



# The effect of changes in habitat conditions on the movement of juvenile Snail Kites *Rostrhamus sociabilis*

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The degradation of habitats due to human activities is a major topic of interest for the conservation and management of wild populations. There is growing evidence that the Florida Everglades ecosystem continues to suffer from habitat degradation. After a period of recovery in the 1990s, the Snail Kite Rostrhamus sociabilis population suffered a substantial decline in 2001 and has not recovered since. Habitat degradation has been suggested as one of the primary reasons for this lack of recovery. As a consequence of the continued degradation of the Everglades, we hypothesized that this would have led to increased movement of juvenile Kites over time, as a consequence of the need to find more favourable habitat. We used multistate mark-recapture models to compare between-site movement probabilities of juvenile Snail Kites in the 1990s (1992-95; which corresponds to the period before the decline) and 2000s (2003-06; after the decline). Our analyses were based on an extensive radiotelemetry study (266 birds tracked monthly over the entire state of Florida for a total period of 6 years) and considered factors such as sex and age of marked individuals. There was evidence of increased movement of juvenile Snail Kites during the post-decline period from most of the wetland regions used historically by Kites. Higher movement rates may contribute to an increase in the probability of mortality of young individuals and could contribute to the observed declines.

**Keywords:** endangered species, habitat degradation, mark-recapture, maximum likelihood estimation, radiotelemetry.

The movement of organisms over time and throughout their potential spatial range is an integral process in population dynamics (Belisle *et al.* 2001, Clobert *et al.* 2001, Macdonald & Johnson 2001). Movements across a spatially varying landscape help maintain a diverse gene pool and

\*Corresponding author. Email: abowling@msu.edu & Holt 1992). Among factors generating spatial heterogeneity, fragmentation can degrade habitats and induce changes in the way animals perceive and move through landscapes (Haddad 1999, Belisle *et al.* 2001, Macdonald & Johnson 2001) and several studies have shown that habitat quality (e.g. resource availability) is a major factor influencing the movement of organisms (Boudjemadi *et al.* 1999, Bennetts & Kitchens 2000, Senar *et al.* 2002). In particular, low-quality habitat can force organisms to disperse at higher rates in search of higher quality habitat (Ims & Hjermann 2001, Lenihan *et al.* 2001, Pettorelli *et al.* 2003). It is probably a complex combination of both habitat fragmentation and habitat quality that determines

protect local populations from extinction (McPeek

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rates and distances of movement (Boudjemadi *et al.* 1999).

As a result, rates of movement can be used as an indication of habitat quality (Belanger & Rodriguez 2002) and may differ among members of a population. In particular, movement can be an especially important process for juvenile cohorts of a population. Their survival and recruitment into the breeding population, which are essential to maintaining a growing or stable population (Harmata et al. 1999, Cushman 2006), are directly affected by their ability to move across the landscape and find the appropriate habitat to support their physiological needs. If high-quality habitats become uncommon in the landscape, organisms may be forced to move at a higher rate and travel longer distances, leading to higher energy expenditure and higher encounter rates with potential sources of mortality (McPeek & Holt 1992).

Wildlife habitat quality may degrade as a consequence of anthropogenic activities. Wetlands and their vegetative communities that support faunal life are particularly susceptible to degradation and subtle changes in hydrology (Mitsch & Gosselink 2007). The Everglades ecosystem is an expansive, once contiguous, wetland of international importance. It is currently subject to extensive restoration plans in response to the progressive fragmentation and habitat loss induced by drainage for agriculture and urban environments. The Comprehensive Everglades Restoration Plan (CERP) is the largest active restoration project in the world (RECOVER 2005). The outcome will add to our knowledge of how to undertake large-scale restoration for other imperilled ecosystems.

Kitchens *et al.* (2002) described the slow degradation of the palustrine system due to uninterrupted inundation of impounded wetlands which had once experienced the natural cycle of dry and wet periods. This type of management was initiated in part (Ogden 2005) to provide short-term drought refuges for conservation-sensitive Snail Kites *Rostrhamus sociabilis*. However, over time, the vegetative communities that provided foraging opportunities have transitioned from prime foraging habitat (Karunaratne *et al.* 2006) to deep aquatic environments unsuitable for Kites (Zweig & Kitchens 2008).

Havens and Gawlik (2005) and Johnson *et al.* (2007) showed the water quality of Lake Okeechobee to be low due to phosphorus loading from upstream sources and unnatural hydrology. Because of the impoundment of the lake, the remnant littoral zone, which is important Snail Kite foraging habitat, suffers the effects of high depths during large water deliveries but dries out quickly with low water deliveries. Thus, although the wet and dry cycle is natural, the fluctuations currently experienced are too extreme. Invasive plants, such as Torpedograss *Panicum repens*, have out-competed the native emergent species during the low water events, with overall negative impacts on the whole littoral zone.

The Snail Kite is a wetland-dependent species which can be found throughout South America (Haas et al. 2009). The subspecies R. sociabilis plumbeus occurs almost exclusively in the greater Everglades ecosystem of southern Florida and is one of the few avian taxa that are confined to the wetland units that constitute the former Greater Everglades (Takekawa & Beissinger 1989, Kitchens et al. 2002). Its population biology is finely tuned to the hydrology of the system, so the Snail Kite is considered to be an important indicator of the success of the Everglades restoration effort (RECOVER 2005, Martin et al. 2008). Snail Kites forage over vegetative communities characterized by sparse emergent herbaceous plants such as *Eleo*charis and Panicum (Bennetts et al. 2006). Their diet consists almost exclusively of the aquatic freshwater Apple Snail Pomacea paludosa (Sykes 1987). During drying events, snails become unavailable to Kites, which must move to less affected areas to increase their chance of survival (Bennetts & Kitchens 2000). Recently, there have been concerns that changes in hydrological regime in the wetlands within the Everglades have led to changes in vegetative communities and lower snail abundance (Darby et al. 2008). Martin et al. (2008) suggested that appropriate habitat for the Snail Kite may have decreased in quality since the mid-1990s, which may explain the failure of Snail Kite population numbers to recover from the effects of a drought in 2001 (Martin et al. 2006a, 2007a, 2008). More specifically, Martin et al. (2008) hypothesized that two processes are occurring simultaneously: (1) habitats are being degraded (vegetative communities are shifting towards those that are less desirable for Snail Kites) (see also Kitchens et al. 2002, Hotaling et al. 2009) as a result of floods and a prolonged hydroperiod from August to January; and (2) an increase in the frequency of drying events (during May to August) compared with that of the mid-1990s has reduced the availability of snails to Kites.

Our aim was to examine changes in the probability of movement of juvenile Snail Kites among wetland regions and to evaluate how this may correlate with habitat condition over time. We compared the movement of juvenile Kites between two time periods: before the population decline that occurred in 2001 (i.e. pre-decline period) and after the decline (i.e. post-decline period).

Bennetts and Kitchens (2000) presented a conceptual model of food availability and dispersal, in which Snail Kites exhibit exploratory behaviour when food resources are high, show little movement when resources are marginal, and must disperse when resources are limited. We hypothesized that the juvenile population during the post-decline period experienced the *leave or starve* point in this model. Other studies have found that Snail Kites escape the effects of disturbances such as droughts by moving to wetlands outside the reach of the disturbances (Beissinger & Takekawa 1983, Bennetts 1993, Bennetts & Kitchens 1997b). These concepts are consistent with the hypothesis that starving birds have higher activity levels which tend to increase the likelihood of a bird leaving its natal area (Astheimer et al. 1992). We predicted that the probabilities of large-scale juvenile movements have increased among all regions in the post-decline period and are related to the degradation of the wetland habitats occupied by Snail Kites.

We considered the size of the wetland regions, distance among wetland regions, and the age and sex of the birds as covariates to explain movement patterns of Snail Kites among wetland regions. Based on the existing literature, we made specific predictions about the directionality of the relationship between the covariates under consideration and movement. Martin et al. (2006b) found that the probability of movement of juvenile Snail Kites decreased with increasing distance among wetlands. They also found that the interaction between the size of the receiving wetland and the distance among wetlands positively influenced the movement probability of juvenile Snail Kites. Therefore, we included these covariates in our models because the effects of habitat type and connectivity on population dynamics are potentially complex (Boudjemadi et al. 1999). Based on these findings, we also predicted: (1) a positive relationship between movement probability and size of the site to which Snail Kites move; and (2) a negative relationship between distance and movement.

We were also interested in how sex may influence the probability of movement. In most avian species, females tend to move further than males (Greenwood & Harvey 1982, Clarke *et al.* 1997, Real & Manosa 2001). Therefore, we predicted that juvenile females had higher movement probabilities than juvenile males.

Finally, we evaluated the effect of variation in age on movement probabilities. When examining monthly movement probabilities, Bennetts and Kitchens (1997a) found that birds younger than 1 year had lower monthly movement rates than adults (i.e. birds > 1 year old). We also accounted for the effect of age on survival because previous studies have shown that younger birds have lower survival rates (e.g. Bennetts & Kitchens 1999).

# **METHODS**

# **Study area**

The study area consisted of the five major freshwater wetland regions and the peripheral wetlands utilized by Snail Kites in central and south Florida (Bennetts & Kitchens 1999). The five main regions are the Kissimmee Chain of Lakes (K), Saint John's Marsh (J), Lake Okeechobee (O), Loxahatchee Slough (L), and the Everglades (E) (Fig. 1). The peripheral areas are wetlands anywhere in the state that are not within these five major wetland regions. These include small lakes, agricultural fields and canals, urban areas (retention ponds), and small ephemeral wetlands.

# **Data collection**

Juvenile birds in 1992–95 and 2003–06 were equipped with VHF radio-transmitters at the nest at the time of fledging ( $\sim 28$  days). The transmitters used for the period 1992–95 weighed 15 g, and those used for the period 2003–06 weighed 12 g (American Wildlife Enterprises, Monticello, FL, USA). The radio-transmitters were attached to the bird with a Teflon harness, constructed with four pieces of Teflon strap held together with degradable thread and designed to fall off the bird in 2 years (approximately the same lifespan as the battery in the transmitter; Bennetts & Kitchens 2000). The radiotracking of animals was conducted



Figure 1. The five major wetland regions used by the Snail Kite in Florida (adapted from Martin *et al.*, 2006b): K, the Kissimmee Chain of Lakes; J, Saint John's Marsh (Upper St. John's River); O, Lake Okeechobee; L, Loxahatchee Slough (West Palm Beach Water Catchment Area/Grassy Waters Preserve); E, the Everglades.

by fixed-wing aircraft. This work was approved by the Institutional Animal Care and Use Committee (approval F#149).

From March 1992 to May 1995, 117 juvenile Snail Kites were tracked by aerial surveys and data on bird locations across the state were collected every 14 days throughout the year, by flying twice per week (for 4–5 h). We covered a different group of wetlands during each flight (4–5 h), enabling us to cover all of the wetland system in our study area through rotation (Fig. 1; Bennetts & Kitchens 2000). From March 2003 to May 2006, 149 juvenile Snail Kites were tracked by aerial surveys and data on bird locations across the state were collected every 30 days throughout the year, by flying over a different group of wetlands during each 4- to 5-h flight during the course of a 5-day period. The data from the first time period were restricted to locations obtained every 30 days for consistency in methodology with the second time period. The lifespan of transmitters used during the two time periods differed: for the pre-decline period they averaged 9 months, but for the postdecline period they averaged 22 months.

Before each survey, half of all radio frequencies were stored in one receiver (Advanced Telemetry Systems, Isanti, MN, USA) and the other half in a second receiver. Each radio receiver was set to scan through its set of frequencies, switching to the next frequency at regular intervals. A small two-element antenna was attached to each wing of the aircraft, which flew at an altitude of  $\sim 500$  m. Transects across major wetlands were flown at a speed of 110-180 km/h. When a signal was detected, we interrupted the scanning to focus on tracking this particular signal until we felt confident (based on the intensity of the signal) that it could be assigned to one of the wetlands included in our study area. After a signal was tracked down, the plane resumed its original transect route.

An individual was considered to have moved when its signal was detected in a different wetland region. Although we sampled the entire range of the Florida population of Snail Kites either once or twice per month, we were unable to detect every marked (radiotagged) juvenile during each sampling occasion. While the radio-transmitters were programmed to change signal pace upon mortality of the individual (i.e. the individual did not move for 6 h or more), often we did not hear a mortality signal, for example because a bird died and its body sank under water. When we had not recorded an individual for one or more previous time steps, or when we did not detect an individual for all subsequent time steps, we accounted for the probabilities of movement and survival within the modelling process described below. We created encounter histories consisting of sighting locations (i.e. wetland region of location) and non-detections for the length of time (by month/year) each radiotagged individual was tracked. Because the statistical models used to estimate movement probabilities accounted for imperfect detection, our estimates of movement for the two time periods should be comparable even with differences in sampling efforts (e.g. transmission power of the radiotransmitter, transect width) and other factors (e.g. altitude, speed) likely to affect detection probabilities of tagged birds.

## Data analysis

### Likelihood-based multistate models

We used likelihood-based multistate models in the program MARK version 5.1 (White & Burnham 1999) to model the probabilities of movement among the different wetland regions. The input for these models was the set of encounter histories created by the 266 radiotagged individuals from both time periods. We used multistate models to estimate probabilities of movement ( $\psi$ ), apparent survival (S) and detection probabilities (p). We used multinomial logit (mlogit) link functions (but used logit link functions when covariates were used to model movement) to enforce the constraint that all movement probabilities out of a stratum should be < 1. To minimize problems associated with the multimodal nature of the likelihood surface, we used simulated annealing as the optimization method (Cooch & White 2007, Ellison et al. 2007). Our analysis followed the general approach of Martin et al. (2006b), although those authors considered both adult and juvenile Snail Kites and only used data from 1992 to 1995. Because search efforts were greater in 1992–95 than in 2003–06, Martin et al. (2006b) used a known fate version of the model (i.e. they fixed S = 1). To accommodate the data collected in 2003-06 we treated S as a nuisance parameter (see below).

This model assumes that all mortality takes place before movement (White *et al.* 2006). It assumes that individuals do not die during transition or while in a new state before they are detected on the next encounter (White *et al.* 2006). Because of this assumption, estimating stratum-specific S parameters can be problematic, especially when the strata are geographical states (White *et al.* 2006). To avoid this problem, and because battery life in the radio-transmitters would be reflected in the S parameters, survival was treated as a nuisance parameter that estimates a combination of survival of the radio-transmitters and apparent survival of the population.

We accounted for possible differences in detection probabilities (e.g. due to different search intensities and observers) by allowing parameter pto vary among the two time periods. We also allowed p to vary by region. Although the data collection protocol did not vary spatially, the actual effort varied widely. Some sites were near major airports and a US Air Force base. Due to the high volume of air traffic and/or military exercises in these areas, we were often forbidden from entering certain airspace, forced to fly at suboptimal altitudes for detection or only allowed optimal altitudes for limited time. Each of the five regions was considered to be a geographical state (Bennetts *et al.* 1999, Martin *et al.* 2006b; Fig. 1), and we estimated movements among the five major wetland regions. We also considered a sixth geographical state that included all peripheral areas (see Martin *et al.* 2006b).

#### Parameter index matrices and design matrices

We modelled the probability of movement among regions as a function of several covariates related to habitat configuration. In particular, we considered patch size and distance among patches. With respect to patch size covariates, we considered the effect of the cumulative area occupied by wetlands in each of the five wetland regions (sites) of the donor site (AD) and of the receiving site (AR; see also Martin et al. 2006b). Distance among patches (d) was a measure of the distance between centroids of donor and receiving sites. These were the same measures of habitat configuration used in a study by Martin et al. (2006b). We used these covariates in our analysis because they appeared to be important factors influencing the movement of Snail Kites (Martin et al. 2006b).

For the models that included a distance and the effect of patch size, we modelled the peripheral areas not as a function of either distance or patch size but rather as having a distinct probability of movement. This was because the peripheral areas encompassed all other locations outside of the major regions and therefore it did not make sense to assign a distance or a patch size value to these areas. We also included models that ignored the effect of distance and patch size. In these models, we modelled movement as varying by geographical state (or region; r). An interaction among covariates is indicated with (\*) and an additive effect is indicated with (+).

We included an age effect in some of the models. Models that considered age as a factor assumed that movement probabilities varied between birds younger than 5 months and birds 5 months or older.

We modelled the apparent survival parameter S as a combination of apparent bird survival and radio-transmitter life. To account for variation in survival due to age, we considered models that included the same two age categories used to

model movement probabilities (see above). We also included models with sex as a covariate only in the post-decline period, because we collected feather samples from juvenile birds at time of capture starting in 2003. The tissue on the end of the calamus was analysed at a University of Florida genetics lab and by Avian Biotech International using molecular sexing techniques.

We modelled movement probabilities as linearlogistic functions of the covariates (Equation 1) (Blums *et al.* 2003, Martin *et al.* 2006b) in which  $\beta_i$  and  $\beta_{AR}$  were the parameters estimated.  $\beta_i$  was the intercept,  $\beta_{AR}$  was the slope for the area of receiving site, X was the vector of covariate values and  $\varepsilon$  was the error term.

$$logit(\psi(AR)) = \beta_i + \beta_{AR}X + \epsilon$$
(1)

#### Goodness-of-fit

We attempted to assess the goodness-of-fit of the fully time-dependent general model with several test statistics including the chi-square and G2 statistics using the program U-Care (Choquet *et al.* 2005); however, the data were too sparse, so we were unable to estimate goodness-of-fit.

#### Model selection

We used the Akaike information criterion adjusted for small sample size (AICc) and AICc weights (w) (Burnham & Anderson 2002) to select the most parsimonious model from all candidate models (i.e. the model that provided the best compromise between bias and precision, the model with the highest weight on a scale from 0 to 1; see Supporting Information Table S1).

#### Effect size

To quantify the effect of a particular factor on movement probabilities from the most parsimonious model, we computed estimates of effect size (ES) as the arithmetic difference between two estimates of interests (i.e. with and without the effect). Estimates of variance and approximate 95% CI were derived using the Delta method (Cooch & White 2007). If the confidence intervals of the effect size overlapped zero, then the difference between the estimates being compared was not considered statistically different.

## RESULTS

The two top models (with a combined AICc weight of 94%; Table 1) indicated that the nuisance parameter S differed only between time periods and was otherwise constant. Detection differed between time periods and geographical regions, and movement differed between time periods and among regions, and indicated that the area of the site to which the birds moved and the distance between sites were predictors of movement by juvenile Snail Kites, but only in the pre-decline period. The most parsimonious model also indicated that movement rates differed between the two periods (Figs 2 and 3). Average monthly probability of movement for the juvenile population of Snail Kites among the five wetland regions was different (ES = 0.040, 95% CI = 0.030-0.049) between the two time periods: 0.007 (95% CI = 0.002-0.011) pre-decline (n = 117 juveniles) and 0.046 (95% CI = 0.038-0.055) post-decline (n = 149 juveniles) (Fig. 4). Movement increased from most regions in the post-decline period as

Table 1. Models of monthly movement rates by Snail Kites in Florida for the pre-decline (1992–95) period vs. the post-decline period (2003–06).

Model	$\Delta$ AICc	W	К	Deviance
$S[\text{pre}(.)\text{post}(.)] p[\text{pre}(r)\text{post}(r)] \psi[\text{pre}(\text{AR} + d)\text{post}(r)]$	0	0.70	56	4011.39
$S[pre(.)post(.)] p[pre(r)post(r)] \psi[pre(AR*d)post(r)]$	2.14	0.24	57	4011.41
$S[pre(r)post(r)] p[pre(r)post(r)] \psi[pre(AR + d)post(r)]$	6.45	0.03	66	3996.48
$S[pre(.)post(.)] p[pre(r)post(r)] \psi[pre(AD)post(r)]$	6.67	0.03	55	4020.19
S[pre(.)post(.)] p[pre(r)post(r)] \u03c6[pre(r)post(r)]	20.01	0.00	74	3992.79

All models show a difference in survival (*S*), detection (*p*) and movement ( $\psi$ ) between the pre-decline and post-decline period. *S*(.) models show no difference in survival among geographical regions, sex or age. Some models vary only with regard to geographical region (*r*). In all models presented above, detection (*p*) varies according to region (*r*) but is different between the sampling periods. The top four models indicate that movement ( $\psi$ ) during the pre-decline period varies as a function of one or more habitat configuration covariates: area of receiving site (AR), area of donor site (AD), and distance (*d*) between donor and receiving sites. The top five models reflect that movement in the post-decline period varies across regions (*r*). Only models with *w* > 0 are presented in this table.



**Figure 2.** Sum of the movement probabilities ( $\psi$ ) by Snail Kites to and from each major wetland region, as well as to and from the periphery of the main Florida distribution range. KCL, Kissimmee Chain of Lakes.

compared with the pre-decline period. Eighteen of 20 movement estimates from wetland regions increased and six of those were significant. Movement rates increased significantly from Everglades (E) to Okeechobee (O) (ES = 0.0271, 95%CI = 0.0132-0.0409), E to Loxahatchee Slough (L) (ES = 0.0573, 95% CI = 0.0335-0.0811), O to E (ES = 0.2959, 95% CI = 0.1679-0.4239), O to L (ES = 0.1158, 95% CI = 0.0084-0.2232), L to E (ES = 0.0780, 95% CI = 0.0232-0.1327) and Kissimmee Chain of Lakes (K) to L (ES = 0.0497, 95% CI = 0.0056-0.0938). Two of five movement estimates from the major regions into the periphery also showed some evidence of increasing between time periods, but the CIs of the estimates spanned zero. Movement probabilities among all regions during both time periods and the differences between time periods are shown in Supporting Information Table S2.

Habitat configuration, specifically area of receiving site and distance, was a major predictor of movement in the pre-decline period (Martin et al. 2006b; Table 1). In the highest ranked model, habitat configuration had an effect on movement in the pre-decline period, but no effect in the postdecline period (Table 1). Although the model that assumed an effect of habitat configuration on movement in the pre- and post-decline period  $(S[pre(.)post(.)] p[pre(r)post(r)] \psi[pre(AR + d)$ post(AR + d)]) received limited support based on AICc weights ( $\sim 0$ ), the estimates of the slope parameters indicated that there was a negative relationship between distance and movement and a positive relationship between movement and AR (Fig. 5). The directionality of this relationship was consistent with our predictions and the findings

© 2012 The Authors Ibis © 2012 British Ornithologists' Union from Martin *et al.* (2006b). We found no evidence that movement was affected by sex or age. Models that included a sex effect received no support from the data based on AICc weights ( $w \sim 0$ ).

Our original *a priori* model set included models with varying age structures for both apparent survival (S) and movement ( $\psi$ ). Unfortunately, no model that included an age structure for movement reached numerical convergence, so we were not able to incorporate age structure into our final model set. However, unlike the study of Martin *et al.* (2006b) our study focused on birds that were radiotagged as fledglings, and tracked exclusively in their initial 22 months of life (the approximate lifespan of the radios).

To address further any possibility that age may influence movement, we reran the analysis with a truncated dataset. This truncated dataset excluded all sightings (from both time periods: pre- and post-decline) that occurred after 9 months. Unfortunately, these age-structured models also failed to converge. Furthermore, the estimates from models within the model set that used the truncated data that did converge displayed problems. The post-decline estimates and confidence intervals were not interpretable because there was insufficient data after truncation to estimate movement probabilities.

## DISCUSSION

The Snail Kite is a highly mobile species and has been described as nomadic in Florida (Bennetts & Kitchens 2000), although Martin *et al.* (2006b, 2007b) found evidence of annual philopatry to specific regions. Snail Kites have been known to



**Figure 3.** Sum of the monthly movement probabilities to and from each region and the periphery. The width of the arrow corresponds to the size of the sum of the  $\psi$ s. (a,b) Sum of movement probabilities from each region and the periphery. (c,d) Sum of movement probabilities to each region and the periphery. (c,d) Sum of movement probabilities to each region and the periphery. Movements (a,c) in the pre-decline period, and (b,d) in the post-decline period. Similar widths are assigned to the sum of movement probabilities within the same 0.05 interval (e.g. if the sum of the  $\psi$ s from one region is in the interval 0–0.05, the width of the arrow is 0.1, and if the sum of the  $\psi$ s from one region is in the interval 0.66–0.70, the width of the arrow is 1.5).

escape the physiological stress associated with drying events by moving to wetlands less affected by these disturbances (Beissinger & Takekawa 1983, Bennetts 1993, Bennetts & Kitchens 1997b). The population has become increasingly vulnerable after the precipitous decline of 2001 and populations have remained low since (i.e. fewer than 1000 individuals; Cattau *et al.* 2008) in the degraded habitat conditions of the Everglades ecosystem. Since the mid-2000s, survival and reproduction rates have decreased substantially: juvenile survival has varied between 0.1 and 0.4, adult survival between 0.6 and 0.9, and the proportion of successful nests between 0.2 and 0.5 (Cattau *et al.* 2008).

In addition, this study suggests that movement rates have increased. Increased movement of juvenile birds may further reduce their chances of survival because of higher energetic costs and mortality risks (Part 1995). For instance, dispersal is known to increase the risk of starvation and predation due to the exploration of new areas (Gaines



Figure 4. Estimates of average monthly movement probabilities by Snail Kites among the major wetland regions used by this species in Florida.

& McClenaghan 1980, Johnson & Gaines 1990, Strickland 1991).

The increase in juvenile movement, despite its potentially high costs, may be explained in the

context of the conceptual framework described by Bennetts and Kitchens (2000). The Snail Kite population during the pre-decline period may have been at the low-risk exploration stage of the conceptual relationship between dispersal and food availability, in which Kites make exploratory longdistance movements when food availability is high in order to gather information for future foraging needs. The population during the post-decline period was possibly in the leave or starve stage of the continuum postulated by Bennetts and Kitchens (2000). Such a scenario could be compatible with the facts that 2004 was a drier year than average and that the only two regions (J and L, Fig. 1) for which movement rates did not increase have been traditionally viewed as important refuges during drought. Therefore, a substantial number of Snail Kites may have responded to general drought and habitat degradation by taking refuge in these two wetland complexes.

We note that there are several limitations that should be considered when interpreting our results. First, habitat quality was not quantified, and therefore our assumption that the higher movement rates are in response to habitat degradation is not causative, but rather strengthens the hypothesis that the post-decline Snail Kite population experienced a different environment with



**Figure 5.** Estimates of monthly movement probabilities for the model that also incorporated the influence of habitat configuration on movement for the post-decline period:  $S[pre(.)post(.)] p[pre(r)post(r)] \psi[pre(AR + d)post(AR + d)]$ . Area of receiving site (AR) is on the *x*-axis. Distance between sites (*d*) is on the *y*-axis. Values are standardized. Probability of movement ( $\psi$ ) is on the *z*-axis. As distance decreases and area of receiving site increases, the probability of movement increases, but the relationship is steeper in the post-decline era.

different resources than the pre-decline population. Secondly, our data did not allow us to estipotential age-specific or sex-specific mate movement probabilities. The models that included these effects did not converge, and hence were unreliable. It is possible that age and sex affect movement probabilities but more data will be needed to discern these differences. Thirdly, our attempts to test radio-transmitter lifespan, and thus age structure differences, between the two time periods with a truncated dataset were inconclusive due to limited sample size. Thus, any Snail Kite movement probability differences between the two time periods attributable to this effect remain unresolved. Future studies of Snail Kite movement will necessitate a larger dataset to address the effects of age on movement rates.

# **Conservation implications**

The Comprehensive Everglades Restoration Plan is one of the most ambitious ecosystem restoration efforts ever undertaken (e.g. Mitsch & Gosselink 2007). Because Florida Snail Kite is one of the few avian taxa that is almost exclusively confined to the wetland units that constitute the former Greater Everglades, it is viewed as an important performance indicator for Everglades restoration (RECOVER 2005, USFWS 2007). Our study suggests that movement of juvenile Snail Kites has increased. Several studies have shown that increased movement can lead to lower survival (e.g. because of increased energetic costs). Thus, an increase in mortality associated with higher movement could further contribute to reducing the probability of persistence of the Snail Kite population in Florida.

Our study provides additional evidence that critical habitat in the Florida range of the Snail Kite population may not be enough to ensure long-term persistence or to maintain former population levels (Martin *et al.* 2008, Zweig & Kitchens 2008). Lake Okeechobee and Water Conservation Area 3A (the largest areas of historical use within the Everglades) are no longer functioning as the primary habitats of Snail Kites because juvenile birds are leaving these areas at higher rates. This seems to indicate that habitat quality has been diminishing.

Because managing agencies are increasingly relying on models to manage natural systems in the Everglades, it is important to obtain reliable estimates of vital rates and movement. For instance, Mooij *et al.* (2002) developed an individual-based model that ties water management scenarios to Snail Kite population dynamics. Movement is an important component of these models and our study, which is based on an extensive dataset, provides an opportunity to update these models with more reliable and current estimates of movement. These models can then be used to improve hydrological management to help the recovery of the Snail Kite. Continued monitoring of the status of the Florida Snail Kite population should remain a priority for the implementation of adaptive management strategies.

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# REFERENCES

- Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scand.* **23**: 355–365.
- Beissinger, S.R. & Takekawa, J.E. 1983. Habitat use by and dispersal of Snail Kites in Florida during drought conditions. *Florida Field Naturalist* **11**: 89–106.
- Belanger, G. & Rodriguez, M.A. 2002. Local movement as a measure of habitat quality in stream salmonids. *Environ. Biol. Fishes* 64: 155–164.
- Belisle, M., Desrochers, A. & Fortin, M.J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82: 1893–1904.
- Bennetts, R.E. 1993. The Snail Kite, a wanderer and its habitat. *Florida Naturalist* 66: 12–14.
- Bennetts, R.E. & Kitchens, W.M. 1997a. *The Demography* and Movements of Snail Kites in Florida. No. 56. Gainesville: USGS/Biological Resources Division, Florida Cooperative Fish & Wildlife Research Unit, University of Florida.
- Bennetts, R.E. & Kitchens, W.M. 1997b. Population dynamics and conservation of Snail Kites in Florida: the importance of spatial and temporal scale. *Colon. Waterbirds* 20: 324–329.
- Bennetts, R.E. & Kitchens, W.M. 1999. Within-year survival patterns of Snail Kites in Florida. *J. Field Omithol.* **70**: 268–275.
- Bennetts, R.E. & Kitchens, W.M. 2000. Factors influencing movement probabilities of a nomadic food specialist:

proximate foraging benefits or ultimate gains from exploration? *Oikos* **91**: 459–467.

- Bennetts, R.E., Dreitz, V.J., Kitchens, W.M., Hines, J.E. & Nichols, J.D. 1999. Annual survival of Snail Kites in Florida: radio telemetry versus capture-resighting data. Auk 116: 435–447.
- Bennetts, R.E., Darby, P.C. & Karunaratne, L.B. 2006. Foraging patch selection by Snail Kites in response to vegetation structure and prey abundance and availability. *Waterbirds* 29: 88–94.
- Blums, P., Nichols, J.D., Hines, J.E., Lindberg, M.S. & Mednis, A. 2003. Estimating natal dispersal movement rates of female European ducks with multistate modelling. *J. Anim. Ecol.* 72: 1027–1042.
- Boudjemadi, K., Lecomte, J. & Clobert, J. 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. J. Anim. Ecol. 68: 1207–1224.
- Burnham, K.P. & Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. New York: Springer.
- Cattau, C., Kitchens, W., Reichert, B., Bowling, A., Hotaling, A., Zweig, C., Olbert, J., Pias, K. & Martin, J. 2008. Demographic, Movement, and Habitat Studies of the Endangered Snail Kite in Response to Operational Plans in Water Conservation Area 3A. Gainesville: U.S. Geological Survey, Florida Cooperative Fish and Wildlife Research Unit, University of Florida.
- Choquet, R., Reboulet, A.M., Lebreton, J.D., Gimenez, O. & Pradel, R. 2005. U-CARE 2.2 User's Manual. CEFE. Availale at: http://www.cefe.cnrs.fr/biostatistiques-et-biologie-des-populations/logiciels (Accessed 16 January 2010).
- Clarke, A.L., Saether, B.E. & Roskaft, E. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* **79**: 429–438.
- Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) 2001. *Dispersal*. Oxford: Oxford University Press.
- Cooch, E.G. & White, G.C. 2007. Program MARK: A Gentle Introduction. Available at: http://www.phidot.org/software/ mark/docs/book/ (Accessed 10 June 2007).
- Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* 128: 231–240.
- Darby, P.C., Bennetts, R.E. & Percival, H.F. 2008. Dry down impacts on Apple Snail (*Pomacea paludosa*) demography: implications for wetland water management. *Wetlands* 28: 204–214.
- Ellison, L.E., O'Shea, T.J., Neubaum, D.J. & Bowen, R.A. 2007. Factors influencing movement probabilities of Big Brown Bats (*Eptesicus fuscus*) in buildings. *Ecol. Appl.* **17**: 620–627.
- Gaines, M.S. & McClenaghan, L.R. 1980. Dispersal in small mammals. Annu. Rev. Ecol. Syst. 11: 163–196.
- Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. 13: 1–21.
- Haas, S.E., Kimball, R.T., Martin, J. & Kitchens, W.M. 2009. Genetic divergence among Snail Kite subspecies: implications for the conservation of the endangered Florida Snail Kite *Rostrhamus sociabilis*. *Ibis* 151: 181–185.
- Haddad, N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecol. Appl.* 9: 612–622.
- Harmata, A.R., Montopoli, G.J., Oakleaf, B., Harmata, P.J. & Restani, M. 1999. Movements and survival of Bald

Eagles banded in the greater Yellowstone ecosystem. *J. Wildl. Manag.* **63**: 781–793.

- Havens, K.E. & Gawlik, D.E. 2005. Lake Okeechobee conceptual ecological model. Wetlands 25: 908–925.
- Hotaling, A.S., Martin, J. & Kitchens, W.M. 2009. Estimating transition probabilities among Everglades wetland communities using multistate models. *Wetlands* 29: 1224–1233.
- Ims, R.A. & Hjermann, D.O. 2001. Condition-dependent dispersal. In Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) *Dispersal*: 203–216. Oxford: Oxford University Press.
- Johnson, M.L. & Gaines, M.S. 1990. Evolution of dispersal theoretical-models and empirical tests using birds and mammals. *Annu. Rev. Ecol. Syst.* **21**: 449–480.
- Johnson, K.G., Allen, M.S. & Havens, K.E. 2007. A review of littoral vegetation, fisheries, and wildlife responses to hydrologic variation at Lake Okeechobee. *Wetlands* 27: 110–126.
- Karunaratne, L.B., Darby, P.C. & Bennetts, R.E. 2006. The effects of wetland habitat structure on Florida Apple Snail density. *Wetlands* 26: 1143–1150.
- Kitchens, W.M., Bennetts, R.E. & DeAngelis, D.L. 2002. Linkages between the Snail Kite population and wetland dynamics in a highly fragmented South Florida hydroscape. In Porter, J.W. & Porter, K.G. (eds) *The Everglades, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*: 183–203. Boca Raton: CRC Press.
- Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W. & Colby, D.R. 2001. Cascading of habitat degradation: Oyster reefs invaded by refugee fishes escaping stress. *Ecol. Appl.* **11**: 764–782.
- Macdonald, D.W. & Johnson, D.D.P. 2001. Dispersal in theory and practice: consequences for conservation biology. In Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) *Dispersal*: 358–372. New York: Oxford University Press Inc.
- Martin, J., Kitchens, W., Cattau, C., Bowling, A., Conners, M. & Huser, D. 2006a. Demography of the Snail Kite in blue cypress marsh complex. Final report 2005. *St. Johns River Water Manag. District Spec. Publ.* SJ2006-SP4: 1–31.
- Martin, J., Nichols, J.D., Kitchens, W.M. & Hines, J.E. 2006b. Multiscale patterns of movement in fragmented landscapes and consequences on demography of the snail kite in Florida. J. Anim. Ecol. 75: 527–539.
- Martin, J., Kitchens, W.M. & Hines, J.E. 2007a. Importance of well-designed monitoring programs for the conservation of endangered species: case study of the Snail Kite. *Conserv. Biol.* 21: 472–481.
- Martin, J., Kitchens, W.M. & Hines, J.E. 2007b. Natal location influences movement and survival of a spatially structured population of Snail Kites. *Oecologia* 153: 291–301.
- Martin, J., Kitchens, W.M., Cattau, C.E. & Oli, M.K. 2008. Relative importance of natural disturbances and habitat degradation on Snail Kite population dynamics. *Endang. Species Res.* 6: 25–39.
- McPeek, M.A. & Holt, R.D. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* 140: 1010–1027.
- Mitsch, W.J. & Gosselink, J.G. 2007. *Wetlands*. Hoboken: John Wiley & Sons, Inc.
- Mooij, W.M., Bennetts, R.E., Kitchens, W.M. & DeAngelis, D.L. 2002. Exploring the effect of drought extent and

interval on the Florida Snail Kite: interplay between spatial and temporal scales. *Ecol. Model.* **149**: 25–39.

- Ogden, J.C. 2005. Everglades ridge and slough conceptual ecological model. *Wetlands* 25: 810–820.
- Part, T. 1995. The importance of local familiarity and search costs for age-biased and sex-biased philopatry in the Collared Flycatcher. *Anim. Behav.* 49: 1029–1038.
- Pettorelli, N., Gaillard, J.M., Duncan, P., Maillard, D., Van Laere, G. & Delorme, D. 2003. Age and density modify the effects of habitat quality on survival and movements of Roe Deer. *Ecology* 84: 3307–3316.
- Real, J. & Manosa, S. 2001. Dispersal of juvenile and immature Bonelli's Eagles in northeastern Spain. J. Raptor Res. 35: 9–14.
- **RECOVER** 2005. *CERP System-Wide Performance Measures. Restoration Coordination and Verification*. West Palm Beach: South Florida Water Management District.
- Senar, J.C., Conroy, M.J. & Borras, A. 2002. Asymmetric exchange between populations differing in habitat quality: a metapopulation study on the Citril Finch. J. Appl. Stat. 29: 425–441.
- Strickland, D. 1991. Juvenile dispersal in Gray Jays dominant brood member expels siblings from natal territory. *Can. J. Zool.* 69: 2935–2945.
- Sykes, P.W.J. 1987. The feeding habits of the Snail Kite in Florida, USA. *Colon. Waterbirds* **10**: 84–92.
- Takekawa, J.E. & Beissinger, S.R. 1989. Cyclic drought, dispersal, and the conservation of the Snail Kite in Florida – lessons in critical habitat. *Conserv. Biol.* 3: 302–311.
- USFWS 2007. Snail Kite 5-Year Review: Summary and Evaluation. Vero Beach, FL: U.S. Fish and Wildlife Service.

- White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120–139.
- White, G.C., Kendall, W.L. & Barker, R.J. 2006. Multistate survival models and their extensions in Program MARK. *J. Wildl. Manag.* 70: 1521–1529.
- Zweig, C.L. & Kitchens, W.M. 2008. Effects of landscape gradients on wetland vegetation communities: information for large-scale restoration. *Wetlands* 28: 1086–1096.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Table S1. All candidate models from which the most parsimonious models were selected.

Table S2. All movement probabilities among the regions and the periphery pre- and postdecline and the effect size between them.

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