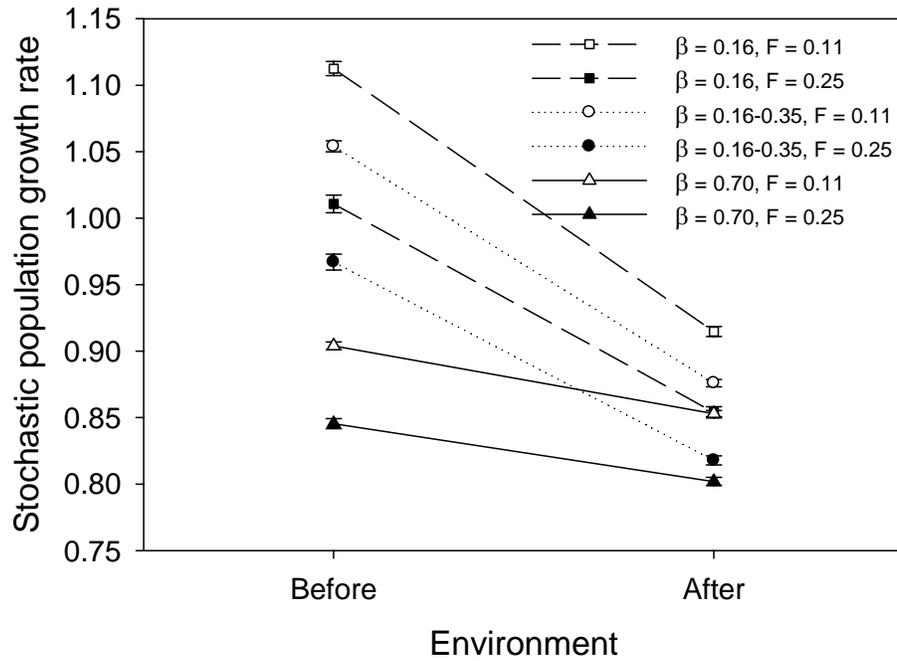


Figure 5-5. Estimates of stochastic population growth rates (λ_s) for environmental conditions before and after 1998. For each environment (i.e., before and after), we simulated two frequency of droughts: $F = 0.25$ (one drought every 4 years) and $F = 0.11$ (one drought every 9 years). Estimates of λ_s were computed for three detections of juveniles ($\hat{\beta}(t) = 0.16$, $\hat{\beta}(t) = 0.16$ to 0.35 and $\hat{\beta}(t) = 0.7$). Error bars correspond to 95% confidence intervals.

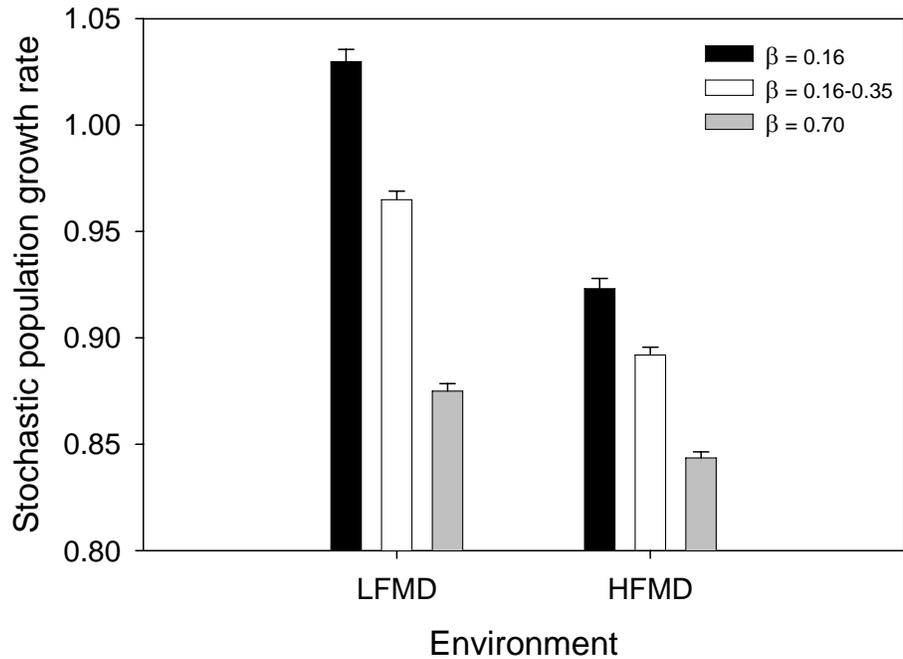


Figure 5-6. Estimates of stochastic population growth rates (λ_s) assuming a low frequency of moderate drying events (LFMD) and a high frequency of moderate drying events (HFMD). LFMD corresponded to the frequency of wet, dry and drought years that were observed during the period 1992 to 1998. HFMD corresponded to the frequency of wet, dry and drought years that were observed during the period 1999 to 2005. Estimates of λ_s were computed for three detection of juveniles ($\hat{\beta}(t) = 0.16$, $\hat{\beta}(t) = 0.16$ to 0.35 and $\hat{\beta}(t) = 0.7$). Error bars correspond to 95% confidence intervals.

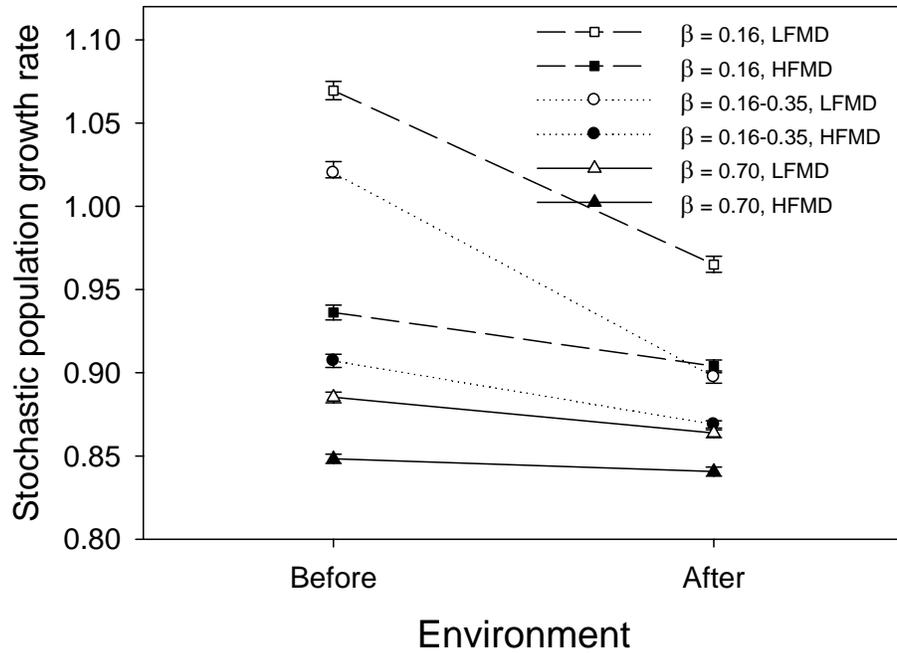


Figure 5-7. Estimates of stochastic population growth rates (λ_s) for environmental conditions before and after 1998. For each environment (i.e., before and after), we simulated environments with two frequencies of wet, dry and droughts: LFMD (frequencies of wet, dry, droughts observed during 1992-1998); and HFMD (frequencies of wet, dry, droughts observed during 1999-2005). Estimates of λ_s were computed for three detections of juveniles ($\hat{\beta}(t) = 0.16$, $\hat{\beta}(t) = 0.16$ to 0.35 and $\hat{\beta}(t) = 0.7$). Error bars correspond to 95% confidence intervals.

CHAPTER 6 CONCLUSION

In this final chapter I synthesized the information presented in the preceding chapters and provided a framework for understanding the population ecology of the Snail Kite and developed a vision for its recovery.

Synthesis of Research Findings

Monitoring of the Snail Kite

During the last decade a growing number of wildlife studies have emerged which estimate detectability. Additionally, strong statements about the importance of estimating detectability have been made decades ago (Pollock et al. 1990, Bennetts et al. 1999b), yet, Rosenstock et al. (2002) showed that out of 224 papers published in major journals, 95% of bird monitoring studies that they reviewed did not account for detectability. Moreover, analyses of uncorrected counts continue to be published in major journals (reviewed in Conn et al. 2004). As indicated by Conn et al. (2004), the controversy about the value of uncorrected counts persists because protocols to estimate detectability are typically more labor intensive and expensive to implement. Furthermore, studies that address both detectability and spatial variation are even less frequent (Yoccoz et al. 2001). As indicated in Chapter 2, the principle that detectability and spatial variation should carefully be considered in monitoring programs appears to take even longer to reach managers. As a consequence, recovery plans for many endangered species are still based on count surveys that do not account for either sources of variability. This is very troubling because, as shown in Chapter 2, primary recovery criteria based on uncorrected counts could have realistically been met, while in fact the species is declining precipitously. Studies such as those from Cassey and Ussher (1999) nicely demonstrate that uncorrected counts can largely underestimate abundance of endangered species; however, these authors did not examine the

biases associated with using count based indices as measures of population change. Yet, this is exactly where the controversy continues to be the most intense. Chapter 2 provides a clear and strong message to conservation biologists and managers to urge them to revise monitoring programs and recovery plans that ignore primary sources of variability.

Analyses in Chapter 2 are based on a superpopulation model that is simple to implement and is well suited to deal effectively with both detectability and spatial variation when estimating population size. This is also a valuable method to estimate fecundity and fertility rates (parameters that are often difficult to estimate appropriately). Bennetts (1998) pointed out that fecundity (i.e., number of young females produced per adult female) is one of the most important reproductive rates to understand Snail Kite dynamics (see also Caughley 1977). Bennetts (1998) proposed to derive this rate from the proportion of birds attempting to breed, the proportion of breeding attempts that are successful and the number of breeding attempts per year, the number of young produced per successful nest and the sex ratio of the young produced. This approach is prohibitively expensive (see Bennetts 1998). A cheaper alternative presented in Chapters 2 and 5 allows for a more direct estimation of fecundity rates. Fertility rates can then be derived from the approach described in Chapter 5 or from the “anonymous reproduction” equation described by Caswell (p.173, 2001).

Accounting for detectability and spatial variation is also important when estimating survival and movement rates (e.g., Williams et al. 2002). Bennetts and Kitchens (1997) implemented a very nice study design to estimate movement and survival rates while accounting for these sources of variation. In Chapters 3 and 4 we expanded some of their analyses (e.g., Bennetts and Kitchens 2000, Bennetts et al. 1999a) to take scale issues into consideration. We

found that a careful consideration of scale both in space (wetlands versus regions) and time (month versus year) was necessary to better understand kite dynamics.

Thus, the research presented in this volume provided compelling evidence that it is critical to consider scale, detectability and spatial variation when estimating movement and demographic parameters of Snail Kites. Although monitoring programs that account for detectability and spatial variations are more costly (Conn, Bailey et al. 2004), in the case of the Snail Kite this investment is clearly necessary.

New information on movement and demography of the Snail Kite

Snail Kites have been described as nomads (Beissinger 1983, Bennetts and Kitchens 2000). Bennetts and Kitchens (2000) estimated the average probability of movement among wetland units to be approximately 0.25 per month. However, when we incorporated additional levels of complexity of the spatial configuration of the system, we discovered a different pattern. In Chapter 3, we found that kites moved extensively among contiguous wetlands, but significantly less among isolated wetlands. Our analyses indicated that kite movement was affected by fragmentation. Results in Chapter 3 also suggest that young birds may be even more affected by fragmentation than adults. Familiarity with the landscapes is particularly important during regional droughts (Bennetts and Kitchens 2000). In Chapters 3 and 4 we found that only a small proportion of kites escaped a regional drought by moving to refugia (wetlands less affected by drought). Many individuals died after the drought. During the 2001 drought adult survival dropped by 16%, while juvenile survival dropped by 86% (possibly because juveniles were less likely to reach refugia). Although kites exhibit extensive exploratory behavior, they also show high levels of annual site tenacity during the breeding season, particularly to their place of birth (see Chapter 4). Fidelity to breeding and natal sites has been given relatively little attention in the past. However, as discussed in Chapters 3 and 4, site fidelity could have a large influence on

movement patterns and survival, and could influence the entire dynamics of the kite population. In Chapter 3 and 4 we found that survival varied significantly among regions. During most years, survival was higher in the southern regions than in the north. In contrast, during the 2001 drought survival of kites occupying the northern regions was higher. This confirmed hypotheses from Takekawa and Beissinger (1989) and Bennetts and Kitchens (1997), which stated that the Kissimmee Chain of Lakes may serve as a refuge habitat. It also emphasized the importance of considering spatiotemporal patterns of variation in habitat conditions when assessing the conservation values of particular wetlands (see Chapters 3 and 4).

Current Status of the Snail Kite and Management Implications

Population size estimates for the period 1997 to 2000 presented by Dreitz et al. (2002) were four to five times greater than the recovery target set by the USFWS, and survival estimates for the period 1992 to 1999 presented by Bennetts et al. (2002) remained high for both adults and juveniles. Although neither Bennetts et al. (2002) nor Dreitz et al. (2002) suggested that Snail Kites were recovering, their results were interpreted by some managers as evidence that the Snail Kite population in Florida was heading toward recovery. However, results presented in Chapters 2 and 5 refute the idea of a Snail Kite recovery. In fact, recent superpopulation estimates (Chapter 2) indicated that the Snail Kite population declined dramatically in recent years. Estimates of stochastic population growth rate and probabilities of quasi extinction presented in Chapter 5 suggest that the Snail Kite is still at high risk of extinction. The sharp decline observed after 2001 was mostly associated with a multiregional drought that occurred in 2001 and affected both survival and reproduction (see Chapters 2, 3, 4, and 5). However, the lack of recovery after 2002 suggests that other factors are limiting the growth of Snail Kites in Florida. The Life Table Response Experiment presented in Chapter 5, suggests that a reduction in recruitment is probably responsible for the lack of recovery. In Chapter 5, we found evidence that both habitat

conversion (caused by prolonged hydroperiod and increased water depth during the Fall), and increase in frequency of drying events (during the Spring and Summer) are responsible for the observed reduction in population growth rate (see Chapter 2).

Chapters 3 and 4 indicate that fragmentation, movement and site fidelity should also be considered when managing the network of wetlands occupied by kites. Although fragmentation is certainly not the cause of the recent decline in kite abundance, Chapter 3 provides evidence that further fragmentation and habitat reduction would reduce the resistance of kites to drought and therefore increase probability of extinctions. The fact that kites respond to fragmentation and to the geographic features of the landscapes (see Chapter 3), leads to the logical recommendation that managers should manage the wetlands occupied by kites as a network and not as independent units (see also Takekawa and Beissinger 1989 and Bennetts and Kitchens 1997, and Kitchens et al. 2002). Given the paradigm that the persistence of good natural habitats requires occasional drying events (see Chapter 5, Bennetts et al. 1998, and Kitchens et al. 2002).

Restoration projects that involve wholesale dry downs of an entire region (e.g., restoration of Lake Tohopekaliga) (Welch 2004) may want to consider the option of conserving water in at least some local patches within the region to be affected to serve as a refuge for Snail Kites. The draw downs of local patches should occur sequentially, allowing a sufficient recovery period for previously dried areas to return to a productive level. Moreover, the pattern of drying and inundation should optimally attempt to mimic as closely as possible the hydrology of the Everglades under a more natural landscape (Fennema et al. 1994).

Finally, findings presented in Chapters 3 and 4 emphasized the importance of considering spatiotemporal patterns of variation in habitat conditions when assessing the conservation values of particular wetlands. For instance, we found that during most years kite survival was higher in

the southern than in the northern regions. However, during drought kite survival in the Kissimmee Chain of Lakes was less impacted by droughts than the southern regions. Therefore, in order to make a correct assessment of the conservation values of habitats one should consider the frequency of droughts in these wetlands.

Perspectives

The population monitoring program of the Snail Kite that has been in place for more than 16 years offers many additional research questions related to conservation, management and population ecology. In this section I present a non-exhaustive list of research directions and ideas that I consider reasonable priorities for conservation and management.

Rescuing the Snail Kite Population from Extinctions Risks Associated with Small Populations

Recent estimates indicate that the Snail Kite population size includes less than 2000 individuals (Chapter 2). Projections presented in Chapter 5 suggest that the population is expected to experience further decrease. Although current estimates of abundance do not suggest that Allee effects and demographic stochasticity are sources of immediate concern (at least in the short term), genetic stochasticity on the other hand may constitute an immediate problem for the Snail Kite population. As explained in Chapter 1, there are other populations of Snail Kites in Cuba and in Central and South America. It is not clear at this point if all these populations constitute different Evolutionary Significant Units (*sensu* Fraser and Bernatchez 2001)). Some authors have noted differences in morphometrics measurements among these populations (Sykes et al. 1995). However, genetic and ecological exchangeability among these populations have not been carefully considered (Beissinger 1988). Nevertheless, establishing the level of gene flow (or genetic divergence) among these populations could be of great conservation value. If gene flow between the Snail Kite population in Florida and other populations (e.g., Cuba, Central America)

is low (i.e., less than one migrant per generation) genetic stochasticity (e.g., due to inbreeding depression) could be a serious concern for the viability of the Snail Kite. Given that population viability analyses presented in Chapter 5 suggest that the Snail Kite population in Florida may reach extremely low numbers of individuals in a relatively short period of time, management considerations to prevent genetic extinction or increase genetic diversity of the Snail Kite population in Florida may need to be considered soon. Captive breeding and supplemental translocations are among the conservation options that deal with these problems. Although captive breeding is a popular recovery technique recommended by management agencies, it is often impractical for many vertebrate populations (Allendorf and Luikart 2007). In the case of the Snail Kite supplemental translocation (i.e., introduction of a few individuals from source populations in Central America (or other populations) into the population in Florida), appears more promising. However, supplemental translocation is risky when populations are not genetically and ecological exchangeable (Allendorf and Luikart 2007). With these concerns in mind, I recommend (1) additional studies about the genetic structure of Snail Kite in Florida (e.g., effective population size, level of heterozygosity etc.); (2) studies to establish the level of genetic exchangeability (e.g., reciprocal monophyly based on mitochondrial DNA); studies to determine the level of gene flow among populations; (4) studies to determine ecological exchangeability (e.g., study of courtship behavior etc.) with populations that could be potential candidates for translocation programs. Evidently these programs will not be substitutes for the need to restore Snail Kite habitats. In the next section I provide some ideas on how to improve habitat management techniques.

Habitat Management Models

Everkite

In 2002, Mooij et al. published an article that described a detailed individual based model of the Snail Kite population in Florida: Everkite. Everkite is a comprehensive spatially explicit model that includes a large number of parameters (e.g., reproduction, survival, movement etc), that are linked to hydrological conditions. This model is a valuable tool to explore questions related to the population ecology of kites, but can also be applied to address management questions, in fact it could be incorporated into an adaptive management framework (see below). More specifically, Everkite can be used to assess the effect of water management scenarios on Snail Kites. At this point many of the biological parameters included in Everkite are based on count data. Updating this model with movement and survival estimates presented in Chapters 2, 3 and 4 would probably improve this model's predictive performance and value for management. In addition, establishing a clear mechanistic link between hydrology, vegetation, Apple Snails and Snail Kites would also be useful.

Adaptive management

Adaptive management is a powerful framework to manage ecological systems (Dorazio and Johnson 2003, Williams et al. 2002). Kitchens et al. (2002) recognized the value of adaptive management to help Snail Kite recovery. In the following section I propose to use adaptive management to address a specific problem related to management of kite habitat; but this framework can be used to resolve many other management issues related to Snail Kite recovery.

As explained in Chapter 5, restoring suitable nesting and foraging kite habitats in WCA3A is key to kite recovery. This restoration effort can be achieved by acting on hydrology. I believe that adaptive management is a method of choice to reach this goal.

Nichols (2001) notes that adaptive management require five prerequisites: (1) specification of an objective function; (2) a model set including predictive models associated to competing hypotheses about how the system will respond to management actions; (3) prior probabilities associated to each predictive model; (4) a finite set of management actions; (5) a monitoring program to keep track of the system state and other variables relevant to the objective.

Once these prerequisites have been met, Nichols (2001) suggests the following four iterative steps: (1) identify the state of the system at time t ; (2) probabilities associated to each predictive model are updated based on information obtained about the system state at time t ; (3) the management action which is expected to produce the optimal return (in term of the initial objective function) is selected; (4) after this management action is implemented we returns to step 1.

We can apply the approach described by Nichols to the implementation of optimal water regimes in WCA3A that will maximize the persistence of kites. A logical objective for this management problem could be to minimize the probability of quasi-extinction of Snail Kite. As explained in Chapter 5, the primary factors that we identified as most critical to kite recovery are: drying events intensity, duration and frequency, and flooding events intensity, duration and frequency. We need to develop models that will predict how kite will respond to management actions (e.g., given intensity, duration and frequency of drying and flooding events). Each model can be assigned a probability based on its credibility (Kendall 2001; Nichols 2001). We should then derive the management action that maximize the return (i.e., minimize probability of quasi-extinction). After implementation of the selected management action, we should reevaluate the predictive models and give more weight to the models whose predictions agreed the most with

the observed changes in the system-state (Kendall 2001; Nichols 2001). Another iteration of the process can then be started.

This adaptive management approach has not yet been rigorously applied to Snail Kite habitat management. Unforeseen difficulties may of course arise during its implementation (e.g., agreement over the finite set of management actions). However, if these difficulties can be surmounted, this approach could prove itself to be a very efficient way to manage kite habitats (Nichols and Williams 2006).

APPENDIX A
SURVEY-SPECIFIC PARAMETER ESTIMATES USED TO COMPUTE ESTIMATES OF
SUPERPOPULATION SIZE

Table A-1. Survey-specific parameter estimates used to compute estimates of superpopulation size for Snail Kites between 2001 and 2005.

<i>Year</i>	<i>Survey</i>	$\hat{\phi}_{ij}$	$\widehat{SE}(\hat{\phi}_{ij})$	\hat{p}_{ij}	$\widehat{SE}(\hat{p}_{ij})$	\hat{N}_{ij}	\hat{B}_{ij}	\hat{N}_{Yij}	\hat{B}_{Yij}
2001	1	0.71	0.08	0.39	0.07	944	-	-	-
	2	0.70	0.07	0.39	0.07	1135	467	-	-
	3	0.69	0.07	0.39	0.07	1190	398	-	-
	4	0.70	0.07	0.39	0.07	827	4	-	-
	5	0.71	0.07	0.39	0.07	487	0	-	-
	6	-	-	0.39	0.08	559	215	-	-
2002	1	0.91	0.10	0.33	0.09	1117	-	-	-
	2	0.91	0.15	0.33	0.09	1174	163	-	-
	3	0.91	0.10	0.32	0.09	1192	126	-	-
	4	-	-	0.32	0.07	870	0	-	-
2003	1	0.98	0.10	0.29	0.09	902	-	-	-
	2	0.92	0.15	0.29	0.09	854	0	-	-
	3	0.98	0.11	0.28	0.09	697	0	-	-
	4	-	-	0.27	0.07	943	260	-	-
2004	1	0.89	0.07	0.27	0.05	1155	-	-	-
	2	0.87	0.07	0.27	0.05	928	0	186	-
	3	0.86	0.08	0.25	0.05	975	169	350	189
	4	0.86	0.08	0.26	0.05	737	0	151	0
	5	0.87	0.08	0.26	0.05	716	82	123	0
	6	-	-	0.26	0.05	716	92	148	41
2005	1	0.88	0.07	0.29	0.06	1371	-	-	-
	2	0.93	0.05	0.29	0.06	1401	195	-	-
	3	0.90	0.06	0.26	0.06	1254	0	-	-
	4	0.93	0.05	0.29	0.05	953	0	14	-
	5	0.89	0.05	0.36	0.09	827	0	31	18
	6	-	-	0.28	0.05	722	0	50	23

^aParameter definitions: $\hat{\phi}_{ij}$, apparent survival probability; \hat{p}_{ij} , detection probability; \hat{N}_{ij} , abundance of adults; \hat{N}_{Yij} , abundance of young of the year; \hat{B}_{ij} , number of new adult individuals in the sampled populations; \hat{B}_{Yij} , number of new young individuals in the sampled population.

APPENDIX B
CONFIDENCE INTERVALS, MODEL SELECTION TABLES AND MOVEMENT
ESTIMATES

Appendix B-1. Method from Burnham et al. (1987) to compute confidence intervals on parameter θ .

When a parameter θ is assumed to be lognormally distributed, lower and upper bounds $\hat{\theta}_L$ and $\hat{\theta}_U$ for an approximate $(1-\alpha)\%CI[\hat{\theta}]$, are computed as:

$$\hat{\theta}_L = \hat{\theta} / C; \text{ and } \hat{\theta}_U = \hat{\theta} * C; \text{ where } C = \exp\left(z_{\alpha/2} \sqrt{\ln(1 + [cv(\hat{\theta})]^2)}\right)$$

$cv(\hat{\theta})$ is coefficient of variation of $\hat{\theta}$; $z_{0.025} = 1.96$ (for 95%CI, $\alpha = 0.05$).

This approach provides a better approximation than normal based 95%CI $[\hat{\theta}] = \hat{\theta} \pm 1.96*$

$\widehat{SE}[\hat{\theta}]$, when parameter θ is strictly positive and/or $cv(\hat{\theta}) > 0.1$ (Burnham and Anderson 2002; Burnham et al. 1987).

Table B-1. Multistate models of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) snail kites among the 5 major regional patches in Florida based on radio-telemetry data. These models evaluate the effect of patch size, distance, regional patch identity alone on movement probabilities. The models presented below are not supported by the data but were developed to evaluate the fit of the models presented in Table 3-1.

Model	ΔAICc	K
a-Movement among regions of juveniles and adults modelled simultaneously		
ψ <i>ad</i> (<i>r</i>) ψ <i>juv</i> (<i>r</i>)	15.2	60
ψ <i>ad</i> (<i>AR</i> * <i>d</i>) ψ <i>juv</i> (<i>AR</i> * <i>d</i>)	16.5	26
ψ <i>ad</i> (<i>AR</i> + <i>d</i>) ψ <i>juv</i> (<i>AR</i> + <i>d</i>)	21.8	25
ψ (<i>AR</i> + <i>d</i>)	22.4	12
ψ (<i>AR</i> * <i>d</i>)	24	13
ψ (<i>r</i> * <i>season</i>)	29.2	90
ψ (<i>AR</i>)	48	11
ψ (<i>r</i> * <i>years</i>)	96.9	120
ψ <i>ad</i> (<i>AD</i>) ψ <i>juv</i> (<i>AD</i>)	103	19
ψ (<i>AD</i>)	104	11
ψ <i>ad</i> (<i>d</i>) ψ <i>juv</i> (<i>d</i>)	118.6	22
ψ (<i>d</i>)	127.1	11
ψ <i>ad</i> (<i>r</i> * <i>seas</i>) ψ <i>juv</i> (<i>r</i> * <i>seas</i>)	134.1	180
ψ <i>ad</i> (<i>seas</i>) ψ <i>juv</i> (<i>seas</i>)	173.4	6
ψ <i>ad</i> (<i>years</i>) ψ <i>juv</i> (<i>years</i>)	184.3	8
ψ (.)	203.2	1
ψ (<i>seas</i>)	186.7	3
ψ (<i>seas</i> * <i>years</i>)	189.2	10
ψ (<i>years</i>)	203.7	4
ψ (<i>t</i>)	215.3	40
ψ (<i>breed</i>)	205.1	2
ψ <i>ad</i> (<i>t</i>) ψ <i>juv</i> (<i>t</i>)	222.1	78
ψ <i>ad</i> (<i>r</i>) ψ <i>juv</i> (<i>d</i>)	933	36
ψ <i>ad</i> (<i>r</i>) ψ <i>juv</i> (<i>AR</i>)	1081	29
ψ <i>ad</i> (<i>AR</i>) ψ <i>juv</i> (<i>AR</i>)	69300	15
b-Juveniles only		
ψ <i>juv</i> (<i>r</i>)	14	30
c-Adults only		
ψ <i>ad</i> (<i>AR</i> + <i>d</i>)	13.6	12
ψ <i>ad</i> (<i>AR</i> * <i>d</i>)	15.4	13

Notes: AICc is the Akaike's Information Criterion adjusted for small sample size. Δ AICc for the *i*th model is computed as AICc_{*i*} - min (AICc). w refers to AICc weight. K refers to the number of parameters. Only models with $w < 0.01$ are presented. "*r*": month; "*r*": region; "*AR*": area of the receiving site; "*AD*": area of the donor site; "*d*": distance; "*seas*": seasonal; "*breed*": breeding season. Models that never reached numerical convergence were not presented.

Table B-2. Multistate models (with survival and detection probabilities equal to 1) of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) snail kites among wetlands in the E and K regions based on radio-telemetry data. The models presented below are not supported by the data but were developed to evaluate the fit of the models presented in Table 3-2.

Model	ΔAICc	K
Movement within the E region		
ψ (<i>cw</i>)	12.4	20
ψ <i>ad</i> (<i>cw</i>) ψ <i>juv</i> (<i>cw</i>)	21.5	38
ψ <i>ad</i> (<i>cw</i>) ψ <i>juv</i> (<i>AR</i> * <i>d</i>)	25.8	22
ψ <i>ad</i> (<i>cw</i>) ψ <i>juv</i> (<i>AD</i>)	39.2	21
ψ <i>ad</i> (<i>cw</i>) ψ <i>juv</i> (<i>AR</i> + <i>d</i>)	40.3	21
ψ <i>ad</i> (<i>cw</i>) ψ <i>juv</i> (<i>AR</i>)	42.4	21
ψ <i>ad</i> (<i>cw</i>) ψ <i>juv</i> (<i>d</i>)	49.3	20
ψ (<i>cw</i> * <i>years</i>)	58.6	72
ψ (<i>AR</i> * <i>d</i>)	60.6	3
ψ (<i>seas</i> * <i>region</i>)	65	120
ψ (<i>AD</i>)	82.4	2
ψ <i>ad</i> (<i>AD</i>) ψ <i>juv</i> (<i>AD</i>)	85	4
ψ (<i>seas</i> * <i>year</i>)	99.3	10
ψ (<i>AR</i> + <i>d</i>)	102	3
ψ (<i>seas</i>)	102.3	3
ψ <i>ad</i> (<i>AR</i> + <i>d</i>) ψ <i>juv</i> (<i>AR</i> + <i>d</i>)	103.2	6
ψ <i>ad</i> (<i>AR</i>) ψ <i>juv</i> (<i>AR</i>)	103.2	4
ψ (<i>AR</i>)	104.2	2
ψ (.)	106.6	1
ψ (<i>d</i>)	107.7	2
ψ <i>ad</i> (.) ψ <i>juv</i> (.)	108.3	2
ψ (<i>breed</i>)	108.5	2
ψ (<i>breed</i> * <i>year</i>)	108.8	7
ψ (<i>years</i>)	109.7	4
ψ <i>ad</i> (<i>d</i>) ψ <i>juv</i> (<i>d</i>)	111.1	4
ψ (<i>t</i>)	111.8	34
ψ <i>ad</i> (<i>years</i>) ψ <i>juv</i> (<i>years</i>)	783.7	7
ψ <i>ad</i> (<i>t</i>) ψ <i>juv</i> (<i>t</i>)	799.6	48
ψ <i>ad</i> (<i>cw</i> * <i>years</i>) ψ <i>juv</i> (<i>cw</i> * <i>years</i>)	1606.1	95

Table B-2 (cont.).

Model	$\Delta AICc$	K
Movement within the K region		
ψ (<i>years*breed</i>)	9.2	7
ψ <i>ad</i> (years) ψ <i>juv</i> (years)	10.1	7
ψ <i>ad</i> (<i>mw</i>) ψ <i>juv</i> (<i>mw</i>)	20.4	24
ψ (<i>t</i>)	29.2	37

Notes: AICc is the Akaike's Information Criterion. $\Delta AICc$ for the *i*th model is computed as $AICc_i - \min(AICc)$. w refers to AICc weight. K refers to the number of parameters. Only models with $w < 0.01$ are presented. "*cw*": contiguous wetland; "*mw*": moderately isolated wetland; "*seas*": season; "*breed*": breeding season. Models that never reached numerical convergence were not presented.

Table B-3. Multistate models of annual survival (ϕ), sighting probabilities (p), and annual movement probabilities (ψ) of adults (ad) and juveniles (juv) snail kites based on banding data. The drought effect during 2000-2002 was denoted D_{1-2} . Constant ϕ during non-drought years (1992-2000 and 2002-2004) was denoted ND . The models presented below are not supported by the data but were developed to evaluate the fit of the models presented in Table 3-3.

Model	$\Delta AICc$	K
$\phi_{ad}^{[E=O \neq K \neq J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	11	80
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	14	76
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(r+t_d) \psi_{ad}(r) \psi_{juv}(r)$	15.6	88
$\phi_{ad}^{[E=O \neq K \neq J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	16	77
$\phi_{ad}(r*ND) \phi_{ad}^K(.) \phi_{ad}^{[E \neq O \neq J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	16.3	82
$\phi_{ad}^{[E=O \neq K \neq J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O \neq J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	16.6	79
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^{[E=O=J \neq K]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	16.7	78
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O \neq J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	16.8	79
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}^{[E=O \neq K=J]}(t) p(r*t) \psi(r)$	17.2	88
$\phi_{ad}^{[E=O \neq K \neq J]}(ND) \phi_{ad}^{[E=O \neq J \neq K]}(D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	17.8	81
$\phi_{ad}(r*ND) \phi_{ad}(r*D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	18.7	84
$\phi_{ad}^{[E=O \neq K \neq J]}(ND) \phi_{ad}^{[E=O \neq J \neq K]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r)$	19.2	81
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r*D_1)$	19.6	88
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	19.7	77
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^{[E=O=J \neq K]}(D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	19.8	75
$\phi_{ad}(r+t) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	22.9	86
$\phi_{ad}(r*ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi(r*D_1)$	22.9	95
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r*t) \psi_{ad}(r) \psi_{juv}(r)$	24.2	87
$\phi_{ad}^{[E=O \neq K=J]}(.) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	36.8	75
$\phi_{ad}(r*ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	42.4	75
$\phi_{ad}(r*ND) \phi_{ad}^K(.) \phi_{ad}^{[E \neq O \neq J]}(D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi(r)$	43.5	80
$\phi_{ad}(r*ND) \phi_{ad}(r*D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi_{ad}(r) \psi_{juv}(r)$	60.7	81

Table B-3 (cont.).

Model	ΔAICc	K
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(r+t_d) p(r+t) \psi(r)$	108.6	44
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(r+t_d) p(t) \psi(r)$	145.8	40
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r * t) \psi(t)$	171.1	76
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r * t) \psi(.)$	192.9	65
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(r) \psi(r)$	226.4	32
$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(t) p(.) \psi(r)$	263.4	29

Notes: AICc is the Akaike's Information Criterion adjusted for small sample size. ΔAICc for the *i*th model is computed as AICc_{*i*} - min (AICc). *w* refers to AICc weight. K refers to the number of parameters. Only models with *w* < 0.01 are presented. “*t*”: time (years); “*r+td*”: additive effect of region and time on ϕ , except during 2001-2002, during which ϕ was time dependent only; “.”: ϕ is constant during 1992-2004. Superscript indicate region specific ϕ ; “=”: regions have identical ϕ ; “≠”: regions have different ϕ .

Table B-4. Annual movement estimates ($\hat{\psi}$), between the 4 major regions used by the snail kite (E, O, K and J) during normal and drought years estimated with model

$$\phi_{ad}^{[E=O \neq K=J]}(ND) \phi_{ad}^K(.) \phi_{ad}^{[E=O=J]}(D_{1-2}) \phi_{juv}(r+t_d) p(r*t) \psi(r*D_1).$$

MOVEMENT					
FROM	TO	$\hat{\psi}$	$\hat{SE}[\hat{\psi}]$	95%CI	Year
E	O	0.017	0.004	0.010-0.026	Normal
E	O	0	0	0	Drought
E	K	0.015	0.003	0.010-0.022	Normal
E	K	0.03	0.012	0.014-0.066	Drought
E	J	0.016	0.003	0.010-0.025	Normal
E	J	0.027	0.017	0.008-0.091	Drought
O	E	0.156	0.024	0.115-0.209	Normal
O	E	0	0	0	Drought
O	K	0.044	0.014	0.024-0.080	Normal
O	K	0.33	0.117	0.146-0.580	Drought
O	J	0.039	0.013	0.076	Normal
O	J	0.018	0.096	0-1	Drought
K	E	0.092	0.021	0.058-0.133	Normal
K	E	0	0	0	Drought
K	O	0.1	0.025	0.063-0.161	Normal
K	O	0	0	0	Drought
K	J	0.084	0.02	0.052-0.133	Normal
K	J	0.14	0.111	0.026-0.497	Drought
J	E	0.155	0.033	0.010-0.231	Normal
J	E	0	0	0	Drought
J	O	0.028	0.017	0.009-0.090	Normal
J	O	0	0	0	Drought
J	K	0.062	0.02	0.033-0.115	Normal
J	K	0.000	0.000	0	Drought

APPENDIX C
SELECTION OF MODELS USED TO ASSESS THE EFFECT OF NATAL LOCATION ON
MOVEMENT AND SURVIVAL

Table C-1. Multistate models of apparent survival (“ ϕ_{AD} ”: survival of adults; “ ϕ_J ”: survival of juveniles) and annual transition probabilities (“ ψ ”) among the four major wetland complexes used by snail kites in Florida between 1992 to 2004. Factors incorporated in the models included: age, region, natal region; and a drought effect on movement and survival.

Model	ΔAIC_c	K	DEV
$r_{\phi_{AD,nd}^{[E \neq L \neq J \neq K]}}(.) r_{\phi_{AD,d}^{[E \neq L \neq J \neq K]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	12.26	84	2586.5
$nr_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) nr_{\phi_{AD,d}^{[K=J]}}(ND) nr_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO=OA \neq ON]}(nr) p(r * t)$	12.32	72	2612.0
$nr_{\phi_{AD,nd}^{[E \neq L \neq J \neq K]}}(.) nr_{\phi_{AD,d}^{[K]}}(ND) nr_{\phi_{AD,d}^{[E=L \neq J]}}(D) \phi_J(t) \psi^{[NO \neq OA \neq ON]}(nr) p(r * t)$	12.63	80	2595.3
$nr_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) nr_{\phi_{AD,d}^{[K]}}(ND) nr_{\phi_{AD,d}^{[E=L=J]}}(D) \phi_J(t) \psi^{[NO \neq OA \neq ON]}(nr) p(r * t)$	13.56	76	2604.8
$nr_{\phi_{AD,nd}^{[E \neq L \neq J \neq K]}}(.) nr_{\phi_{AD,d}^{[K]}}(ND) nr_{\phi_{AD,d}^{[E \neq L \neq J]}}(D) \phi_J(t) \psi^{[NO \neq OA \neq ON]}(nr) p(r * t)$	14.15	82	2592.6
$r_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) r_{\phi_{AD,d}^{[K=J]}}(ND) r_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr * D_m) p(r * t)$	14.17	88	2579.8
$nr_{\phi_{AD,nd}^{[E=L \neq J \neq K]}}(.) nr_{\phi_{AD,d}^{[K]}}(ND) nr_{\phi_{AD,d}^{[E=L \neq J]}}(D) \phi_J(t) \psi^{[NO \neq OA \neq ON]}(nr) p(r * t)$	15.07	79	2599.9
$nr_{\phi_{AD,nd}^{[E=L \neq J \neq K]}}(.) nr_{\phi_{AD,d}^{[K]}}(ND) nr_{\phi_{AD,d}^{[E=L=J]}}(D) \phi_J(t) \psi^{[NO \neq OA \neq ON]}(nr) p(r * t)$	15.19	77	2604.3
$nr_{\phi_{AD,nd}^{[E \neq L \neq J \neq K]}}(.) nr_{\phi_{AD,d}^{[E \neq L \neq J \neq K]}}(D) \phi_J(t) \psi^{[NO \neq OA \neq ON]}(nr) p(r * t)$	17.72	84	2591.9
$r_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) r_{\phi_{AD,d}^{[K=J]}}(ND) r_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(nr * t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	21.2	103	2554.6
$r_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) r_{\phi_{AD,d}^{[K=J]}}(ND) r_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(\text{age} * r * t)$	24.53	119	2523.2
$r_{\phi_{AD,nd}^{[E=L=J=K]}}(.) r_{\phi_{AD,d}^{[E=L=J=K]}}(D) \phi_J(t) \psi^{[NO \neq OA \neq ON]}(nr) p(r * t)$	29.48	75	2622.8
$r_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) r_{\phi_{AD,d}^{[K=J]}}(ND) r_{\phi_{AD,d}^{[E=L]}}(D) \phi_J(t) \psi^{[NO \neq ON=OA]}(nr) p(r * t)$	33.08	72	2632.7
$r_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) r_{\phi_{AD,d}^{[E=L \neq K=J]}}(ND) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	46.74	74	2642.2
$r_{\phi_{AD}^{[E \neq L \neq J \neq K]}}(t) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	49.4	116	2554.6
$r_{\phi_{AD,nd}^{[E \neq L \neq J \neq K]}}(.) r_{\phi_{AD,d}^{[E \neq L \neq J \neq K]}}(ND) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	49.7	76	2640.9
$r_{\phi_{AD,nd}^{[E=L \neq J=K]}}(.) r_{\phi_{AD,d}^{[E=L \neq K=J]}}(ND) \phi_J(nr * D) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	51.63	73	2649.2
$r_{\phi_{AD,nd}^{[E=L=J=K]}}(.) r_{\phi_{AD,d}^{[E=L=K=J]}}(ND) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	59.84	73	2657.4
$\phi_{AD}(r * nr * D) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	61.2	119	2559.8
$\phi_{AD}(r * nr) \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	68.6	88	2634.2

Table continues next page

Table C-1 (cont.)

Model	ΔAICc	K	DEV
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(\cdot) \psi^{[NO \neq ON \neq OA]}(nr) p(r * t)$	82.81	65	2697.2
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(\text{age} * t)$	91.54	50	2737.3
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi(r) p(r * t)$	102.05	76	2693.2
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(t)$	102.49	40	2768.9
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi^{[NO=ON \neq OA]}(nr) p(r * t)$	112.14	72	2711.8
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi^{[NO=ON=OA]}(nr) p(r * t)$	119.47	68	2727.6
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(r)$	161.3	32	2844.2
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi^{[NO \neq ON \neq OA]}(nr) p(\cdot)$	188.26	29	2877.3
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi(t) p(r * t)$	239.47	76	2830.7
$\Gamma_{\phi_{AD,nd}^{[E=L \neq J=K]}(\cdot)} \Gamma_{\phi_{AD,d}^{[K=J]}(ND)} \Gamma_{\phi_{AD,d}^{[E=L]}(D)} \phi_J(t) \psi(\cdot) p(r * t)$	253.09	65	2867.5
$\phi(\text{age} * r * t) \psi(r * t) p(r * t)$	337.12	275	2472.5

Notes: Only models with Δ AICc > 11 (see Table 4-1 for models with Δ AICc < 11). AICc weights are not presented in digital appendix S1 because $w \sim 0$ for all models. For other notations see Table 4-1.

APPENDIX D CLUSTERING ANALYSIS

Cluster analyses are numerical methods that allow the identification of groups in multivariate data (Venables & Ripley 2002). We conducted an agglomerative hierarchical clustering analysis on a $m \times n$ matrix (Everitt 2005). The rows (m) corresponded to the years (from 1992 to 2006), and the columns (n) to hydrological variables.

To avoid the dependence on the choice of measurements units, we standardized the measurements based on recommendations from Kaufman and Rousseeuw (1990):

$$z_{ig} = \frac{x_{ig} - m_g}{s_g}$$

where m_g is the *arithmetic mean* of variable g , x_{ig} is the i th observation of variable g ($i = 1$ to n), and s_g is the *mean absolute deviation*:

$$s_g = \frac{1}{n} \left\{ |x_{1g} - m_g| + |x_{2g} - m_g| + \dots + |x_{ng} - m_g| \right\}$$

We selected 5 biologically relevant hydrological variables:

- minimum water levels for the entire year.
- average water levels for the period March to June (which is more biologically relevant to kites than average water levels for the entire year, see Martin et al. (2006) and Mooij et al (2007)).
- proportion of wetlands affected by dry conditions (< 1 SD below the annual minimum for the period March-June, see Bennetts and Kitchens 1997 and Martin et al. 2006).
- duration of drying event (i.e., number of days for which water levels fell below 1 SD below the mean annual minimum, see Bennetts and Kitchens 1997).
- duration of moderate dry conditions (i.e., number of days for which water levels fell below the mean annual minimum).

The results of the agglomerative hierarchical analysis are summarized in Figure D-1.

From this analysis we could identify 3 groups of years:

Group 1 (G1): 1992 and 2001

Group 2 (G2): 1999, 2000, 2002, 2004 and 2006

Group 3 (G3): 1993, 1994, 1995, 1996, 1997, 1998, 2003 and 2005

This grouping was consistent with grouping based on visualization of Table D-1. Figure D-1 shows that G1 included the driest years, G2 included years with more moderate dry conditions, G3 included years with the wettest conditionsers with other wet years (Figure D-1). Therefore based on Table D-1 and Figure D-1 we identified 3 categories:

- 1-Drought years: years included in G1. Note from Table 7-4 that 2001 was a more intense drought with a greater spatial and temporal extent than 1992.
- 2-Moderately dry years: years included in G2.
- 3-Wet years: years included in G3.

Table D-1. Five hydrological variables used to conduct the hierarchical agglomerative clustering analysis. (1) Annual minimum water levels at station 3A65 (MWL); (2) average water levels for the period March to June (WL (Mar-Jun)) at station 3A65; (3) spatial extent of wetlands affected by dry conditions; (4) duration of drying event (i.e., number of days for which water levels fell below 1 SD below the mean annual minimum, see Bennetts and Kitchens 1997) (Duration II); (5) duration of moderate dry conditions (i.e., number of days for which water levels fell below the mean annual minimum) (Duration I).

Year	MinWL	WL (Mar-Jun)	Duration I	Duration II	Spat. Ext.
1992	7.92	8.60	54.00	14.00	54%
1993	9.13	9.68	0.00	0.00	9%
1994	8.93	9.36	0.00	0.00	0
1995	9.09	9.70	0.00	0.00	0
1996	8.95	9.31	0.00	0.00	8%
1997	8.89	9.30	0.00	0.00	0
1998	8.49	9.53	17.00	0.00	0
1999	8.46	8.94	39.00	0.00	17%
2000	8.31	8.86	19.00	0.00	0
2001	7.83	8.35	107.00	30.00	72%
2002	8.37	9.00	30.00	0.00	0
2003	8.90	9.31	0.00	0.00	0
2004	8.25	8.83	45.00	0.00	8%
2005	8.62	9.16	0.00	0.00	0
2006	8.36	8.86	48.00	0.00	25%

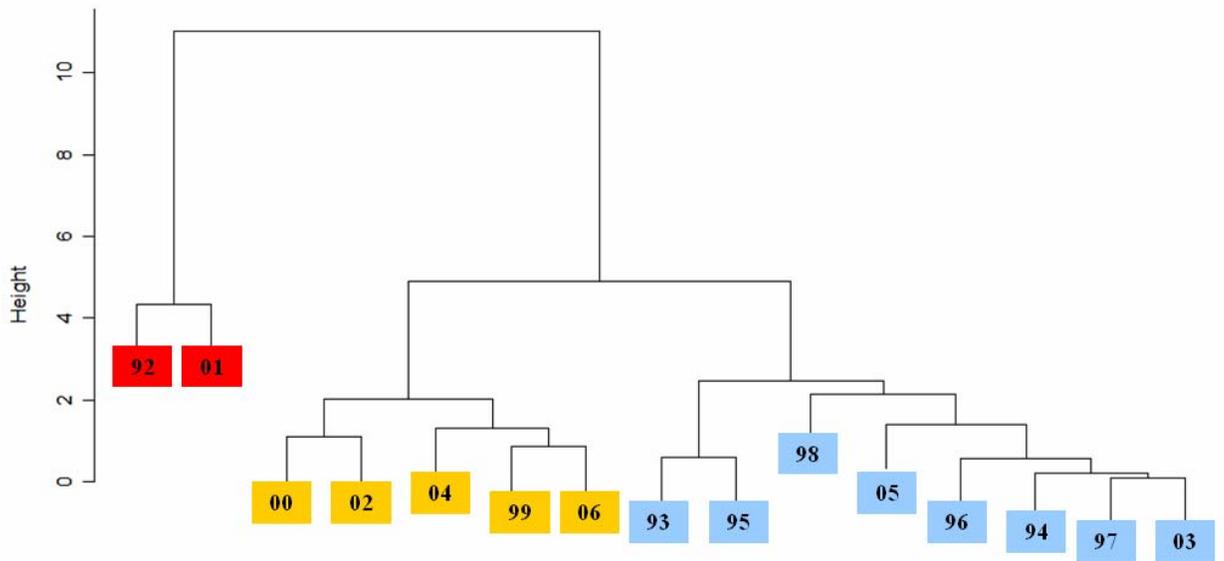


Figure D-1. Agglomerative hierarchical analysis which categorized years from 1992 to 2006 into wet years (blue), moderately dry years (yellow) and drought years (red).

APPENDIX E
ESTIMATION OF Q(T)

Estimates of $q(t)$ can be obtained based on estimates from Bennetts (1998).

$$q(t) = \frac{m_a}{m_s} = \frac{S_a \times \delta_a \times \alpha_a \times Y_a}{S_s \times \delta_s \times \alpha_s \times Y_s}$$

Where S_i corresponds to nest success (subscripts indicate the age class to which the parameter pertains to, adults: “a” and subadults:”s”); δ_i is the number of breeding attempts per year; α_i is the proportion of birds attempting to breed; Y_i is the number of young per successful nest; and the sex ratio is assumed to be 50:50 (see Beissinger 1995). Beissinger (1995) assumed no difference in nest success and number of young per successful nest. Based on a radiotelemetry study, Bennetts (1998) estimated $\hat{\delta}_a(1995) = 1$ (i.e., 100% of the adult Snail Kites attempted to breed in 1995 which was a wet year), and $\hat{\delta}_s(1995) = 0.33$. Based on his radiotelemetry study, Bennetts estimated $\hat{\alpha}_a(1995) = 1.4$, but did not get an estimate for α_s . Therefore we set $\alpha_s = 1$ based on Beissinger (1995), which noted most subadults nest later in the season.

Thus, based on Bennetts estimates $\hat{q}(1995) = \frac{0.3 \times 1 \times 1.4 \times 1.9}{0.3 \times 0.33 \times 1 \times 1.9} = 4.24$

In contrast, based on Beissinger (1995), $\hat{q}(t) = 8$ during lag years, 8.8 during wet years, and 1 during drought (however this latter estimate was based on less reliable data). We used $\hat{q}(t)$ based on Bennetts estimates because these estimates were more recent and based on a more robust methodology. Varying $q(t)$ from 4 to 8.8 had little effect on population growth rates and other relevant measures.

APPENDIX F DETECTION OF JUVENILES

Estimates of detection of juveniles $\hat{\beta}(t)$ were available for 2004 and 2005 only (Martin et al. 2007b). In contrast, estimates of detection of adults were available for the period 1997 to 2005.

Martin et al. (2007b) found that detection for the adults increased linearly over time between 1997 and 2005. They suggest that this increase in detection was the result of an increase in search effort. Thus, we fitted a linear regression to their data (Table 2, MC data); the dependent variable was detection of adults $\hat{\beta}_a(t)$ and the independent variable was “year” (t). We found a significant relationship ($F = 24.63$, $df = 1$ and 6 , $P = 0.0025$, $R^2 = 0.80$): $\hat{\beta}_a(t) = -38.1158 + 0.0192 \times t$.

We adjusted this equation for detection of juveniles so that detection in 2005 would equal 0.35, which was the estimate obtained by Martin et al. (2007b). We obtained the following equation: $\hat{\beta}(t) = -38.146 + 0.0192 \times t$. We computed annual detection of juveniles using the latter equation, except for 2004 for which an estimate of detection was available ($\hat{\beta}(t)$ in 2004 was 0.16). Martin et al. (2007b) emphasized that this estimate was unusually low, probably because of logistical problems that occurred in 2004. Thus, detection for this analysis varied between 0.16 and 0.35. Martin et al. (2007b) cautioned about these estimates of detection for juveniles because of scattered data. Therefore, in order to assess the robustness of our analyses we also repeated our analyses based on a conservative overestimate of juveniles, $\hat{\beta}(t) = 0.70$, which was basically twice the estimate obtained in 2005. When detection of juveniles was considered to be 0.70, we assumed a constant detection for all years. We also conducted our

analyses assuming a constant detection probability of $\hat{\beta}(t) = 0.16$. It is probably safe to assume that the average detection of juveniles during our study period was between 0.16 and 0.70.

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