

EFFECTS OF AGING AND THE ENVIRONMENT ON SNAIL KITE DEMOGRAPHY: A  
REASSESSMENT OF SNAIL KITE (*Rostrhamus sociabilis plumbeus*) VITAL RATES

By

BRIAN ENGEBOS REICHERT

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To Conservation

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Brian Engebos Reichert

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The Snail Kite (*Rostrhamus sociabilis plumbeus*) is a long-lived species. In this work, banded individuals were observed at age 25, and successfully reproducing until 18 years of age. The Snail Kite's life-history pattern has been described by relatively high, stable adult survival, variable juvenile survival, and low annual adult fecundity. These patterns are generally characteristic for populations whose reproductive output is closely tied to environmental stochasticity.

Snail Kites, like most wild populations, face risks associated with both intrinsic (i.e. aging) and extrinsic (i.e. environmental) sources of mortality. The objective of this work was to assess their relative impacts on Snail Kite vital rates. Thus, we use a capture-mark-recapture framework to model age-dependent survival and breeding. The results of which provide evidence of senescent declines in both survival and the breeding probabilities of adult kites.

As a dietary specialist, the Snail Kite is heavily dependent upon its primary food resource, the freshwater Florida apple snail (*Pomacea paludosa*), whose availability varies according to local hydrologic conditions. Therefore, the Snail Kite population provides an excellent opportunity to evaluate hypotheses related to the interactions of aging and the environment. Using range-wide drought events (2000-2002 and 2007) and the occurrence of range-wide

habitat degradation we provide convincing evidence that the annual survival probabilities of senescent kites are disproportionately affected by droughts relative to the survival probability of prime-aged adults, and that the cost of reproduction which decreases Snail Kite survival is exacerbated during periods of low resource availability. Accounting for these additional sources of variation within vital rates may be particularly important to accurately compute estimates of population growth rate, and probabilities of quasi-extinctions.

Finally, we use our results to assess the current population age structure and discuss the potential implications of an aging Snail Kite population on future conservation objectives.

## CHAPTER 1 INTRODUCTION

The Florida Snail Kite (*Rostrhamus sociabilis plumbeus*) is an endangered raptor whose population is confined to the remaining freshwater marshes and littoral wetlands of central and southern peninsular Florida (Bennetts and Kitchens 1997). Similar to most species native to the South Florida Environment, the Snail Kite population has been adversely affected by human alterations in the landscape, specifically widespread drainage and changes to the natural hydrologic regime (Bennetts and Kitchens 1997; USFWS 1999; Martin *et al.* 2008; Sykes 1983). In addition to drainage efforts, impoundments, invasive species, and nutrient loading have severally degraded the natural processes within the Snail Kite's historical range: the Kissimmee-Okeechobee-Everglades watershed (Sykes 1979; Duever *et al.* 1994; Sklar *et al.* 2002; Sklar *et al.* 2005).

The life-history strategies of the Everglade's flora and fauna have been shaped in response to extreme spatial and temporal climatic variation, the same precipitation-driven patterns which dictated the natural hydrology of the system. As it has been recognized that a successful restoration of the Everglades ecosystem is contingent upon reestablishing the "natural" hydrologic regime (CERP) species, such as the Snail Kite, have been selected as performance measures of restoration efforts because they exhibit numerical changes in population size, movement probabilities, and vital rates in response to changes in habitat quality (i.e. hydrology) (RECOVER 2005).

Although reliable estimates of population size were not available until 1996 (Dreitz *et al.* 2002), early accounts and recent studies both provide convincing evidence that the changes in Snail Kite population size correspond directly to environmental conditions, especially hydrology (Sykes 1983; Beissinger 1988; Martin *et al.* 2006; Cattau 2008). After reaching an estimated

level of 3,400 individuals in 1999, the Snail Kite population has subsequently halved twice in the last decade: once from 2000-2002 and again from 2006-2008 (Cattau 2008). The population was estimated at 685 individuals in 2008, and preliminary calculations suggest no significant change in 2009 (Cattau, unpublished). As the Snail Kite's population growth is a function of its vital rates, long-term monitoring has focused on how these vital rates change in relation to the Snail Kite's environment. If changes in Snail Kite demography provide a reliable barometer for Everglades restoration, recent dramatic declines in population size, fecundity, and juvenile survival are indications of an ailing ecosystem.

The vital rates, or demographic parameters, addressed in this body of work are of interest from both ecological and conservation perspectives. Generally speaking, vital rates can be used to describe and predict the life-cycle of a population of interest (Caswell 2001). They can also be used as a qualitative means for gaining insight into the relationships between the individuals of a population and their surroundings. For example, assessing the trends in Snail Kite survival and breeding probabilities over a period of habitat degradation or environmental disturbance can be used as an indicator of how individuals respond to changes in habitat quality. Furthermore, identifying how changes in the population's environment may adversely affect the vital rates of one age cohort more than another provides important information about Snail Kite population dynamics, which are critical for predicting population responses to management alternatives (Ralls *et al.* 2002).

As a dietary specialist, the Snail Kite's behavior and thus its demography are strongly dependent upon the availability of its primary food resource, a freshwater apple snail (*Pomacea paludosa*) (Beissinger 1995; Bennetts 1998a; Mooij *et al.* 2002; Martin *et al.* 2007a; Cattau 2008). Wide-spread drying events decrease apple snail availability, requiring Snail Kites to

increase their effort in search for adequate foraging habitat, or refugia (Bennetts and Kitchens 1997). The longer the duration and greater the spatial extent of a drying event the greater its potential impact can be on Snail Kite survival (Martin *et al.* 2006; Bennetts and Dreitz 1997). Thus, a general lack of refugia, resulting from habitat degradation or conversion during times of resource depletion (i.e. drought) exacerbates this effect by extending the necessary distance to travel, and increasing the individual fitness necessary to arrive at suitable habitat. Individuals less than a year old, who are less physiologically fit, and/or less experienced in finding refugia, experience higher rates of mortality (Bennetts and Kitchens 1997; Martin 2007). These phenomena are thought to have played an important role in the population's recent dramatic declines (Martin *et al.* 2008).

In Chapter 2 we model this drought effect on the survival on yet another potentially less adept portion of the population, senescent adults. We compare models testing hypotheses with regard to senescence and drought, the results of which suggest that both aging and age-specific drought effects limit overall adult survival. This is a finding of significant importance, as changes in adult survival have the most affect on the population growth rate of long lived avian species (Saether and Bakke 2000; Stahl and Oli 2006).

In addition to survival, Snail Kite reproductive effort is also thought of to be affected by resource availability (Beissinger 1988; Bennetts and Kitchens 1997). As an iteroparous species, an individual makes the decision whether or not to attempt breeding at multiple occasions during their lifespan. Cued in part by environmental factors, it must make a trade-off between attempting to breed and maximizing their probability of survival (Curio 1988; Erikstad *et al.* 1998). Sources of individual heterogeneity, such as age and experience, interact with these

environmental conditions, and become factors in determining the outcome of their decisions and their life-history patterns.

In Chapter 3 we use known patterns in Snail Kite life-history to generate a set of candidate models which test for the effects of aging and environment on the probability of individuals attempting to breed. Utilizing a robust multistate design that adjusts for the misclassification of breeding state designations, we provide robust estimates of breeding probabilities for the first time. We assess the direct and indirect costs of reproduction on Snail Kite survival and future breeding, assess recent trends in breeding probabilities, and provide an age-specific distribution for the breeding proportion of the population.

Chapter 4 assesses the significant findings in the context of Snail Kite conservation. We discuss potential concerns related to recent changes in the age structure of the Snail Kite population and provide recommendations for future analyses.

The early inclusion of the Snail Kite to the Endangered Species Act, in 1967, and its use as a performance measure for the management of wetland habitats, especially the Comprehensive Everglades Restoration Project (RECOVER 2005) has generated an unusually large amount of information relative to most endangered species, of which we tend to have limited demographic data. The long-term Snail Kite monitoring project was implemented with the intent of providing future researchers the opportunity to test predictions and adjust models by incorporating new information about long-term processes, such as aging (Bennetts and Kitchens 1997). This iterative modeling process and the adaptive approach to management are critical for the successful recovery of the Snail Kite (Nichols *et al.* 1980; Bennetts and Kitchens 1997; Martin *et al.* 2007a).

Adult fecundity and survival have the most impact on the rate of population growth, and therefore the persistence of the Snail Kite in Florida (Nichols *et al.* 1980; Beissinger 1995, Martin *et al.* 2008). Nichols *et al.* (1980) suggested that further research should focus primarily on “the clarification of relationships between these rates and environmental factors which affect their magnitude.” The following study is an attempt to further our understanding of these relationships by testing hypotheses regarding the effects of aging and environment on adult Snail Kite survival (Chapters 2 and 3 ) and breeding probabilities (Chapter 3). The public dissemination of this information is absolutely critical for its use in future conservation tools and by managers interested in Snail Kite conservation and its eventual recovery.

CHAPTER 2  
INTERACTIVE EFFECTS OF SENESCENCE AND NATURAL DISTURBANCE ON THE  
ANNUAL SURVIVAL PROBABILITIES OF SNAIL KITES

**Introduction**

On an individual level, senescence can be defined as a decrease in survival and/or reproductive output that results from physiological deterioration with increasing age (Partridge and Barton 1993; Abrams 1993). Jones *et al.* (2008) disentangled these two manifestations of senescence and concluded that addressing survival alone provides “reliable information on overall senescence”. Understanding the role of senescence, and age-specific survival in nature is important for numerous issues in ecology (condition-dependent mortality; (Williams *et al.* 2006; Caswell 2007; Roach *et al.* 2009), evolution (e.g., life-history theory; (Jones *et al.* 2008), and conservation (e.g., population projections; (Beissinger and Westphal 1998)

Nonetheless, empirical tests of the evolutionary theories of aging first presented by Medawar (1952), Hamilton (1966), and Williams (1957) have relied heavily on controlled populations in laboratory settings (Rose and Charlesworth 2002; Charlesworth and Hughes 1996; Charlesworth 2000; Kirkwood and Austad 2000; Partridge and Gems 2002; Carey *et al.* 1992; Kawasaki *et al.* 2008). These studies elucidated many of the physiological mechanisms responsible for senescence and demonstrated several important tradeoffs inherent to different life history strategies. However, several authors have recently questioned whether the inferences drawn from laboratory studies of senescence are applicable when studying patterns of survival in naturally occurring populations (Kawasaki *et al.* 2008; Monaghan *et al.* 2008; Williams *et al.* 2006; Roach *et al.* 2009).

Developments in the techniques of data collection and analyses, specifically those involving marked individuals, have allowed researchers to conduct formal tests for the effects of aging on the survival probabilities of individuals in wild populations (Nichols *et al.* 1997;

Gaillard *et al.* 2004). A growing consensus in the current literature favors the use of longitudinal data over cross-sectional data when evaluating senescence at the individual level (Monaghan *et al.* 2008; Nussey *et al.* 2008; Roach *et al.* 2009). A commonly cited reason is the inability of cross-sectional data, such as that used in life tables, to incorporate imperfect detection probabilities (Nisbet and Cam 2002; Nichols *et al.* 1997; Gaillard *et al.* 2004). Longitudinal studies (i.e. those that follow multiple cohorts of marked individuals through time via capture-mark-recapture or mark-resight methods) generate capture histories of individuals, and thus, provide a framework for dealing with re-sight probabilities that are less than one (Nichols *et al.* 1997).

The use of longitudinal analyses has led to an increasing number of studies that have demonstrated the presence of senescence in wild populations of birds (Newton and Rothery 1997; Loison *et al.* 1999; Gaillard *et al.* 2004; McDonald *et al.* 1996; Pugsek *et al.* 1995), mammals (Loison *et al.* 1999), and fish (Reznick *et al.* 2004). However, a paucity of studies exists that explore the ecological consequences of senescence, particularly the interactive effects between aging and natural disturbance (Williams *et al.* 2006).

Sources of mortality in individuals of wild populations can be divided into ‘intrinsic’ mortality, which results from aging-related factors (e.g. cancer, stroke, cardiovascular failure), and ‘extrinsic’ mortality, which results from factors external to the organism (e.g. extreme weather, predation (Abrams 1993). Condition-dependent mortality may occur when there is an interaction between ageing-related factors and external stressors (Abrams 1993). Therefore, extrinsic mortality, which is truly independent of age, is differentiated from condition-dependent mortality, in which external factors adversely affect one age cohort more than another. In general, wild populations are exposed to higher levels of external stressors than captive

populations (Ricklefs, 2000), thus wild populations may face greater risks of both extrinsic and condition-dependent mortality. Although several authors have hypothesized that condition-dependent mortality is pervasive in natural systems, few studies have provided empirical evidence showing that senescent individuals of wild avian populations become more vulnerable to environmental stressors as they age (Williams *et al.* 2006). In fact, earlier studies provided evidence to the contrary (Ricklefs 2000; Ricklefs and Scheuerlein 2001; Coulson and Fairweather 2001), which supported the hypothesis that senescence in survival of wild avian populations is driven by catastrophic “intrinsic causes of death that kill independently of the external environment” implying that birds in wild populations “...do not become more vulnerable to extrinsic mortality factors with increasing age” (Ricklefs 2000; Ricklefs 2008). The intent of this study is not to separate the intrinsic and extrinsic causes of mortality, but rather to identify the interaction phenomenon, termed as condition-dependent mortality, in a wild avian population.

The Snail Kite (*Rhostrhamus sociabilis plumbeus*) population in Florida provides an excellent opportunity to evaluate hypotheses related to senescence and condition-dependent mortality in a natural context. The Snail Kite is an endangered species whose range is limited to the remaining freshwater wetlands of central and southern Florida (Kitchens *et al.* 2002). A long-term monitoring study of Snail Kite demography and movement, which includes marking birds with individual alpha-numeric bands, has been ongoing since 1992 (Martin *et al.* 2007a), and other less intensive studies that also involved marking individuals date back to the mid-1970s (Bennetts *et al.* 1999). The Snail Kite is a long-lived species, with early studies discovering that Snail Kites could live and reproduce up to at least 18 years of age; however only a small number of such old individuals were identified (Bennetts and Kitchens 1997). Some of these same

individuals have now been re-sighted at age 25. Obtaining an adequate sample size of older individuals is commonly reported to be the limiting factor when testing for the presence of actuarial senescence in wild populations (Nichols *et al.* 1997; Nussey *et al.* 2008). Until now sufficient data has been lacking to test for age-specificity in Snail Kite survival rates among older individuals (>12 years) compared to prime-aged adults (1-12 years). To obtain a sufficient sample size of known-age individuals in the older age class, we utilized resight data collected since 1992 that included known-age individuals marked as nestlings during intermittent studies from 1976 to 1991 and individuals that were marked during the long-term monitoring study that has been ongoing since 1992. Past studies have shown that adult survival does not change substantially over time except during catastrophic events (Bennetts and Kitchens 1997; Martin *et al.* 2006).

As a dietary specialist, the Snail Kite is dependent upon the availability of its primary food resource, the freshwater Florida apple snail (*Pomacea paludosa*). During droughts, the availability of apple snails to kites decreases (Beissinger and Takekawa 1983; Bennetts and Kitchens 1997), and previous authors have shown that droughts negatively affect Snail Kite survival probabilities (Beissinger 1995; Bennetts and Kitchens 1997; Martin *et al.* 2006). During the period of 2000-2002, the majority of the Snail Kite range in Florida experienced a period of extremely dry conditions, characterized as a drought by Martin *et al.* (2006), who found that apparent survival of adults (> 1 year old) decreased by 16%, while the apparent survival of juvenile Snail Kites (< 1 year old) decreased by 86%; however, these authors only considered two age classes that did not distinguish potential effects on older individuals. This environmental perturbation provides us the opportunity to evaluate the hypothesis of condition-dependent mortality in senescent individuals.

The objectives of our study were two-fold. First, we employed capture-mark-recapture (CMR) methodologies on longitudinal data, to test for age-dependent annual survival among adult Snail Kites. Authors have noted that inadequate sample sizes (Nichols *et al.* 1997) and the effects of individual heterogeneity (Nisbet and Cam 2002) may mask evidence of senescence. In order to address these concerns, we take advantage of a large, longitudinal data set (2,084 individuals, 3,746 re-sights) spanning a 33 year period (1976-2008) from multiple cohorts of a long-lived bird. Second, we used a range-wide drought event, already shown to have a negative effect on Snail Kite survival probabilities (Martin *et al.* 2006), to test for an interactive effect between aging and an environmental disturbance, as evidence of condition-dependent mortality in a naturally occurring population. We predict that the range-wide drought will have a disproportionate effect on the annual survival probabilities of senescent Snail Kites compared to younger adults.

## **Methods**

### **Data Collection and Field Methodology**

Resight data from marked individuals was collected annually from 1992 to 2008 as part of a long-term monitoring project of the Snail Kite subspecies population in Florida, U.S.A. The entire range of the Snail Kite in Florida was systematically searched via airboat during each of the four to six intra-annual survey occasions, and marked individuals were identified using a 15-60x spotting scope. Detailed descriptions of the field methodologies and study site can be found in Bennetts & Kitchens (1997; 1999), Dreitz *et al.* (2002), and Martin *et al.* (2006).

For the purposes of this study, we only included individuals captured and banded as nestlings in our analyses, which limited our sample to known-age Snail Kites. Individuals were banded just prior to fledging (approximately 18-27 days post hatching), using unique alphanumeric colored leg bands which can be easily identified in field with the use of a spotting

scope (Martin *et al.* 2007b). We also included 74 individuals captured and banded as nestlings (149 re-sights) from 1976 to 1991 even though re-sight data for these birds were not available until systematic surveys began in 1992. Of the 74 individuals, 50 survived past age 12 and added to the sample size of the oldest age class (13 years and older). We assumed a 50:50 sex ratio (Bennetts and Kitchens 1997; Martin 2007).

### **Statistical Modeling**

We modeled encounter histories in Program MARK 5.1 (White and Burnham 1999) using extensions of the Cormack-Jolly-Seber (CJS) model for open populations (Cormack 1964; Jolly 1965; Seber 1965; Lebreton *et al.* 1992) which accounted for varying age-classes. The models included parameters for both apparent survival (surviving and returning to the sample area) and detection (the probability that an individual that is alive and in the study area is re-sighted) (Cooch and White 2008).

To include the individuals banded prior to 1992, we fixed detection probabilities to zero for occasions when the population was not sampled (Cooch and White 2008). The model notations and their biological meanings are explained in Tables 2-1, 2-2, and 2-3. Model selection was based on Akaike's Information Criterion adjusted for small sample sizes, AICc (Burnham and Anderson 2002).

### **Annual resight probabilities**

We modeled survival in a step-wise manner, where we first parameterized resighting probability, and then subsequently used the most parsimonious parameterization of resighting probability to further model variation in apparent survival (Nichols *et al.* 1997). To find the most parsimonious model for resight probabilities, we used the general parameterization of survival, which included all possible time and age class specific survival parameters for the period 1976-2008.

As first discussed by Loison *et al.* (1999) and later by Nisbet and Cam (2002) one commonly overlooked source of bias in senescence analyses is related to the theory of age-specific emigration. In other words, the probability of an individual temporarily leaving an area during sampling efforts can be co-linear with age (either increasing or decreasing). To address this potential pitfall, we included models that allowed re-sight probability to vary by time and age-class. Similarly, we included models with drought effects identical to those used to test for age-drought interactions on survival. A comparison of estimates and associated 95% confidence intervals of the drought effects parameters was used to assess whether the resight probability of older individuals decreased as a function of drought. The most parsimonious structure on resight probability was retained for all subsequent modeling of survival. For this reason, descriptions of models in Tables 2-2 and 2-3 do not explicitly list resight probability parameterizations.

Another commonly overlooked phenomenon in senescence analyses is the potential confounding between age-related marker loss and senescence. In other words, markers used to band individuals in the early stages of a study may be more susceptible to deterioration and eventually falling off. Having no direct means for testing or controlling for this hypothesis, we acknowledge this potential confounding in regards to estimates of senescence. Nevertheless, marker loss would not confound estimates of the interaction between drought and senescence, as we have no reason to believe that older individuals would lose their bands at a higher rate than prime-aged individuals during droughts.

### **Age specificity and senescent declines in survival probabilities**

Models which incorporate mathematical functions that make specific assumptions about the declines in survival (increase in mortality) with age are used as a means to test hypotheses about senescence (Nichols *et al.* 1997; Loison *et al.* 1999; Ricklefs and Scheuerlein 2002; Gaillard *et al.* 2004). The Weibull, a power function which assumes an additive effect of

mortality, has been described as the most appropriate function for modeling senescent trends in avian populations (Ricklefs and Scheuerlein 2001). Therefore, as a formal test for a senescent decline in the survival probabilities within the Snail Kite population we compared a model which constrained survival to be a function of a two parameter Weibull model (Gaillard *et al.* 2004) against a model with constant adult survival. Models which allowed the Weibull to start at different ages were included to test for the onset of senescence. Model averaged survival estimates were used to test for age-dependent adult survival.

In addition, a set of models were also developed that made no assumptions about the rate that survival changes with age. Understanding the age structure underlining vital rates such as survival probabilities provides important information for modeling population dynamics (Caswell 2001; Charlesworth 1980). Thus, we tested for age class-specific survival probabilities by comparing models which constrained apparent survival to 2 and 3 age classes against a fully age-dependent model and a model for which adult survival is held constant for all ages (Table 2-2) (Loison *et al.* 1999; Gaillard *et al.* 2004).

### **Age class-specific drought effects**

Hypotheses regarding the potential effects of the 2000-2002 drought on the survival probabilities of the oldest age classes of Snail Kites were tested using the age-class structure of the most parsimonious model determined by the aforementioned test of age specificity in survival probabilities. Models were compared which constrained age-class specific survival by 2 time periods (drought and non-drought). The years 2000-2002 were modeled as a 2 parameter time-specific drought effect. Testing for age-specific drought effects, we compared models with no drought effects against models with additive and interactive drought-age class interactions. The additive model assumed the effect of drought to be equal for both adult age classes (years 1-12; and 13+). We compared this model to an interactive, or condition-dependent, model which

included an additional drought parameter assigned to the oldest age class. Beyond model selection, we assessed the significance of this additional parameter as further evidence to either support or reject the hypothesis that the drought had greater negative consequences on the older individuals than compared to the prime-aged individuals.

### **Goodness of Fit**

To assess goodness of fit we utilized the median c-hat approach (Cooch and White 2008) on a subset of the data which included only the years 1992-2008, during which there was a continuous search effort, using the model  $(\Phi(t)1(.))^{2-3}, (.)^4; p(t)1(t)^{2-4}$ . The approach yielded a  $\hat{c} < 1$ . Therefore there was no need to adjust for over-dispersion.

## **Results**

### **Time and Age Class-Specific Resight Probabilities**

The most parsimonious model was one that allowed detection to vary by time, yet differ between age classes 1 and (2-3), which correspond to ages 0 and 1+ respectively (Table 2-1, model 1). Models which included a drought effect for years 2000-2002 on detection probabilities scored high AICc values and were therefore poorly supported by the data. However, models that allowed detection to vary by time performed consistently better than models which assumed detection to be constant over time (Table 2-1). Model (4) which constrained the detection of the oldest age class to a 2 parameter drought effect, did not perform well in model selection. Additionally, the estimated coefficient for the drought effect in model (4) indicated that drought did not have a significant effect on the detection of the oldest individuals ( $\beta_{\text{DROUGHT}} = -0.6435$ , 95% CI = -1.52 to 0.239). Based on the results of the analysis, we used the two age class, fully time-dependent model parameterization of detection probabilities without drought effects for all subsequent tests on these data.

### **Decreasing Survival Probabilities with Age**

Consistent with general avian life-history theory, we found a decrease in survival probabilities beginning later in life, in this case at age 13 (Table 2-2) (Figures 1 and 2). The most parsimonious model constrained survival probabilities as a function of the Weibull curve (Table 2-2, model 1), and model selection indicated that this model fit the data better than discrete age-class models. Consequently, model averaged survival estimates were strongly influenced by the model that incorporated the Weibull function, as it received 78.7 percent of the AICc weight (Table 2-2, Figure 2-2). However, important differences among discrete age-class models were also elucidated during model selection. Namely, discrete age-class models that allowed survival to vary between prime-aged and senescent adults (Table 2-2, models 2 and 3) out-performed those that held adult survival constant (Table 2-2, models 5, 6, and 10). Furthermore, models that assumed unique survival parameters for each age (in years) (Table 2-2, models 7, 8, and 9) were all poorly supported by the data (Table 2-2).

### **Evidence of Age Class-Drought Interaction**

Generally, models which included drought effects outperformed those without drought effects (Table 2-3). The best fit model (Phi (t) 1 DE\*2-3,4) includes an additional interactive drought parameter for the oldest age class (13+ years). This model received 72.4 % of the AICc weight versus 24.6 % model weight which was given to the additive drought model. Analyzing the beta parameter of the interaction variable reveals a significantly negative interactive relationship between drought and old age ( $\beta_{\text{DROUGHTXOLDAGE}} = -0.4727$ , 95% CI = -0.9255 to -0.0199). Model averaged estimates for both adult age classes during drought and non-drought years are presented in Figure 3.

## Discussion

The present study offers two major findings. First, we found evidence of senescence in survival using both the point estimates of differing adult age classes (Figure 1) and by using a traditional survival function, the Weibull model, as a direct test for a senescent decline in survival probabilities in a naturally occurring avian population. Secondly, we found evidence that the survival of older individuals was considerably lower than younger adults during a drought. This result suggests an interaction between age dependent survival probabilities in older age classes and natural disturbance events, one form of condition-dependent mortality.

In the past, comparative analyses have yielded results which allow evolutionary biologists to make generalizations about the pervasiveness of senescence among taxonomic groups (Jones *et al.* 2008; Holmes and Austad 1995; Ricklefs and Scheuerlein 2001). When compared to mammals, birds are considered to have relatively slower rates of aging which are expressed later in their lifetime. For some avian populations, individuals simply do not live long enough to express senescent declines in survival. A relatively large data set of a long-lived species, such as the Snail Kite, provides investigators with the opportunity to test for senescent declines in survival probabilities. However, the lack of a consensus in the results of similar longitudinal studies on senescence in wild avian populations suggests that additional sources of variation exist which determine the degree to which senescence is expressed beyond that of taxonomic classes (Jones *et al.* 2008). In fact, our results suggest that the expression of senescence may also be dependent upon the ecological interactions (i.e. drought) specific to a population of interest.

Sudden environmental perturbations (e.g. hurricanes, droughts, freezes) undoubtedly have fitness consequences for individuals in wild populations. Depending on the resiliency of the population, these consequences can have widespread, long-lasting impacts on its demography. The strong relationship between Snail Kite life history and the current water levels in its critical

habitat, through its dependency on the freshwater apple snail as its sole food resource, provides an opportunity to test hypotheses about the effects of natural disturbances on senescence. To date, few studies (e.g. Waide 1991; Swilling *et al.* 1998; Labisky *et al.* 1999; Jones *et al.* 2001; Gaillard *et al.* 2003) have addressed the effects of environmental disturbances on the demography of vertebrate populations. Of these studies, only Gaillard *et al.* (2003) directly tested hypotheses regarding disproportional impacts on senescent versus prime-aged adults. For their analysis, they utilized CMR data to assess the impacts of a hurricane on the survival and reproduction of a roe deer population in Europe. No evidence was found to suggest that the extreme weather event had greater impacts on the senescent cohort than to the rest of the adult population.

Our results suggest that an increasing vulnerability to extrinsic causes of mortality may be an important causal factor of ageing related mortality in wild avian populations. Aging related mortality in avian populations may indeed be a result of increasing vulnerability to catastrophic intrinsic mortality (Ricklefs and Scheuerlein 2001; Coulson and Fairweather 2001). However, according to our data, environmental disturbances exacerbate an individual's vulnerability to these catastrophic events. Our results provide empirical evidence of condition-dependent mortality in a naturally occurring avian population.

### **Conservation Implications**

In addition to its implications regarding our understanding of aging processes, our study emphasizes the importance of examining the interaction between senescence and natural disturbance. Indeed, we found evidence that survival of older individuals was considerably lower than younger adults during the drought. The magnitude of the difference among these estimates suggests that future estimates of population growth rate and probabilities of quasi-extinction should account for these sources of variation (Beissinger 1995; Martin *et al.* 2009). In addition,

given the growing interest in applying decision theory to solve management problems (Bakker and Doak 2009; Martin *et al.* 2009) and given the fact that the Snail Kite has been selected as one of the performance measures of Everglades restoration, estimates accounting for senescence and condition-dependent mortality may contribute to the improvement of existing management models (Mooij *et al.* 2002).

Table 2-1. CMR models expressing hypotheses about annual, re-sight probabilities (detection) of Snail Kites in Florida, 1976-2008. Models used one single parameterization to constrain survival by age class and time.

	Model	AICc	Delta AICc	AICc Weight	# Par	Biological Hypothesis
(1)	p (t)1 (t)2-3	9567.967	0	0.99394	107	Detection varies by time and ages (0), (1+).
(2)	p (t)1 (t)2 (t)3 (t)4	9578.2131	10.2461	0.00592	125	Detection varies by time and ages (0), (1-4), (5-12), (13+)
(3)	p (t)1 (t)2 (t)3	9586.131	18.164	0.00011	122	Detection varies by time and ages (0), (1-12), (13+)
(4)	p (t)1 (t)2-3 (DE)4	9589.3536	21.3866	0.00002	109	Detection varies by time for ages (0), (1-12); drought effect for ages (13+)
(5)	p (t)1-3	9604.0352	36.0682	0	91	Detection varies by time only
(6)	p (.)1 (t)2-3	9617.9748	50.0078	0	92	Detection is constant for age (0) and varies by time for ages (1+)
(7)	p (t)1 (.)2-3	9696.4237	128.4567	0	92	Detection varies by time for age (0) and is constant for ages (1+)
(8)	p (.)1 (.)2 (.)3 (.)4	9710.4357	142.4687	0	79	Detection is constant but different between ages (0), (1-4), (5-12), (13+)
(9)	p (.)1 (DE)2-3	9739.7377	171.7707	0	78	Detection is constant for age (0); drought effect for ages (1+)
(10)	p (.)1 (.)2-3	9740.3208	172.3538	0	77	Detection is constant but different between ages (0) and (1+)
(11)	p (DE)1 (DE)2-3	9740.6865	172.7195	0	79	Separate drought effects for ages (0) and (1+)
(12)	p (.)1 (.)2 (.)3	9742.393	174.426	0	78	Detection is constant but different between ages (0), (1-12), and (13+)

Table 2-2. CMR models describing age class-specific, apparent annual survival probabilities of Snail Kites banded in Florida, 1976-2008. Age classes were determined a priori using biologically relevant criteria (see Methods).

	Model	AICc	Delta AICc	AICc Weight	# Par	Biological Hypothesis
(1)	Phi (.)1 (.)2-3 W~(4)	9990.96	0	0.78712	38	Survival is constant and different between ages (0), (1-12); survival is function of Weibull for ages (13+)
(2)	Phi (.)1 (.)2-3 (.)4	9995.16	4.20	0.09642	37	Survival is constant yet different between ages (0), (1-12), (13+)
(3)	Phi (.)1 (.)2 (.)3 (.)4	9996.46	5.50	0.05030	38	Survival is constant yet different between ages (0), (1-4), (5-12), (13+)
(4)	Phi (.)1 W~2-4	9996.53	5.57	0.04850	37	Survival is constant for age (0); survival is function of Weibull for ages (1+)
(5)	Phi (.)1 (.)2 (.)3-4	9999.55	8.59	0.01074	37	Survival is constant yet different between ages (0), (1-4), (5+)
(6)	Phi (.)1 (.)2-4	10000.48	9.52	0.00673	36	Survival is constant yet different between ages (0), (1+)
(7)	Phi (.)1 (.)2-3 (Jones <i>et al.</i> ) <sup>4</sup>	10007.76	16.80	0.00018	49	Survival is constant yet different between ages (0), (1-12); survival is fully age dependent beginning with age 13, (13-26)
(8)	Phi (.)1-32 (full- age)	10014.22	23.27	0.00001	60	Survival varies with all ages
(9)	Phi W~(full age)	10075.26	84.30	0.00000	36	Survival is function of Weibull starting at age (0)
(10)	Phi (.)1-4	10241.78	250.82	0.00000	35	Survival is constant for all ages

Table 2-3. CMR models expressing hypotheses pertaining to age class-specific drought effects on adult Snail Kites.

Model	AICc	Delta AICc	AICc Weight	# Par	Biological Hypothesis
(1) Phi (t)1 (DE* 2-3, 4)	9621.03	0	0.724	62	Time-specific survival for age class 1; interactive drought/age class effect
(2) Phi (t)1 (DE+ 2-3, 4)	9622.96	1.93	0.276	61	Time-specific survival for age class 1; additive drought/age class effect
(3) Phi (t)1 (DE)2-3 (.)4	9648.00	26.98	0	61	Time-specific survival for age class 1; drought effect for age class (2-3); constant survival for age class 4
(4) Phi (t)1 (.)2-3 (DE)4	9746.88	125.85	0	61	Time-specific survival for age class 1; drought effect for age class 4; constant survival for age class (2-3)
(5) Phi (t)1 (.)2-3 (.)4	9764.33	143.30	0	60	Time-specific survival for age class 1; constant but different survival for age classes (2-3) and 4

Notes: Drought effects are 2-parameter time effects combining drought (2000-2001) and non-drought years (1992-1999, 2002-2007). Age class structure taken from model (2) in Table 2. (see Table 2 for age class descriptions)

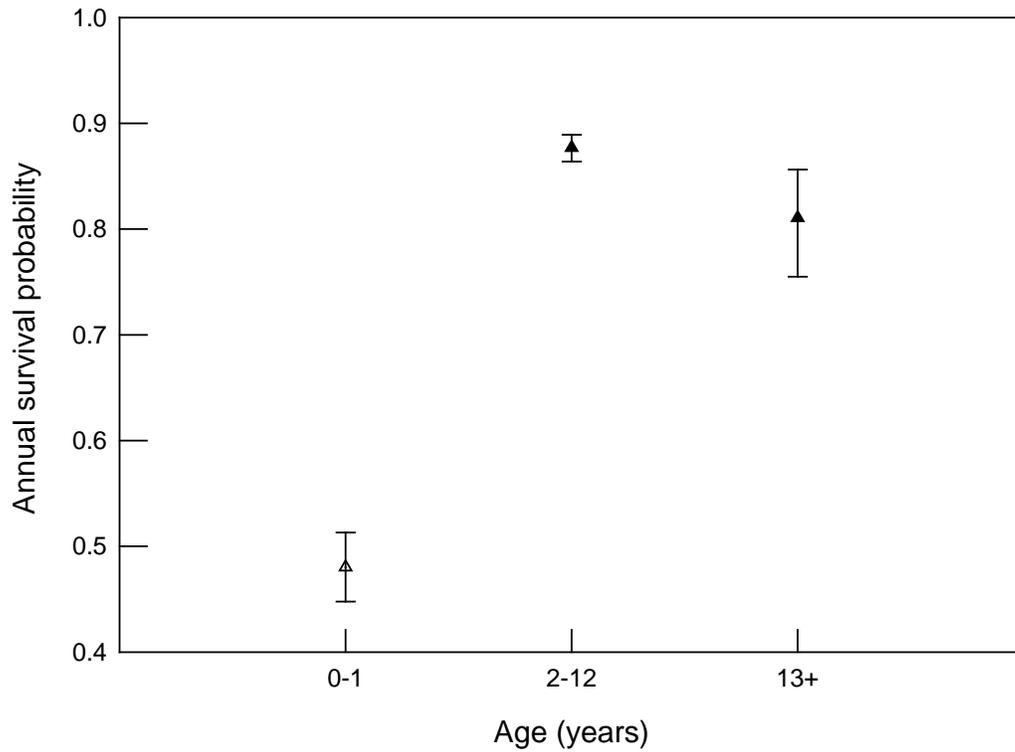


Figure 2-1. Age-class specific apparent annual range-wide survival estimates for the Snail Kite population in Florida, USA. Estimates are from the best fit age-class model (Table 2, model 2). The non-overlapping error bars (95% CI) for the declining estimates of the two adult age classes (2-12 years and 13+ years) suggest senescence in survival beginning with 13 years of age.

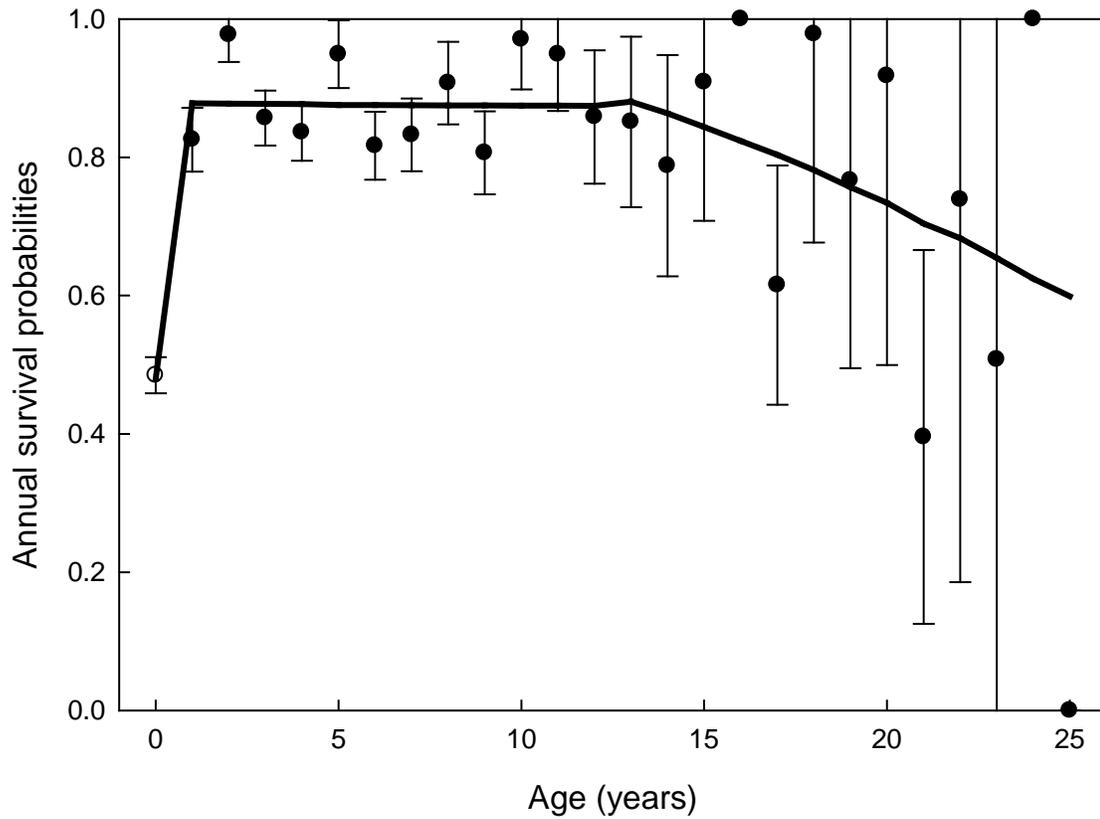


Figure 2-2. Annual survival probabilities as a function of age (●) with standard errors, estimated from the fully age dependent model. Solid line represents estimates from model incorporating the Weibull function beginning at age 13 ( $\Phi(.1(.).2-3 W\sim(4)$ ).

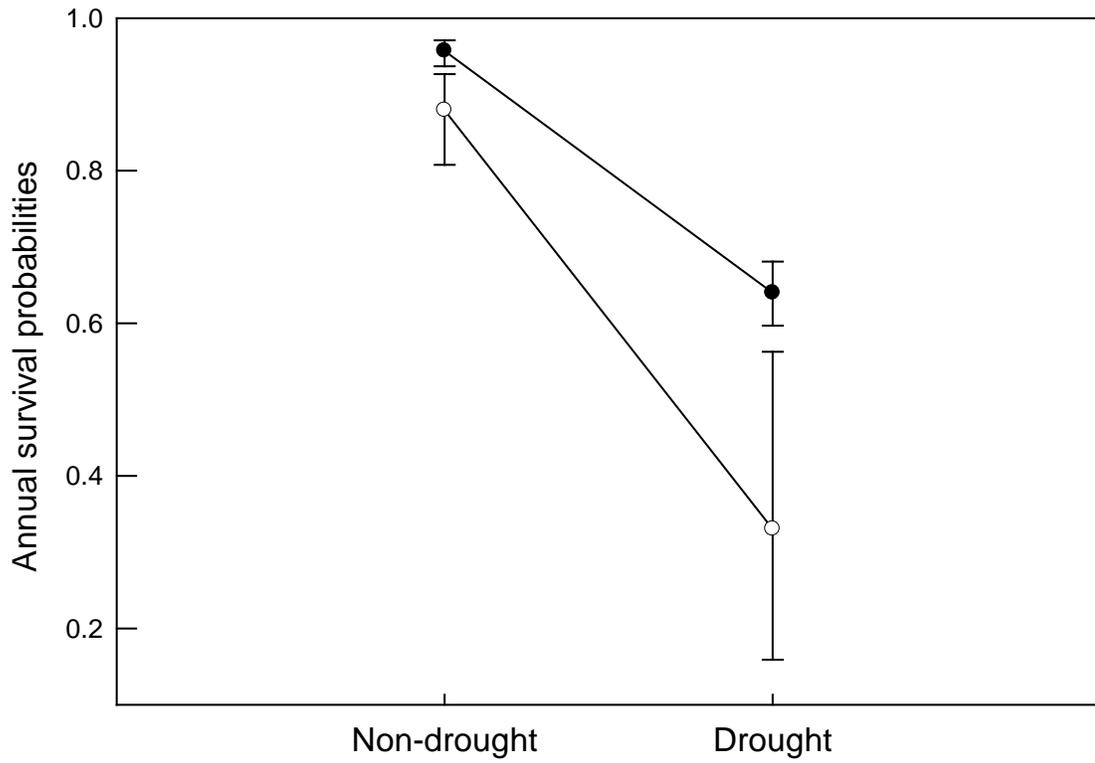


Figure 2-3. Model averaged estimates and 95% CI (Table 3) of age-class specific apparent annual survival for the two adult Snail Kite age classes (2-12 years, “●”) and (13+ years, “○”) during periods of drought (2000 to 2002) and non-drought (1992-1999; 2003-2008).

CHAPTER 3  
EFFECTS OF AGE AND THE ENVIRONMENT ON SNAIL KITE BREEDING  
PROBABILITIES: TESTING FOR COSTS OF REPRODUCTION

**Introduction**

Identifying sources of variation within reproductive vital rates has been a central theme in studies of life-history theory, population ecology, and conservation biology (i.e. Williams 1957; Charlesworth 1980; Gaillard *et al.* 1998). Vital rates, such as breeding probabilities, or projected proportions of individuals attempting to breed are commonly used in stage or age based matrix modeling procedures (Caswell 2001; Fujiwara and Caswell 2002). Factors influencing these rates (i.e. age-structure and the environment) can be important determinants of population dynamics, which make them of great interest to both wildlife demographers and conservation biologists. Changes in the proportion of individuals attempting to breed in a small population can have pronounced effects on its population dynamics. When available, precise estimates should be used to make predictions of population growth rates (Coulson *et al.* 2001). However, this requirement is rarely met, as producing precise estimates can require long-term datasets and labor intensive field sampling. These restrictions can result in researchers having to utilize estimates based on theoretical models and small sample sizes for use in management tools (i.e. population viability analysis) (Beissinger 1995). This is especially true for endangered species whose demographic data is typically limiting. Therefore, long-term datasets that allow estimation of breeding probabilities, especially those that exist for small populations, may not only improve our general understanding of population dynamics and evolutionary ecology, but also provide robust estimates of vital rates for conservation practitioners. The urgency for an iterative process which incorporates the re-examination of demographic parameters using long-term datasets increases when confronted with a federally endangered species whose population has recently undergone

dramatic declines, (Ralls *et al.* 2002) as is the case for the Snail Kite (*Rostrhamus sociabilis plumbeus*) (Figure 3-1), in Florida, USA (Cattau *et al.* 2008).

The Snail Kite is a long-lived species with individuals recently observed nesting and successfully reproducing up to 18 years of age (this work). Its life-history patterns have been described with relatively high, stable adult survival, variable juvenile survival, and low annual fecundity rates (Nichols *et al.* 1980). These patterns are generally characteristic for populations whose reproductive output is closely tied to environmental stochasticity (Schaffer 1974; Nichols *et al.* 1980). Although Snail Kite reproductive output is thought to be strongly affected by local hydrology and thus resource availability (Beissinger 1995; Bennetts and Kitchens 1997; Martin, 2007; Bennetts 1998a), very little is known about the degree to which reproductive effort varies in response to these same factors.

From our knowledge, Bennetts *et al.* (1998a) has been the only other attempt to estimate Snail Kite breeding proportions from empirical data. Earlier estimates relied on anecdotal observations and theoretical Snail Kite models (Nichols *et al.* 1980; Beissinger 1995) which defined a breeding attempt to begin with nest construction. Bennetts *et al.* (1998) defined Snail Kite breeding attempts in the context of estimating nest success. Because nest building is a part of male courtship (Beissinger 1988) and one male may build several nests prior to establishing a pair bond (Bennetts *et al.* 1998), including uninitiated nests (those found before egg laying) would produce biased estimates of nest success. Therefore, Bennetts *et al.* (1998) considered Snail Kite breeding attempts to occur only once eggs had been laid.

For the purpose of this study, we define ‘attempting to breed’ as a decision process with a behavioral outcome. An individual begins to re-allocate energetic resources for breeding long before egg-laying is initiated. Even before pair bonds are established, an individual must make

the decision to breed. As Snail Kites must cope with a limited energetic resource, energy that is invested in courtship (e.g. nest construction) limits the time and effort available to forage for one's own survival. This is especially relevant for Snail Kites who may initiate courtship and build nests for as many as five separate females (Bennetts *et al.* 1998).

The definition for a breeding attempt used in this study is a more sensitive indicator of the decision to initiate breeding behavior, which can be viewed as the trade-off between allocating resources for breeding or maximizing self survival (Stearns 1989). Evolutionarily, this process and its outcomes are influenced by the costs of reproduction on survival and future breeding potential, that are thought to vary with age (Sedinger *et al.* 2001) and environmental conditions (resource availability) (Hecht Orzack and Tuljapurkar 2001). In addition to parental care and nest success, breeding probabilities can be a necessary component for assessing reproductive effort (Nichols *et al.* 1994). In this case, breeding probabilities provide information about behavioral responses to environmental conditions; information that cannot be assessed when only considering parameters of reproductive output.

Models that generate breeding probabilities can be used to test hypotheses about the costs of reproduction (Nichols *et al.* 1994; Orell and Belda 2002) as well as evolutionary ecology (Nichols and Kendall 1995; Cam and Monnat 2000). A thorough understanding of these relationships is important for testing hypotheses on how population dynamics will be affected by management activities, especially when efforts are to be focused on improving habitat to stimulate reproduction. Empirical studies which test for sources of variation in Snail Kite breeding probabilities such as age structure and environmental effects are sorely lacking. And in general, few studies have assessed breeding probabilities that account for the misclassification of breeding status assignment, an assumption frequently violated when states are based on field

observations. In this study, we take advantage of a long-term dataset (1976-2009) to assess the effects of age and the environment on the costs of reproduction in Snail Kites, through the use of a recent development in robust multi-state mark-recapture models that adjusts for misclassification bias.

### **Age Effects**

Most avian populations exhibit age-specific reproduction. These patterns typically begin with relatively low probabilities of breeding for young or inexperienced individuals, until their first attempt (Wooller and Coulson 1977; Weimerskirch 1992; Cezilly *et al.* 1996; Sedinger *et al.* 2001). In longer-lived species, this period of low breeding probability tends to be prolonged (Bell 1980), as seen in wandering albatross (Weimerskirch 1992) and Greater Snow Geese (Reed *et al.* 2003). Breeding probabilities and reproductive performance increase with age (Cam and Monnat 2000; Reed *et al.* 2003) and experience until they reach a plateau that corresponds to prime aged adults, when individuals can maximize reproductive effort during peak individual fitness. In some populations, this plateau is followed by a senescent trend in reproductive output, resulting from physical deterioration or decreased foraging ability (Catry *et al.* 2006); as well as a decline in an individual's breeding probability (Cam *et al.* 2002).

Age-specific reproductive patterns have been attributed to either direct or indirect costs of reproduction on survival and future breeding, resulting in a life-history trade-off. Studies suggest that long-lived species tend to maximize their lifetime reproductive success by restricting annual reproductive efforts to levels below that of their full potential (Stearns 1976), especially during early life stages when fitness and breeding experience are low (Ricklefs 1977; Saether *et al.* 1993). This ensures that individuals minimize the direct cost of reproduction on survival for any given season, which results in sustained high adult survival, thus increasing their chances of

future breeding events and maximizing their lifetime reproductive success (“restraint” hypothesis) (Curio 1988; Charlesworth 1980).

We use Snail Kite age-classes (Chapter 2) to model the effects of age on breeding probabilities and test for age-dependent costs of reproduction on survival. Given the relatively low rate of juvenile survival and the occurrence of actuarial senescence within the Snail Kite population (Chapter 2) we predict an age-dependent pattern of breeding probabilities similar to that described above.

### **Environmental Effects**

Although the observed patterns would differ, it is reasonable for one to expect that reproductive restraint may also occur when populations of long-lived species are subjected to harsh breeding environments. When environmental conditions result in resource depletion, young breeders may delay breeding (Tuljapurkar 1990) and experienced individuals may skip breeding until conditions improve (Erikstad *et al.* 1998). For those individuals who do not restrict reproduction in response to harsh environments, one would expect direct costs of reproduction on survival and future breeding attempts as a potential trade off (Williams 1966). A lack of consensus exists among the few empirical studies that have tested for environmental effects on the costs of reproduction as it relates to breeding and survival probabilities, especially when survival is known to be age-dependent (Chapter 3). For example, although snow cover affected the reproductive output (i.e. breeding propensity, nest success) of Greater Snow Geese, no evidence was found to support that it affected the breeding probabilities of first time breeders (Reed *et al.* 2003). In contrast, breeding experience and sea surface height, as an index of available food resources, were shown to have effects on both their survival and breeding probabilities of Blue Petrels (Barbraud and Weimerskirch 2005).

Similarly, when environments remain permanently varied, and unpredictable, some theoretical models suggest that reproductive effort may become ‘fixed’ at low levels (Stearns 1977; Hastings and Caswell 1979). At this point only the fittest individuals may attempt to breed.

If Snail Kites are required to reach a physiological threshold before they consider allocating resources for breeding, quality environmental conditions with high availability of their primary food resource, the freshwater Florida apple snail (*Pomacea paludosa*), must exist during the time leading up to breeding. As with the case for many endangered species, habitat loss and degradation have played significant roles in its population decline (Martin *et al.* 2008). While recent widespread droughts (2000-2001 and 2007) have negatively affected adult survival by forcing kites to make long distance movements in search of more suitable habitat (Martin *et al.* 2006), the conversion of vegetative communities in response to water management (Zweig and Kitchens 2008) has greatly reduced the reproductive potential of primary Snail Kite breeding areas (Martin *et al.* 2008). As a result, recent reproductive distribution has shifted away from the traditionally most productive wetland units (Water Conservation Area 3A) (Figure 3-2). This shift in spatial distribution corresponds temporally to a decrease in adult fertility and juvenile recruitment (Cattau *et al.* 2008). Based on these trends, we hypothesize that the total breeding capacity of the Snail Kite’s range has decreased, and as a result we predict that range-wide breeding probabilities have decreased over time as well.

As Snail Kites rarely nest over less than 20 cm of water (Sykes 1987) and dry conditions tend to cause apple snails to aestivate (Kushlan 1975) effectively decreasing resource availability to foraging Snail Kites, we also predict a decrease in breeding probabilities during low water years, such as those characterized as droughts by Martin (2007). Because Snail Kite survival is known to decrease during drought years (Martin 2007), we predict that kites nesting during

drought years will have even lower survival than those that do not and will be less likely to nest in the following season.

## **Objectives**

Our first objective was to test for direct and delayed costs of reproduction on Snail Kite survival and breeding probabilities. Then, by assessing how aging, drought, and habitat degradation affect these costs, we attempt to describe the life-time reproductive strategy of the Snail Kite. The proportions of breeding Snail Kites are estimated directly for the years 1996 to 1999 and compared against theoretically derived estimates. The results are intended for use in future conservation tools, such as comparative population viability analysis.

## **Methods**

### **Field Methods and Data Collection**

Snail Kites were banded just prior to fledging (18-27 days post hatching) from 1976 through 2008. The entire Snail Kite breeding range (Figure 3-2) was systematically surveyed via airboat during each of the four to six intra-annual survey occasions from 1992 through 2009, as part of a long-term monitoring project of the Snail Kite subspecies population in Florida, U.S.A. (Bennetts & Kitchens 1997; Dreitz *et al.* 2002; Martin *et al.* 2006). Beginning in 1996, information on a banded individual's breeding status was collected. Corresponding to the height of the Snail Kite breeding season, surveys were conducted between February 28th and June 30th annually, in which it is assumed that all individuals return to breeding areas. Individuals were identified by alphanumeric colored leg bands which can be easily identified in field with the use of a spotting scope (Martin *et al.* 2007b). Encounter histories were generated in the style of the multistate robust design (MSRD).

An individual was recorded as attempting to breed if they were observed actively displaying breeding, nesting, or courtship behavior (Table 3-1). For the purposes of this study,

we only included individuals captured and banded as nestlings in our analyses, which limited our sample to known-age Snail Kites (2,197 individuals, and 2,577 recaptures), but allowed for tests of age-specific breeding probabilities.

It is important to note that the Snail Kite population in Florida is considered to be a closed population. Currently, no evidence exists to suggest that individuals actively emigrate to other Snail Kite populations (i.e. Cuba). Thus the inferences made can be applied at the population level, as the areas surveyed incorporate the extent of the population's breeding habitat.

### **Statistical Modeling**

Breeding probabilities can be viewed as either the probability that an individual will transition into a specific breeding state conditional on its current breeding status, or as a projected proportion of breeding individuals within a population, unconditional to prior breeding status. The breeding probability of most iteroparous vertebrate populations is best described through the use of long-term mark-recapture data implemented into a multistate model that incorporates some variation of at least two states, either breeding or non-breeding (Nichols *et al.* 1994). Model developments have provided researchers with the capacity to account for less than perfect recapture rates (Nichols *et al.* 1994) and more recently, unobservable states (for a review, *see* Kendall 2004). For the purposes of this study we utilize a full likelihood version of the multi-state mark-recapture model (Schwarz *et al.* 1993; Brownie *et al.* 1993) in the framework of the closed robust design (CRD) (Pollock 1982) that adjusts for bias attributed to the misclassification of individuals into a particular breeding state (Kendall *et al.* 2003; 2004, unpublished manuscript). The model is a variation of Kendall *et al.* (2003; 2004) that uses individual encounter histories. As in the CRD, multiple secondary sampling occasions (range-wide surveys) which are conducted within each primary session (years) are used to estimate the probability of detecting an individual ( $p_{ij}^B$  or  $p_{ij}^N$ ) and the probability of detecting an individual is

breeding, given you detected the individual ( $\delta_{ij}^B$ ) separately (Kendall 2004). Similar to the original CRD, sub-sampling parameters are then used to derive detection probabilities for the primary sessions. The expanded number of parameters required in this model type demands a significant amount of data. In order to avoid problems with parameter estimation we collapsed surveys down to two intra-annual efforts. The assumptions of this model are similar to those of the original CRD (Pollock 1982). Kendall (1999) outlines specific cases when these assumptions can be relaxed without introducing additional bias. To meet the assumptions of geographic and demographic closure within primary sessions, the end of the first sub-sampling period for each year occurs after all individuals have come into the sampling area (Kendall 1999).

Adjusting for misclassification bias is important when an individual's state is determined based on field observations and the assignment of an individual to a biological state is less than perfect. For example, in this study the breeding state of an adult Snail Kite is determined through field observations based on Snail Kite behavior. Individuals observed demonstrating reproductive behavior can be unambiguously classified as attempting to breed. While individuals that are not exhibiting these behaviors are classified as non-breeding, but in reality may in fact be breeding or non-breeding. This scenario is not unlike the one presented in Kendall *et al.* (2004) in which adult female manatees are designated as breeders with complete accuracy due to the presence of an attendant calf, while females without calves are apparent non-breeders (Kendall *et al.* 2004). In both cases, not accounting for misclassified state assignments can produce breeding probabilities which tend to be biased low and underestimate the difference in survival probabilities between breeding states (Kendall *et al.* 2003; 2004) (i.e. the cost of reproduction on survival, Nichols 1994).

The misclassification models treat individuals whose breeding status is not known with complete accuracy as a mixture. The likelihood accounts for the probabilities associated with both breeding states. In a scenario with two breeding states, breeder and non-breeder, where misclassification is unidirectional, (i.e. only individuals observed displaying breeding behavior are known to be attempting to breed with certainty) the mixture is comprised of both non-breeders and breeders who were not actively exhibiting breeding behavior when they were observed in the field. For complete model explanations see Kendall *et al.* (2003; 2004) and Kendall (2004).

For the purpose of including age structure in the analysis we used only the encounter histories generated by Snail Kites banded as nestlings. As kites are not known to breed until at least nine months post fledging, all individuals were assigned to a “young” state upon their initial capture (banding). Biologically, the null model assumes stage-based reproduction, where young are not capable of breeding until the onset of their first breeding season, at which time all young from the previous year become either breeding or non-breeding with the same probability as all other adults. For modeling procedures, we fixed the probability of a “young” individual remaining as a young to equal zero, and the detection of this state to equal one for all subsampling and primary sessions. Because it is not possible for breeders or non-breeders to become young, we fixed these transition probabilities to equal zero as well. Additionally, since the breeding state of young is known with complete accuracy, we were also able to fix the probability of ascertaining its state ( $\delta_{ij}^J = 1$ ). Table 3-2 provides an example of the encounter histories used and their associated probabilities modified from those presented in Kendall (2004). Program MARK 5.1 (White and Burnham 1999) was used for model implementation.

A set of candidate models was developed to test hypotheses on the effects of age and the environment (drought and long-term habitat degradation) on Snail Kite survival ( $S$ ) and breeding state transitions ( $\Psi$ ) (Tables 3-3 and 3-4). Hypotheses for age class-specific breeding probabilities were adopted from previous analyses which indicated age structure in survival probabilities, and specifically senescent declines in adult survival beginning at age 13 (Chapter 2). The models in Table 3-3 include both “full age” (i.e. one parameter for each age) and parameters for two, three, and four age classes (AC) adopted from Chapter 2. In addition to ageing effects, Table 3-4 includes models which address hypotheses about the effects of drought and habitat degradation. For these models, notation where ‘DE’ = Drought Effects; parameter/s were used to distinguish between specified drought years and non-drought years, ‘PDE’ = Post Prought Effect; parameter/s were used to distinguish between the year after a drought occurred (2002 and 2008 only) and other years, ‘DP99’ = Degradation Period Effects beginning in 1999; one parameter was used for years 1996-1998; one parameter was used for years 1999-2009, and ‘AC’ = age class; when survival ( $S$ ) or state transitions ( $\Psi$ ) varied by specified age classes. When ‘DP99’ and ‘DE’ were used in combination for the same model, drought years after 1999 were not included as ‘post degradation’ years but were kept as drought years. Refer to Tables 3-3 and 3-4 for complete model descriptions and their associated biological hypotheses.

AICc model selection was used to compare the fit between models and thus the relative influence of age, drought (‘DE’), and habitat degradation (‘DP99’) on the transition probabilities between breeder states (young, breeder, and non-breeder). Model estimates were used to assess the costs of reproduction on survival and the probability of attempting to breed during and one year after a harsh environmental disturbance (i.e. droughts and habitat degradation). It is important to note that the costs of reproduction to Snail Kites could be realized in demographic

parameters beyond the scope of this study. For example, we did not test for responses of body condition, clutch size, or long term breeding probabilities to increased reproductive effort. Testing for these relationships may provide additional insight into the actual mechanisms driving the costs of reproduction, such as energy allocation or long-term life history trade-offs.

Along with the estimation of breeding and survival probabilities, the model we used also directly estimates the proportions of individuals in each state, at a certain time, assuming that individuals from all states are equally likely to be in the study area (Kendall 2004). Model averaging was used to obtain estimates of breeding proportions for each year, which we applied to robust estimates of population size obtained from an earlier analysis (Martin 2006; Cattau *et al.* 2008) and calculated the annual number of Snail Kites breeding from 1998 through 2008.

## **Results**

### **Aging Effects**

Models that ignored environmental effects, but constrained breeding probabilities by age out performed those which held breeding probabilities constant (Table 3-3). Model selection suggested that environmental effects explained more variation in breeding probabilities than age alone (Table 3-3), yet model estimates elucidate patterns of age-specific variation in the costs of reproduction on breeding probabilities and survival.

Model selection within age models suggests an age-dependent trend in the probability of attempting to breed, as seen in the estimates from model 1, tables 3-3 (Figures 3-3 and 3-4). This model constrains adult Snail Kite breeding probabilities to 3 age classes: ages 2-4 years, 5-12 years, and 13+. Of note is a significant declining trend in the transition of non-breeders to attempt breeding in the subsequent year (Figure 3-3) and the simultaneous increase in the probabilities of breeders becoming non-breeders with age (Figure 3-4). These results suggest that as individuals age they are more likely to become non-breeders and stay in the non-breeding

state. Age class-specific decreases in breeding attempts provide evidence of reproductive senescence, which begins at age five, seven years earlier than the onset of actuarial (survival) senescence in adult Snail Kites.

### **Drought Effects**

A model which included drought effects on breeding probabilities for the years 2001 and 2007, with one year post drought effects (2002 and 2008) (model 1, Table 3-4) was best supported by the data (AICc weight = .989). Generally, models that included drought effects for years 2001 and 2007, performed better than comparable models that considered 2000 as a drought year, for example (model 1 versus model 2).

Despite that model 1 (Table 3-4) received nearly all of the Akaike weight (.941), separate breeding probabilities for the 2007 drought were not estimable. We suspect that this problem was an artifact of sparse data during the 2007 drought.

The relatively poor fit of models which equated the drought in 2007 as having the same effect on breeding probabilities as the conditions in 2001, and the declines in estimated breeding proportions (Figure 3-8) suggest that the drought in 2007 had less effect on range-wide breeding than the 2001 drought. We agree with previous authors that the 2007 drought did in fact have negative effects on Snail Kite survival (Figure 3-5) (Cattau *et al.* 2008). But we also hypothesize that the 2007 drought had less effect on breeding probabilities than the 2001 drought because greater than 70 percent of the reproduction for that year occurred in the Kissimmee Chain of Lakes, an area of the Snail Kite range traditionally considered to serve as a refuge during harsh conditions (Martin *et al.* 2006).

We assessed the impact that drought years had on the costs of reproduction by comparing the survival of breeders versus non-breeders during drought years (2001 and 2007) and non-drought years (1996-2000; 2003-2006) (Figure 3-5). As fully time dependent detection

probabilities did not allow for the estimation of survival during drought years, we had to include a model that assumed equal detection probabilities for breeding and non-breeding adults respectively, during drought years (2001 and 2007) (model 3, Table 3-4). The results from this model indicate that the drought exacerbated the costs of reproduction on survival probabilities of the breeding individuals, especially for the oldest adults. Models which included post drought effects (PDE) were well supported by the data (Table 3-4). However, a comparison of estimates for those years to non-drought years reveals no significant lag effects from droughts on breeding probabilities or survival.

### **Effects of Long-Term Habitat Degradation**

Models that included degradation effects (DP99) were also well supported by the data. In fact, the best fit model (model 1, Table 3-4) included effects of habitat degradation for breeding state transitions. Estimates from this model suggest a decrease in the probability of individuals attempting to breed beginning in 1999 (Figure, 3-7). The figure illustrates that the decrease in individual adult breeding probabilities in the post degradation period (after 1998) is largely due to a lack of non-breeders attempting to breed ( $\Psi_{\text{PreDP99}}^{\text{NB}} = 0.37$ ;  $\Psi_{\text{PostDP99}}^{\text{NB}} = 0.06$ ), as the individuals who were already breeding continued at the same rate ( $\Psi_{\text{PreDP99}}^{\text{BB}} = .611$ ;  $\Psi_{\text{PostDP99}}^{\text{BB}} = .619$ ).

An evaluation of age class-dependent survival estimates suggests a disproportionate decrease in the survival of older breeding adults after 1998 (Figure 3-8). Survival estimates between breeders and non-breeders did not differ significantly. Therefore, the decrease in adult survival can be attributed to habitat degradation and not to additional costs of reproduction. A finding that is supported by previous work (Chapter 2) suggesting that less fit Snail Kites experience lower survival during times of resource limitation, whether it be a result of droughts or habitat degradation.

## Discussion

Compared to shorter-lived, more fecund avian species, long lived birds provide a convenient framework to test for the costs of reproduction, as effects can be manifested over a longer period of time (Weimerskirch 1992). If costs of reproduction are driving the decision to breed, one would expect to observe decreased survival and/or breeding probabilities in the breeding proportion of a population (Clutton-Brock 1984; Nichols *et al.* 1994). We indeed found evidence that indicates a direct cost of reproduction on Snail Kite survival, which becomes exacerbated during droughts and disproportionately affects older individuals. Our results did not suggest any cost of reproduction on subsequent breeding probabilities, as the best fit models estimated the probability of breeders attempting to breed in a subsequent year to be greater than not breeding. An exception occurs only during drought years when the proportions of kites attempting to breed declines significantly.

As we predicted, Snail Kite breeding probabilities decreased during times of low resource availability, which suggests that some Snail Kites have the capacity to persist through droughts by forgoing breeding attempts and allocating the remaining resources for their own survival. We did not find an increased cost of reproduction due to habitat degradation, although adult survival has decreased since 1998. Habitat degradation and other long term processes seem to decrease individual physiological fitness (as seen in survival) and cause kites to forgo breeding attempts.

Although this is the first time that flexibility in Snail Kite reproductive effort has been formally addressed, several authors have noted similar hypotheses, although typically in regards to nest abandonment (Beissinger 1988; Bennetts and Kitchens 1997). For other avian species, theoretical models have predicted similar responses, such as seabirds (Erikstad *et al.* 1998; Hecht Orzack and Tuljapurkar 2001), but here we provide empirical evidence to support these models.

Another important result of this study is the description of age-specific breeding probabilities. A profile of the cumulative annual probabilities of becoming a breeder throughout a Snail Kites life (Figure 3-5) illustrates that the highest probability of attempting to breed happens within the first 5 years. Although we did not test individual fitness directly our results suggest that aging in Snail Kites results in a physiological deterioration as a result of allocating resources for early breeding, which decreases an individual's attempts to breed and probability of surviving later in life (Chapter 2). Most studies of reproductive senescence focus on declining rates of reproductive performance, such as inefficient foraging, fecundity, or nest success (Cтры *et al.* 2006). These results provide additional insight into reproductive senescence, suggesting a decrease in reproductive effort. As evolutionary life history models suggest that reproductive effort should increase with age (Charlesworth and Leon 1976), a decrease in effort seen in breeding attempts may reflect the failure of older individuals to reach a fitness threshold required for breeding (Tuomi *et al.* 1983) or an environment with limited resources where only the fittest individuals are able to gain access to breeding opportunities.

We identified a decreasing proportion of breeders in the Snail Kite population after 1998. This may indicate an aging population, with older individuals less likely to breed (Figure 3-3) however, it may also be indicative of a system with increasingly limited resources for breeding. As discussed, Snail Kite reproduction has geographically shifted away from the traditionally most productive regions, such as the Everglades and Lake Okeechobee, and is now limited to the Kissimmee Chain Of Lakes; Lake Tohopekaliga in particular (Cattau *et al.* 2008). It is not unreasonable to suspect that the reproductive capacity of the system has decreased. The population, which was once supported by potential reproductive units throughout its range, is now restricted to breeding in much fewer areas. As resources would limit the number of potential

breeders only the most fit may gain access to breed, where less fit individuals, (i.e. young and old) become non-breeders (Rodenhouse et al. 1997).

An alternative hypothesis is that the adult breeders from areas no longer able to support reproduction (i.e. Water Conservation Areas, Figure 3-2), forgo breeding and move north to the Kissimmee Chain of Lakes or other marginal habitats. Once again, the resources in these wetlands cannot support the same level of breeders as their range once could. The strong natal site fidelity exhibited in Snail Kites suggests that this process could continue year after year until natal areas or refugia provide suitable habitat for reproduction, or kites senescence and experience increased mortality associated with making continued long distance movements (Martin *et al.* 2006; 2007a).

### **Breeding Probabilities and Breeder Proportions**

Addressing sources of variation in Snail Kite breeding probabilities has also allowed us to model annual breeding probabilities and directly estimate breeding proportions (Figure 3-9) and thus, the number of breeding Snail Kites over time (Figure 3-10). Until now robust estimates of Snail Kite breeding proportions have not been available.

Early efforts to model the stochastic growth rate of the Snail Kite population have assumed reductions in breeding probabilities during drought years based on theoretical models (Nichols *et al.* 1980; Beissinger 1995). Using estimates based on a sample of 23 birds fixed with radio telemetry backpacks over a period of two years (Bennetts 1998b) the most recent modeling efforts assumed adult breeding probabilities to be equal to 1 during wet years and .33 during drought years (Martin *et al.* 2008). Comparatively, our results indicate that breeding proportions are far lower than previously assumed, and that more variation exists within estimates than can be explained by drought and non-drought years alone.

Figure 3-9 illustrates the proportions of breeding Snail Kites by year from 1996 to 2009. Of note is the relatively high proportion of breeders in 2000, a year that was considered to be a drought year in some of our models. The relatively poor fit of these models suggests that although the drought began in 2000, dry conditions did not begin until after the 2000 nesting season had finished. Therefore, dry conditions in 2000 would have affected juvenile and adult survival (Cattau *et al.* 2008), but not the breeding probabilities. As we had expected, these results provide evidence that Snail Kite breeding probabilities are in fact more sensitive to conditions earlier in the breeding season. We recommend that future analyses of Snail Kite breeding probabilities take this into consideration.

### **Post Hoc Assessments**

Assessing Snail Kite breeding proportions elucidates that the highest breeding proportion between 1996 and 2009 occurred in 2003, when greater than 70 percent of the population attempted to breed (Figures 3-9 and 3-10). This may have been a result of the dry conditions which occurred in 2001, which were conducive to snail egg laying and hatching, which in turn, may have increased snail abundances in 2002 and led to a proliferation of available resources during the onset of the 2003 breeding season (Darby, personal communication).

This work provides evidence that the conditions leading up to the breeding season are important for promoting Snail Kite breeding attempts. Understanding not only the causes of negative effects on breeding probabilities, but environmental effects which promote breeding attempts will be a major component for restoring Snail Kite reproduction and thus the recovery of the Snail Kite population in Florida.

Table 3-1. Snail Kite behavior warranting designation of ‘breeder’ state.

Behavior category	Field observation
Nesting	Flushing from or occupying visible nest. Flushing from perch and circling $\leq 12$ m above, giving alarm calls. Feigning attacks at observers with talons extended, while giving alarm calls
Courtship	Males carrying sticks to nest building site Males feeding females, or fledglings Females feeding fledglings
Reproduction	Copulation

Notes: 'Breeder' state refers to individuals attempting to breed, and makes no assumptions about the degree of energetic investment, only that an individual has decided to attempt breeding during a particular breeding season.

Table 3-2. Examples of two occasion mark-recapture histories, associated probabilities, and notation definitions.

Encounter History	Likelihood
BN	$S_1^B * (\Psi_1^{BB} * p_2^{B(1-\delta)} + \Psi_1^{BN} * p_2^N)$
NB	$\pi_1 * S_1^N * \Psi_1^{NB} * p^{B(\delta)} + (1-\pi_1) * S_1^B * \Psi_1^{BB} * p_2^{B(\delta)}$
YB	$S_1^Y * \Psi_1^{YB} * p_2^{B(\delta)}$
YN	$S_1^Y * (\Psi_1^{YB} * p_2^{B(1-\delta)} + \Psi_1^{YN} * p_2^N)$

Notes:  $S_1^B$  = probability of a breeder surviving in time 1.  $\Psi_1^{NB}$  = probability of individual transitioning from a non-breeder to a breeder in time step 1.  $\pi_1$  = probability that a kite seen for the first time in year 1 and not exhibiting breeding behavior is in fact a non-breeder.  $p^{B(\delta)}$  = probability that a breeder is detected and seen exhibiting breeding behavior.  $p^{B(1-\delta)}$  = probability that an individual attempting to breed is detected, but not observed exhibiting breeding behavior.

Table 3-3. Models representing hypotheses on the effects of age, droughts, and habitat degradation on the range-wide breeding probabilities of Snail Kites in Florida, USA.

#	Model	# Parm	$\Delta$ AICc	Akaike Weight	Biological Hypothesis
(1)	S (AC (0,1-12,13+)) Psi (AC (0,1-4, 5-12, 13+))	112	0.00	1	Survival varies by age class; breeding probabilities vary by age classes (0, 1-4, 5-12, 13+ years).
(2)	S (Full age) Psi (Full age)	149	79.15	0	Survival varies by individual ages; breeding probabilities vary by individual ages.
(3)	S (AC (0,1-12,13+)) Psi (Full age)	133	183.73	0	Survival varies by age class; breeding probabilities vary by individual ages.
(4)	S (AC (0,1-12,13+)) Psi (.)	114	211.22	0	Survival varies by age class; breeding probabilities were constant across time and for all ages
(5)	S (AC (0,1-12,13+)) Psi (AC (0,1-12,13+))	118	237.40	0	Survival varies by age class; breeding probabilities vary by age class.
(6)	S (Full age) Psi (Full age) p(NB=B)	130	417.13	0	Survival varies by individual ages; breeding probabilities vary by individual ages; detection is the same for breeders and non-breeders.

Table 3-4. Models representing hypotheses of environmental effects on the range-wide breeding probabilities, and age class dependent survival of Snail Kites in Florida, USA.

#	Model	# Parm	$\Delta$ AICc	Akaike Weight	Biological Hypothesis
(1)	S (AC * DE(00-01,07)) Psi (DP99; DE(01,07); PDE(02,08))	143	0	0.941	Survival varies by age class and is drought dependent (2000-01 differ 2007); breeding probabilities differed beginning in 1999, were drought dependent (2001 differ 2007), with one year lag effects (2002 differ 2008).
(2)	S (AC * DE(00-01,07)) Psi (DP99; DE(00-01,07); PDE(02,08))	142	5.5	0.059	Survival varies by age class and is drought dependent (2000-01 differ 2007); breeding probabilities differed beginning in 1999, were drought dependent (2000-01 differ 2007), with one year lag effects (2002 differ 2008).
(3)	S (AC * DE(00-01,07)) Psi (AC (1-4, 5-12, 13+) (DP99) DE(01=07) PDE(02=08) pB(01) = pNB(07))	146	27.67	0	Survival varies by age class and is drought dependent (2000-01 differ 2007); breeding probabilities differed beginning in 1999, were drought dependent (2001 = 2007), with one year lag effects (2002 = 2008), adult detection was equal during droughts.
(4)	S (AC * DE 00-01=07) Psi (DE (01,07))	119	39.27	0	Survival varies by age class and is drought dependent (2000-01 = 2007); breeding probabilities were drought dependent (2001 differ 2007)
(5)	S (AC * DE 00-01) Psi (DE (01-07))	122	56.46	0	Survival varies by age class and is drought dependent (2000-01 = 2007); Breeding probabilities were drought dependent (2001 = 2007)
(6)	S (AC * DE 00-01=07) Psi (AC * DE (01,07))	124	99.76	0	Survival varies by age class and is drought dependent (2000-01 = 2007); Breeding probability is age-class dependent and varied between 2001 and 2007 drought
(7)	S (AC * DE (00-01)) Psi (DE (00-01); PDE(02))	124	102.2	0	Survival varies by age class and 2000-01 drought; Breeding probability varied by 2000-01 drought and one year drought lag effect (2002).
(8)	S (AC * DE 00-01) Psi (DE (01-02))	124	103.9	0	Survival varies by age class and 2000-01 drought; Breeding probability varied by 2001-02 drought years
(9)	S (AC * DE 00-01) Psi (DE (00-01))	123	105.4	0	Survival varies by age class and 2000-01 drought; Breeding probability varied by 2000-01 drought years

Table 3-4. Continued

(10)	S (AC * DE (00-01)) Psi (AC * DE (00=01))	130	139.7	0	Survival varies by age class and is dependent on 2000-01 drought; Breeding probability is age-class dependent and varied by 2000-01 drought.
(11)	S (AC * DE (00-01)) Psi (AC * DE (01=02))	132	141.7	0	Survival varies by age class and is dependent on 2000-01 drought; Breeding probability is age-class dependent and varied by 2000-01 drought.
(12)	S (AC * DE (00-01=07)) Psi (AC * DP99; DE (00-01=07); PDE (02=08))	137	147.9	0	Survival varies by age class and is drought dependent (2000-01 = 2007); breeding probabilities are age-class dependent, differed beginning in 1999, were drought dependent (2000-01 = 2007), with one year lag effects (2002 = 2008).
(13)	S (AC * DE (00-01=07)) Psi (DP99; DE(00-1=07); PDE (02=08))	134	150.9	0	Survival varies by age class and is drought dependent (2000-01 = 2007); breeding probabilities differed beginning in 1999, were drought dependent (2000-01 = 2007), with one year lag effects (2002 = 2008).
(14)	S (AC * DE (00-01=07)) Psi (DE (00-01=07); PDE(02=08))	131	156.8	0	Survival varies by age class and is drought dependent (2000-01 = 2007); breeding probabilities were drought dependent (2000-01 = 2007), with one year lag effects (2002 = 2008).
(15)	S (AC * DP99) Psi (AC * DP99)	122	181.6	0	Survival varies by age class and differed beginning in 1999; breeding probabilities vary by age class and differed beginning in 1999.
(16)	S (AC) Psi (DP99)	110	218.9	0	Survival varies by age class; breeding probabilities differed beginning in 1999.
(17)	S (AC) Psi (AC * DE(00-01=07))	109	347.2	0	Survival varies by age class, breeding probabilities vary by age class and were drought dependent (2000-01 = 2007).
(18)	S (AC) Psi (DE (00-01=07))	103	350.7	0	Survival varies by age class, breeding probabilities were drought dependent (2000-01 = 2007).

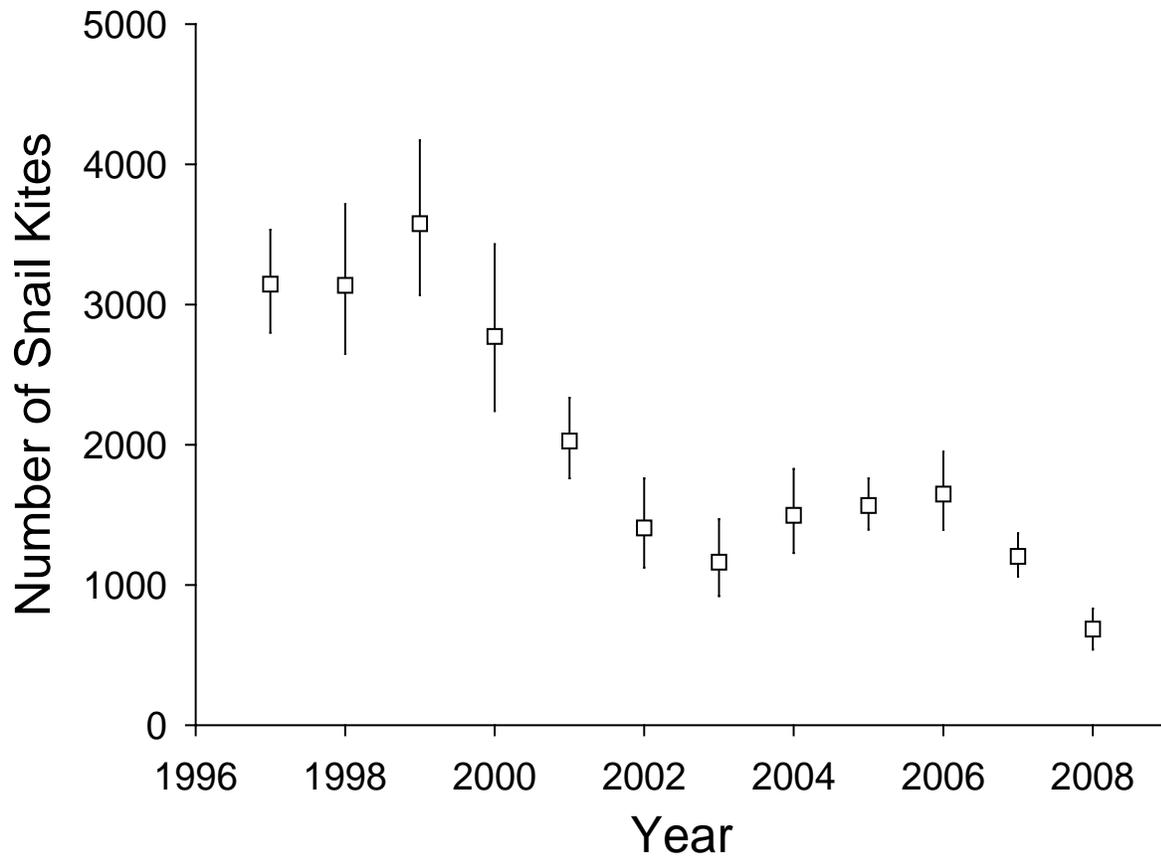


Figure 3-1. Population size of Snail Kites estimated using the super-population approach (Cattau *et al.* 2008).

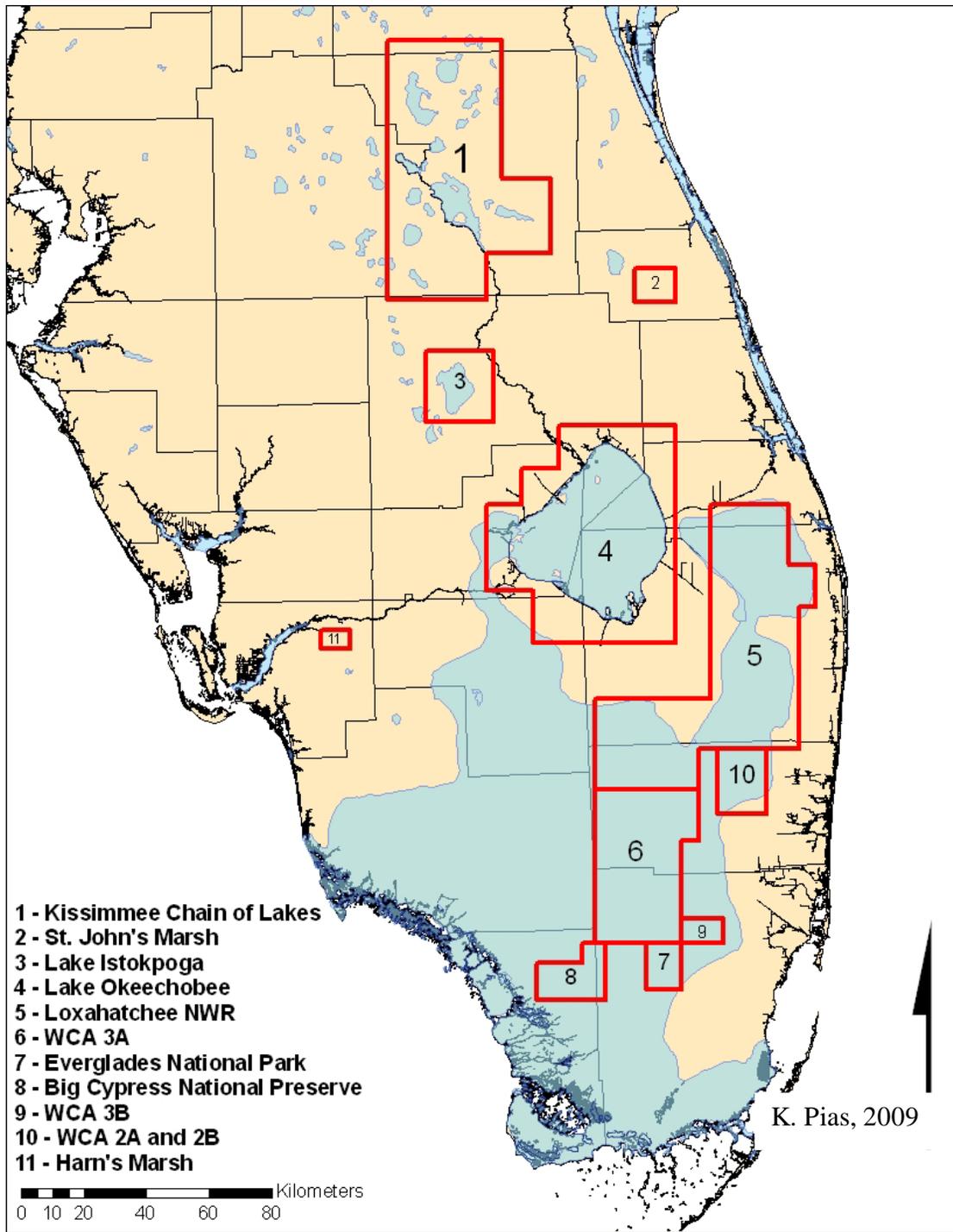


Figure 3-2. Wetland units included in annual surveys; also representative of Snail Kite breeding areas.



Figure 3-3. Age class-specific probabilities and associated standard error of adult Snail Kite non-breeders attempting to breed in subsequent years.

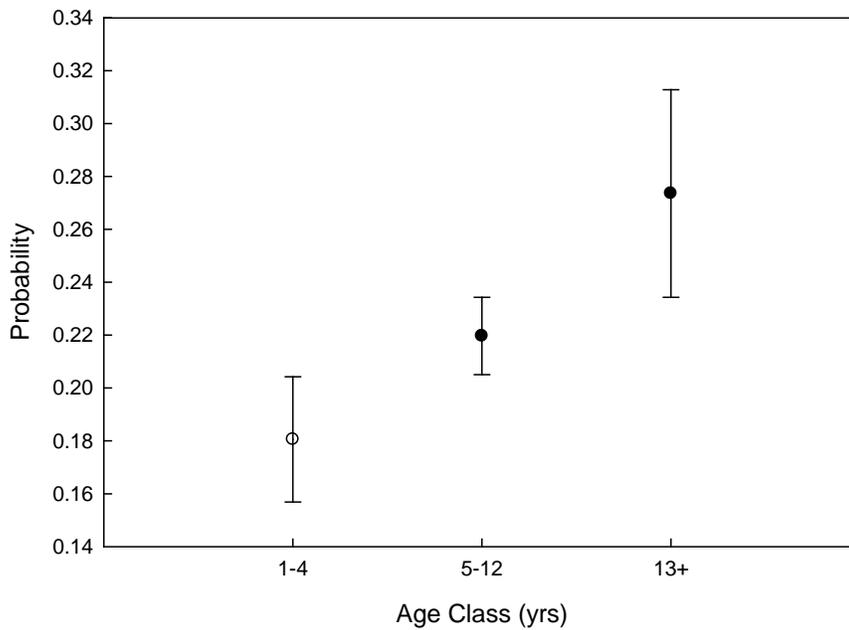


Figure 3-4. Age class-specific probabilities and associated standard error of adult Snail Kite breeders not attempting to breed in subsequent years.

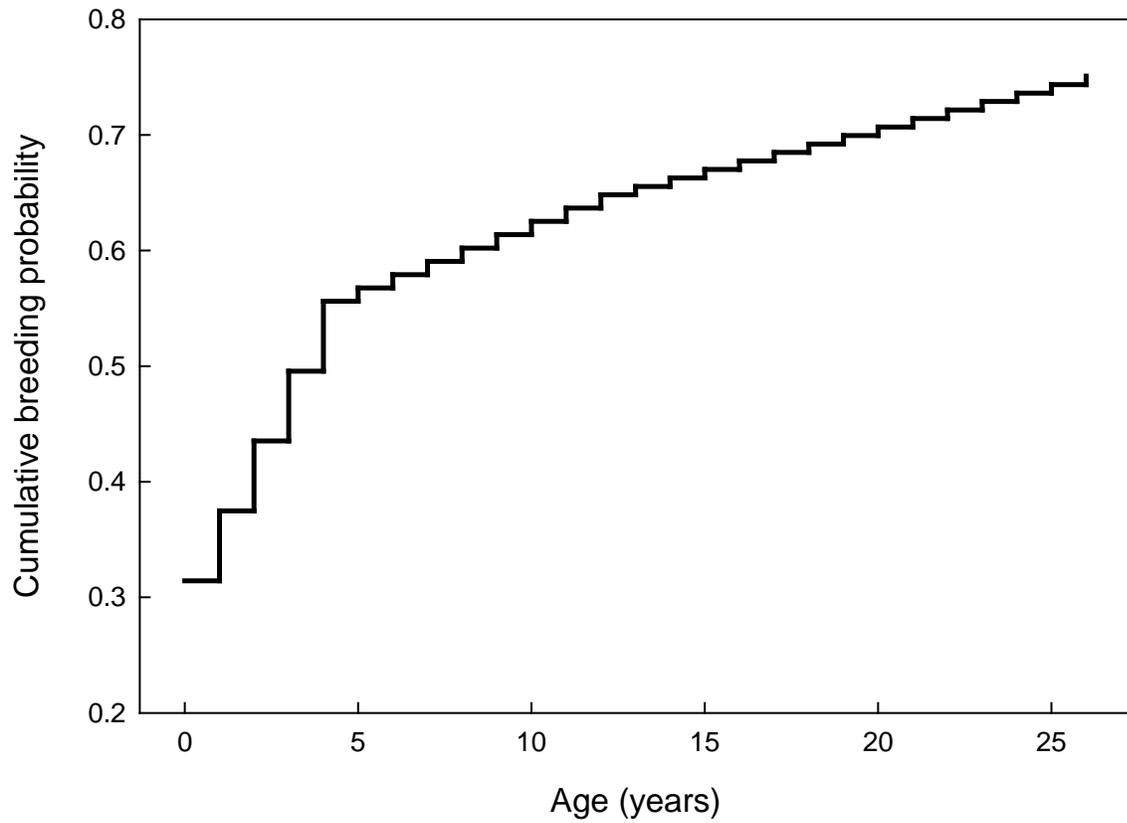


Figure 3-5. Cumulative probability of an individual Snail Kite attempting to breed through-out life span.

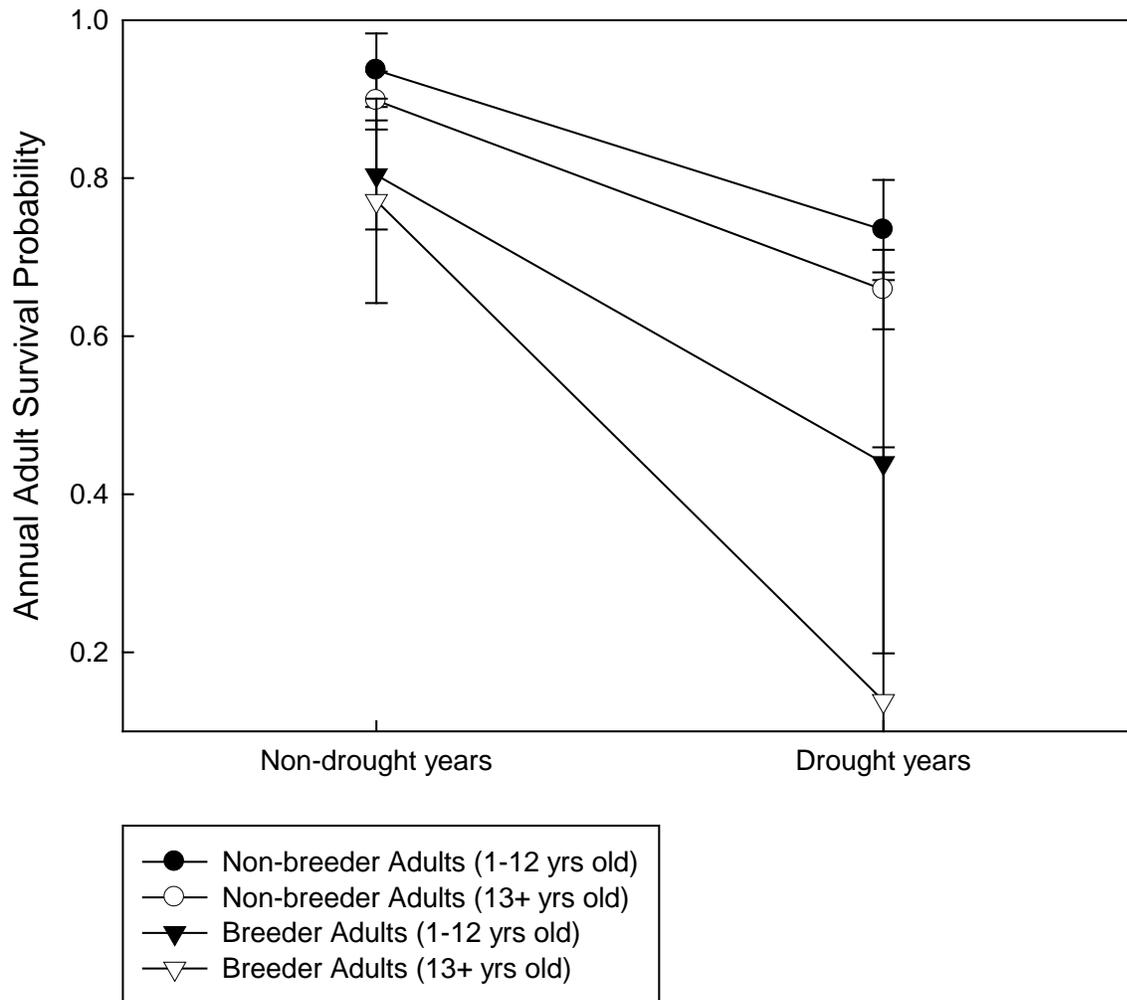


Figure 3-6. Evidence of droughts increasing the costs of reproduction on Snail Kite survival probabilities.

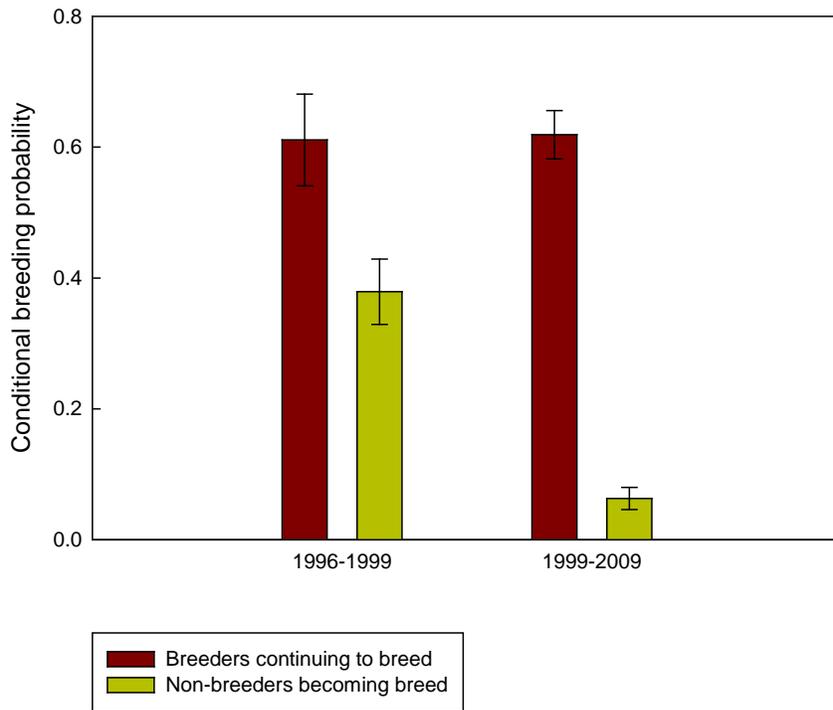


Figure 3-7. Effects of habitat degradation on adult Snail Kite conditional breeding probabilities.

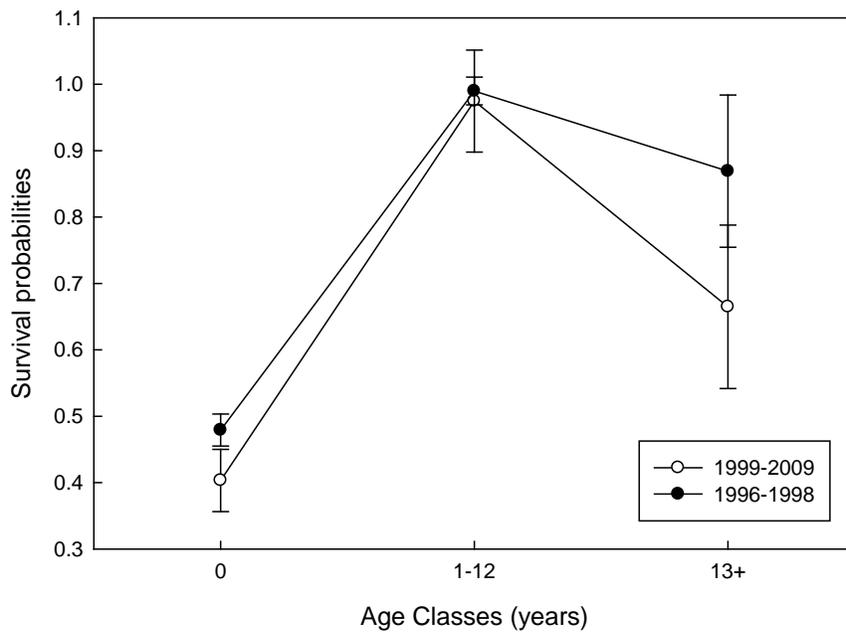


Figure 3-8. Effect of habitat degradation on Snail Kite survival probabilities (model 8, Table 3-4)

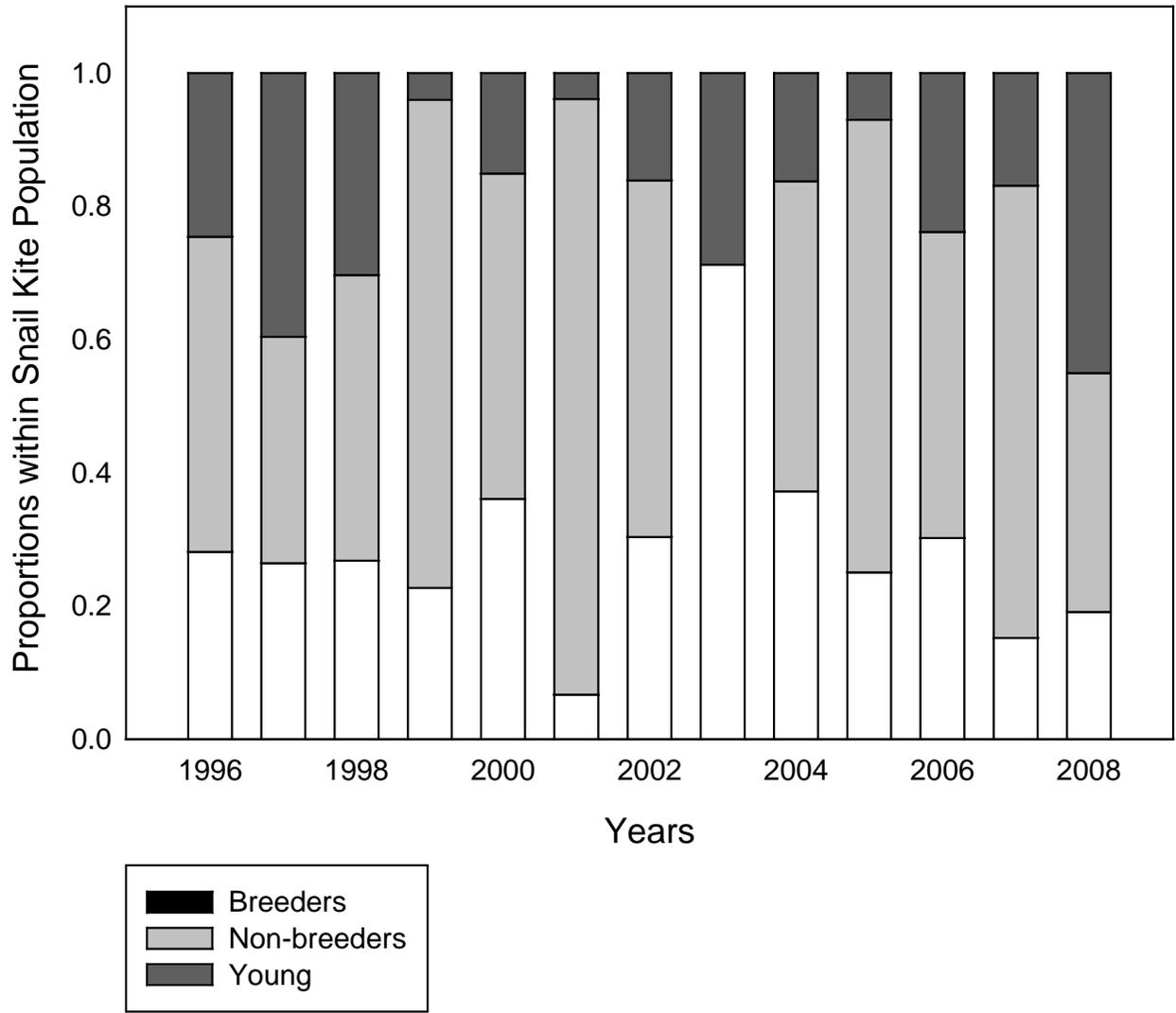


Figure 3-9. Proportions ( $\omega$ ) of Snail Kite population in different breeding states.

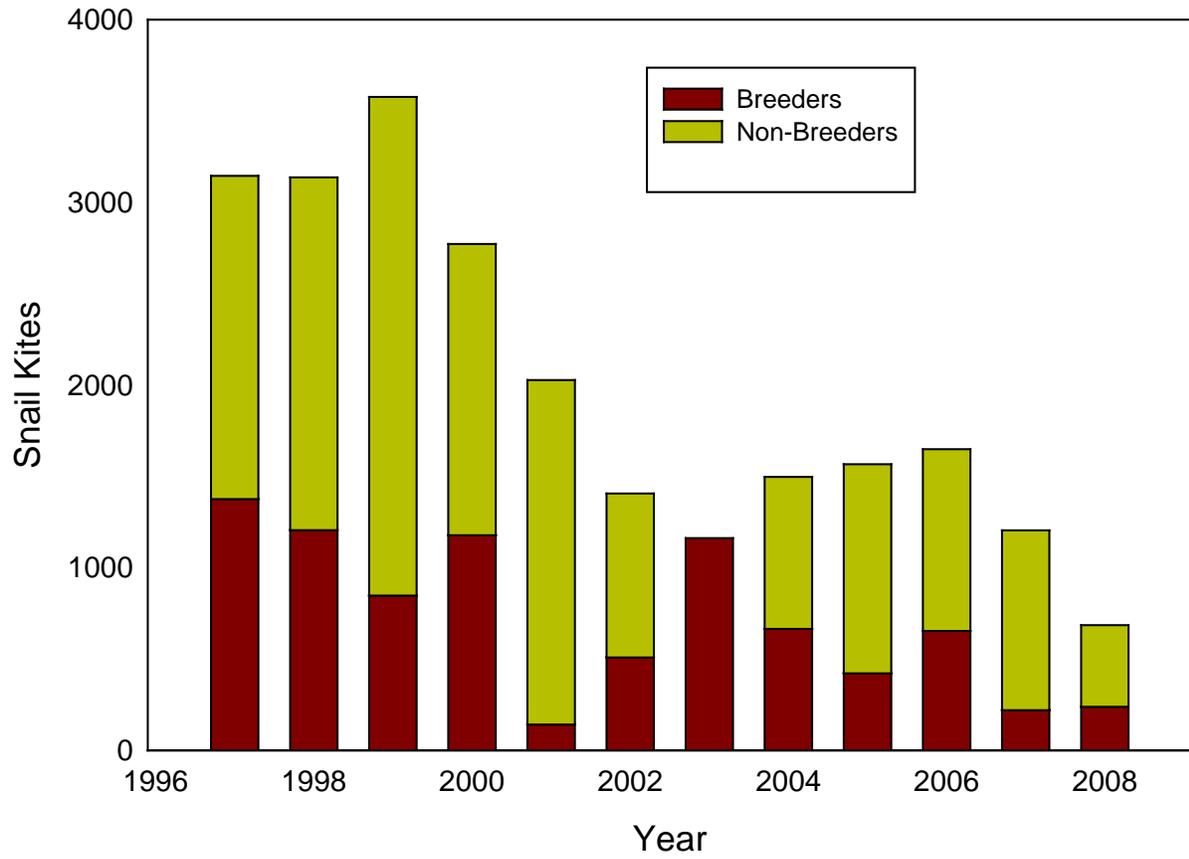


Figure 3-10. Numbers of Snail Kites attempting to breed since 1998.

## CHAPTER 4 CONSERVATION IMPLICATIONS

### **Age-Structure and Snail Kite Demography**

The findings in this work provide convincing evidence of an age structured life history pattern in Snail Kites. Here, we put these findings into the context of the current state of the Snail Kite population, and discuss what age dependent survival and breeding means for the future of Snail Kite population dynamics.

As stated, the Snail Kite population has declined rapidly since 1999. Efforts to model the stochastic growth rate of the Snail Kite population found that the growth rate fell substantially after 1998 (.90), and that > 80% of this decrease could be attributed to a reduction in Snail Kite fertility (Martin *et al.* 2008). The sensitivity analysis indicated that changes in adult survival and fertility had the largest effect on the population growth rate ( $\lambda$ ). Our results describe additional variation to these two parameters which have yet to be considered for Snail Kite population dynamics. We suggest that these concepts be included in a future population viability analysis. Without such an analysis it is difficult to make accurate quantitative assessments of population level effects.

Figure 4-1 illustrates the relative changes in Snail Kite age distribution over time using the proportions of banded individuals re-sighted annually and adjusted for age-specific detection probabilities. The number of young (< 1 yr old) in this figure is the number of banded fledglings per year, which is not included into annual population estimates, as recruitment is variable and does not occur until the beginning of an individual's second breeding season (Bennetts and Kitchens 1997; Martin 2007). However, we included banded fledglings because we think it is telling of several

important issues in Snail Kite demography, and has been the focus of recent conservation efforts.

The number of fledglings produced in a given year provides an idea of the relative potential for recruitment in the following year. As a general trend, the number of younger birds in the population has decreased since 1998, supporting the conclusions made by Martin *et al.* (2008).

Beginning in 1998, a decreasing proportion of Snail Kites are in the (1-4) year old age class, and the population becomes dominated by older individuals. We suspect that prior to 1998, recruitment of younger birds had been supplementing the population. In the second half of 2000, adult survival (especially that of the oldest adults, see Chapter 2) decreased as a result of the range-wide drought. This drought effect corresponded to decreasing breeding probabilities (Chapter 3). Reduced reproductive effort failed to supply the population with new individuals. Recent reports suggest that depressed reproduction has continued through 2008 (Cattau *et al.* 2008) and 2009 (Cattau unpublished). As the population becomes older, the majority of Snail Kites, who are currently middle-aged, will enter a senescent state and experience decreased survival rates (Chapter 2) and be potentially less capable of breeding (Chapter 3). We hypothesize that if adult fecundity does not increase over the next five years, the Snail Kite population could experience yet another dramatic decline resulting from the demographic process associated with Snail Kite aging, which were described in this body of work.

The general aging of the population is also evident in the increase of the average age of breeding adults, which we estimated using band re-sights from individuals identified as breeders to have increased from 5.8 in 1996 to 10.0 in 2009. Although we

recognize this to be an ad hoc methodology, we recommend that additional studies be conducted that investigate age-specific parameters of reproductive output (i.e. nest success, fecundity, breeding attempts per year, etc.) and factors that may promote reproduction of older individuals, such as improving the nesting substrate or foraging base in the natal areas of older individuals (Martin *et al.* 2006).

Recently, criticism has been expressed regarding the validity of the documented demographic trends. It is important that these issues are addressed, so as to assure that doubt does not exist regarding the current emergency state of the Snail Kite population among those in positions to effectively manage for its recovery.

Considering that the Snail Kite population in Florida is closed to demographic and geographic movement, and that banded individuals have the same mortality rate as unbanded individuals, there is no reason to think that our sample is not an adequate representation of the total Snail Kite population. Therefore, there is no reason to believe that the observed, decreasing trends in population size, fertility, adult survival, juvenile survival, and now breeding probabilities are not in fact real and occurring at the population level.

As the Snail Kite population in Florida continues to decrease, providing managers and conservation biologists with reliable estimates of survival and reproduction becomes increasingly important as a means of accurately projecting the effects of competing management strategies on the Snail Kite population as a guide to species recovery. Unfortunately, the information provided here elucidates sources of variation which are limiting Snail Kite vital rates. It is difficult to predict the true quantitative impacts of these results on the projected Snail Kite population. Nonetheless, continuing to test

predictions and redefining our hypotheses accordingly, is an imperative step in the adaptive process of conserving the Snail Kite population in Florida.

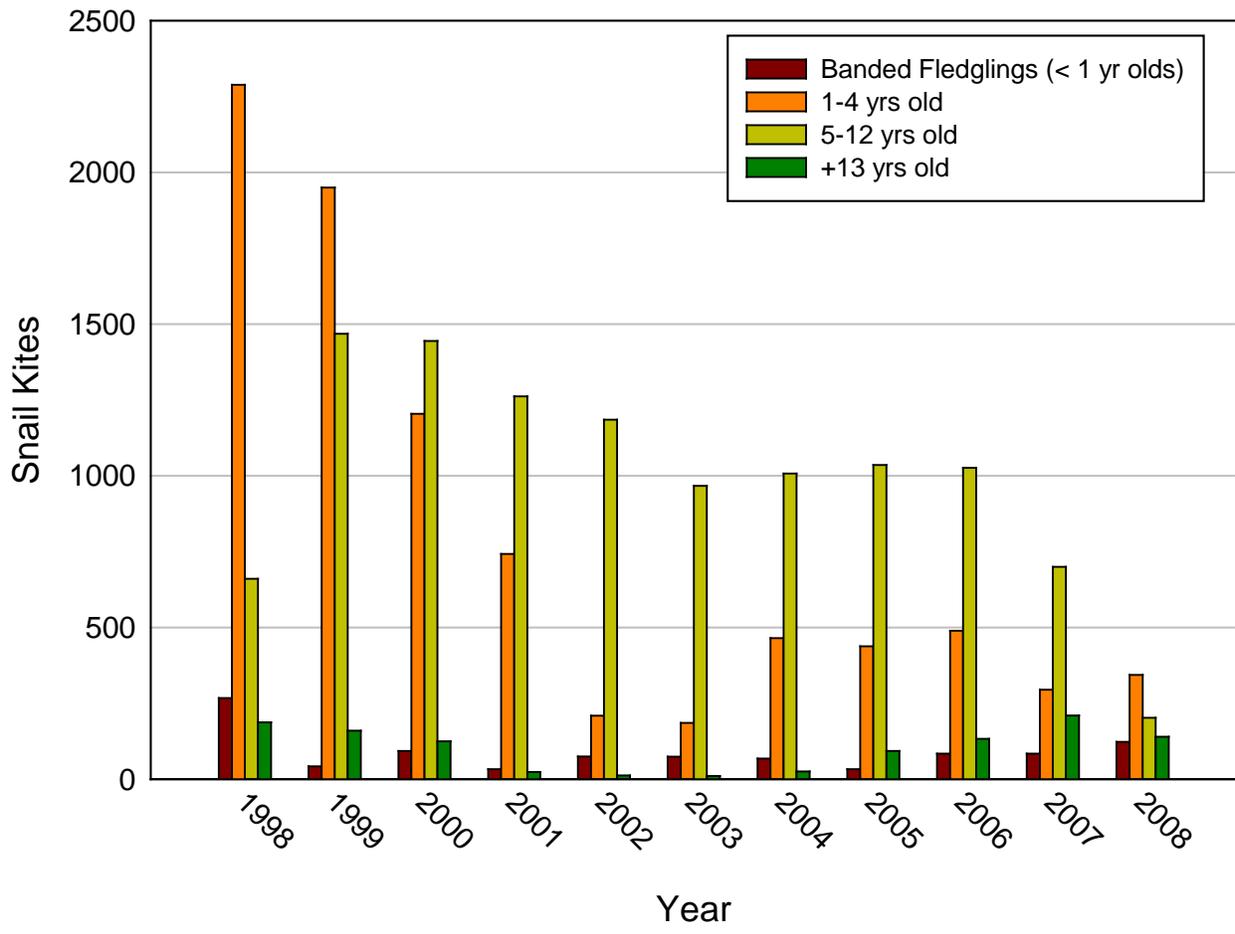


Figure 4-1. Age distribution of banded Snail Kites. Numbers of adults were adjusted for age-specific annual detection probabilities (Chapter 2).

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## BIOGRAPHICAL SKETCH

Brian Engebos Reichert was born in Milwaukee, Wisconsin in 1982. He obtained a B.S. in Fisheries, Wildlife, and Conservation at the University of Minnesota, St. Paul in 2005. Beginning in 2003, Brian worked as a field technician with the Minnesota Cooperative Fish and Wildlife Research Unit on several projects including the investigations into: the fall movements, habitat use, and survival of the American Woodcock in the Western Great Lakes Region, long-term monitoring of breeding Eastern Prairie Population Canada Geese at Cape Churchill, Manitoba, Canada; compiling the breeding bird and master avian species lists for Wapusk National Park, Cape Churchill, Manitoba, Canada; Wood Frog and Boreal Chorus Frog distribution and habitat associations in Wapusk National Park. In 2006, Brian moved to Florida and began working as a field ecologist for the Florida Fish and Wildlife Cooperative Research Unit on the long-term monitoring of Snail Kite demography and its habitat.