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Population Dynamics and Conservation of Snail Kites in Florida: The Importance of Spatial and Temporal Scale

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Abstract.—It has been suggested that the primary regulatory factor of Snail Kite (*Rostrhamus sociabilis*) populations in Florida is periodic drought. Consequently, the need for drought refugia has been previously identified as essential to the viability of kites. However, rainfall patterns across Florida are quite variable and the spatial and temporal patterns of drought have been largely ignored. We suggest that the primary response of Snail Kites to local drying events is behavioral; birds simply move to a different location. Small localized drying events occur at a relatively high frequency, whereas widespread droughts that encompass the entire range of Snail Kites in Florida are relatively rare. The occurrence of simultaneous drying events also is inversely correlated with distance between wetlands, resulting in greater asynchrony of drying events at larger spatial scales. Consequently, a large spatial extent helps to ensure that some refugia are available during most droughts. This enables individuals to escape the effects of droughts by moving.

Several management recommendations have focused on maintaining continuous inundation of wetland habitats; however, the lack of periodic drying can detrimentally affect the kites' nesting and foraging habitat. We suggest that ensuring adequate refugia from drought can, and should, be accomplished by maintaining suitable habitat across a large enough area (including habitats in several different watersheds) to include climatic variability, rather than by prolonging local inundation. A broad spatial extent enables areas to incur periodic drying (necessary for plant communities) on a rotational basis through climatic variability. Monitoring also must occur over time periods long enough to detect not only the short-term response of birds to a given drying event, but also the long-term response of the habitat to water management regimes.

Key words.—Conservation, drought, population dynamics, *Rostrhamus sociabilis*, Snail Kite, spatial scale, temporal scale.

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During the past 2 decades there has been an increased awareness of the importance of scale in investigations and conservation of birds and other organisms (e.g., Wiens *et al.* 1986, Morris 1987). Perceptions of biological patterns and processes are not independent of the spatial and temporal scales on which they are viewed (Wiens 1989). For example, factors such as resource abundance and disturbance that influence demographic processes or patterns of distribution at a local spatial scale may be expressed quite differently at a regional scale.

In 1991, we began a study of the demography and movements of the endangered Snail Kite (*Rostrhamus sociabilis*) in Florida (Bennetts and Kitchens 1997). The purpose of our research was to better understand Snail Kite population dynamics and the influence of environmental conditions. Our emphasis was on obtaining reliable estimates of demographic and dispersal parameters, using a combination of radio telemetry and capture-recapture techniques. These estimates were to be used in a variety of management and modeling contexts. The importance of spatial and temporal scale to population dynamics and conservation of Snail Kites soon became apparent. Here, we present a summary of our current understanding on this topic. Our work is continuing and many of the ideas herein will be tested through continued field study and modeling.

THE STUDY POPULATION

The United States population of Snail Kites is restricted to Florida and is currently estimated to be approximately 1,500 individuals (V. J. Dreitz *et al.*, unpubl. data). It has been speculated that Snail Kites may move between Florida and Cuba (Beissinger *et al.* 1983); however, no supporting evidence has emerged for this hypothesis. Within Florida, Snail Kites are somewhat nomadic (Sykes 1983a, Bennetts 1993), often moving to new locations several times per year throughout their range (Bennetts and Kitchens 1997). Thus, for management and conservation purposes, we believe that the Florida population should be considered as one geographically closed population.

THE IMPORTANCE OF SPATIAL EXTENT

It has been suggested that the primary regulatory factor of the Florida population of Snail Kites is periodic drought (Beissinger 1986, Takekawa and Beissinger 1989). Florida apple snails (*Pomacea paludosa*) are aquatic and have a limited capacity to survive dry conditions (Little 1968, Darby *et al.* 1996). Consequently, droughts may result in periodic reductions in the abundance and/or availability of kite food resources (Kushlan 1975, Sykes 1979). We agree with Beissinger (1986) and Takekawa and Beissinger (1989) that the Florida population of Snail Kites is limited by droughts. However, we also believe that the spatial and temporal patterns of drought events are essential components to understanding how Snail Kites have persisted in Florida.

Droughts occur at periodic intervals of about 5-10 yrs (Thomas 1974, Beissinger 1986, Duever *et al.* 1994). However, like most disturbance processes, the frequency and spatial extent of such events are not independent (Sousa 1984). Rainfall patterns across Florida are quite variable and small localized drying events occur at a relatively high frequency (McVicar and Lin 1984). In contrast, widespread droughts that encompass the entire range of Snail Kites in Florida are relatively rare (MacVicar and Lin 1984, Duever *et al.* 1994, Bennetts and Kitchens 1997). The occurrence of simultaneous drying events also is inversely correlated with distance between wetlands. Drying events in wetlands that are far apart and in different watersheds are much less likely to occur simultaneously (Bennetts and Kitchens 1997). Thus, at larger spatial scales, there is greater asynchrony of drying events than occurs at smaller spatial scales.

This asynchrony of drying events over a broad spatial extent could enhance persistence at both a population and individual level. At the population level we propose an extension of Den Boer's (1968, 1981) concept of "spreading of risk". Den Boer suggested that populations exhibiting a metapopulation structure (i.e., consisted of spatially segregated subpopulations) in variable environments are more stable because the risk of catastrophic events (e.g., disturbance) is spread among the subpopulations. This concept is more simply understood by the popular analogy of not having all of one's eggs in a single basket. However, as Den Boer recognized, all subpopulations could eventually experience local extirpation if there were no dispersal among subpopulations to enable recolonization.

We propose that the persistence and stability of the Florida Snail Kite population is enhanced by a mechanism similar to concept of risk spreading. A key distinction is that our data suggest that the Florida population of Snail Kites is a single population, rather than a metapopulation comprised of local subpopulations. However, this population moves freely, within a network of local habitats (Fig. 1). Thus, we consider risk in relation to habitat (i.e., a meta habitat comprised of local subhabitats) rather than subpopulations, although birds obviously respond to habitat changes. The risk of drying events is spread across the landscape unequally through spatial extent and heterogeneity of rainfall. As the spatial extent of the habitat network increases, the probability that some habitats will remain inundated during a given drought also increases. Thus, even if Snail Kites lacked mobility, a larger spatial extent would enhance persistence in some habitats during any given drought.

The fitness of individual birds also may be enhanced by an asynchronous and variable environment. Birds may be less sensitive to localized disturbance events because of

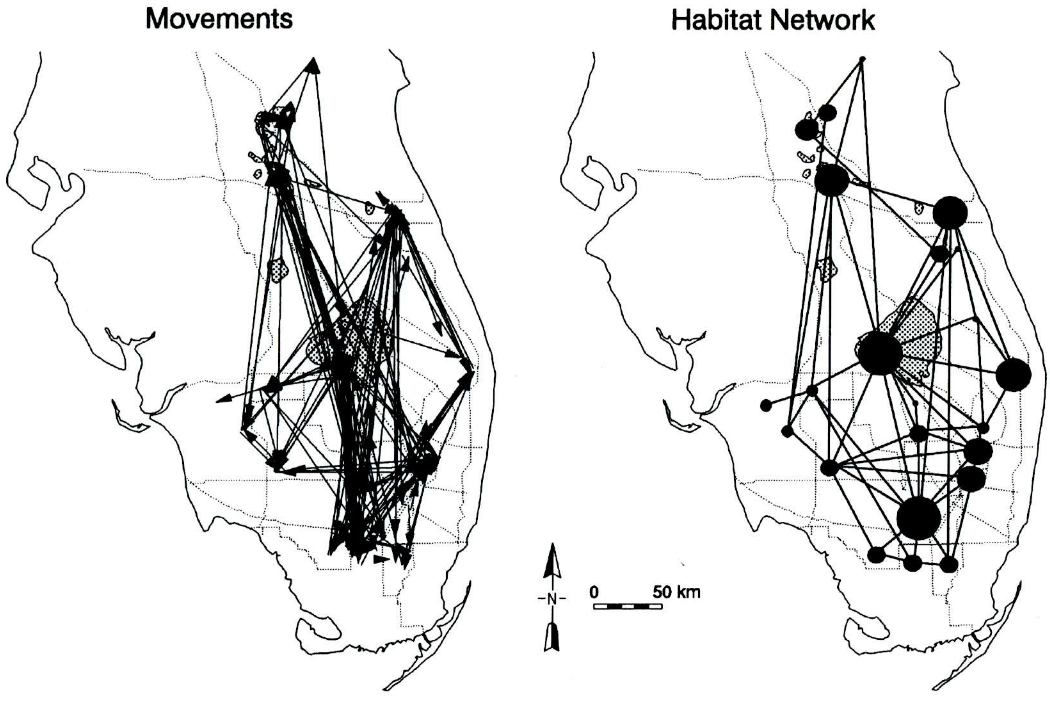

Figure 1. Map of South Florida showing inter-wetland movements (arrows) of adult radio-tagged Snail Kites over a 1-year period from April 1992-April 1993 (left). These movements illustrate a network of habitats used by Snail Kites (right). We have shown data for this limited time period to minimize cluttering. The complete habitat network is substantially more detailed.

their ability to escape such events (Wiens 1989). Asynchrony of disturbance would help to ensure that some refugia are available during most disturbance events. Dispersal of Snail Kites to refugia habitats during droughts is well known (Sykes 1983a, Beissinger and Takekawa 1983, Takekawa and Beissinger 1989). Snail Kites are often considered nomadic (Sykes 1983b, Sykes *et al.* 1995) and our data from 271 radio-tagged individuals indicated that Snail Kites in Florida frequently moved throughout their range (Bennetts 1993, Bennetts and Kitchens 1997). This high mobility in combination with spatial heterogeneity of rainfall may enable Snail Kites to persist in an environment that experiences frequent depletion of local food resources.

We have hypothesized that the primary response of Snail Kites to local drying events is behavioral; birds simply move to a different location (Bennetts and Kitchens 1997). However, as droughts become increasingly widespread, both survival and reproduction may decrease as local food resources and refugia become less available (Sykes 1983a, Beissinger 1986, Takekawa and Beissinger 1989; Fig. 2).

THE IMPORTANCE OF TEMPORAL SCALE

We suggest that temporal scale, particularly with respect to water management, also is a key factor in the conservation of Snail Kites and Florida's wetlands. Several recommendations have focused on maintaining continuous inundation of wetland habitats (e.g., Stieglitz 1965, Stieglitz and Thompson 1967, Beissinger 1988). It has also been suggested that small wetland units be kept inundated during periodic drying events (Sykes 1983a, 1983b; Takekawa and Beissinger 1989). A critical issue that has been largely ignored by these recommendations (but see Sykes 1983a) is that the lack of periodic drying can detrimentally effect the kites' nesting and foraging habitat (Bennetts *et al.* 1994, Bennetts and Kitchens 1997). Virtually

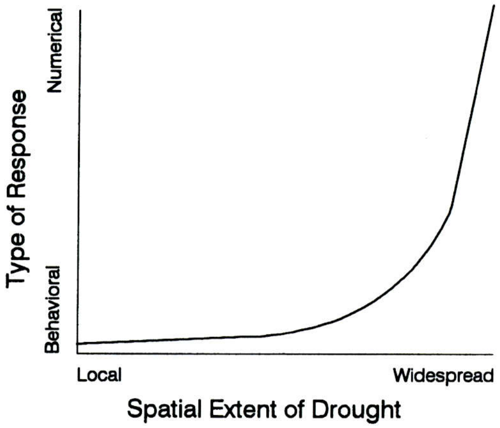

Figure 2. Hypothesized relationship between the spatial extent of droughts and whether the response by Snail Kites is likely to be behavioral (i.e., movement) or numerical (i.e., change in survival and/or reproduction).

all woody vegetation used as nesting substrates, and gramminoid species that are an essential component of foraging habitat, require periodic drying to reproduce and/or survive (Craighead 1971, Gunderson and Loftus 1993, Gunderson 1994). Thus, management that prolongs inundation may result in long-term degradation of the very habitat it is intended to protect. Shifts in the distribution of Snail Kites over the past 2 decades indicate a decreased use in several areas experiencing nearly continuous inundation. However, as a result of water impoundment behind levees, the effects of prolonged inundation and increased water depth are highly confounded (Bennetts and Kitchens 1997). We suggest that any management or evaluation of Snail Kite habitat must consider not only the short-term response of birds to a given drying event, but also the long-term response of the habitat to water management regimes.

IMPORTANCE OF THE INTERPLAY BETWEEN SPATIAL AND TEMPORAL SCALE

We agree with previous authors (e.g., Sykes 1979, Beissinger 1988, Bennetts *et al.* 1988, Beissinger 1995, Sykes *et al.* 1995) that suitable Snail Kite habitat is inundated for relatively long periods (e.g., 1-5 yr average return interval of drying events); however, excessive inundation (e.g., > 5-yr average return interval) probably results in habitat deterioration (Bennetts *et al.* 1988, 1994). The interplay between spatial and temporal scales may provide an answer to this apparent paradox. We also agree with previous authors (e.g., Takekawa and Beissinger 1989) that availability of refugia during drought is essential for the persistence of Snail Kites in Florida. However, we believe that ensuring adequate refugia can, and should, be accomplished by maintaining suitable habitat across a large spatial extent (including habitats in several different watersheds), rather than by prolonging local inundation or attempting to keep small areas inundated within areas experiencing local drying. Managing refugia over a broad spatial extent enables areas to incur the periodic drying (necessary for plant communities) on a rotational basis through climatic variability, rather than trying to "fight" natural rainfall patterns. Attempting to increase stability in a dynamic ecosystem is not only difficult but undesirable ecologically. Periodic disturbance events such as fire, hurricanes, and drought are integral parts of south Florida's landscape patterns (Davis *et al.* 1994). The behavioral responses of Snail Kites to drying events appear well adapted to cope with natural climatic variability.

The uncertainty of specific spatial and temporal patterns of drought at a local scale necessitates habitat conservation at a regional scale to ensure persistence. Currently designated critical habitat occurs almost entirely within the Everglades and Lake Okeechobee watersheds (Federal Register 42 [155]:40685-40688; 50 CFR Ch. 1 [10-1-94 edition]). This spatial configuration of protected habitat ignores what we believe is the primary mechanism (large spatial extent of quality habitat) enabling Snail Kites to persist in the dynamic environment of Florida. The proximity of these 2 watersheds results in a high occurrence of simultaneous drying events (Bennetts and Kitchens 1997). Previous authors (e.g., Sykes 1983a, 1983b; Takekawa and Beissinger 1989) stressed that protection of drought refugia is necessary; however, we believe that spatial configuration of those refugia is equally important. Protection of habitats in watersheds outside of the Everglades and Lake Okeechobee (e.g., St. Johns River and Kissimmee River basins) is essential if refugia are expected to be available during droughts.

Protection, management, and monitoring of habitat must be implemented over a spatial extent broad enough to encompass climatic variability within the Snail Kite's range and over time periods long enough to measure habitat deterioration. When they represent only a portion of the population at one location, local and/or short-term evaluations of Snail Kite population dynamics have a high probability of producing spurious conclusions. Behavioral (i.e., movement) and demographic (numerical) responses in these evaluations are easily confounded. Although in this paper we have emphasized the importance of spatial and temporal scale in relation to natural climatic variability, we must also recognize anthropogenic influences on habitat quality and hydrologic regimes. Habitat loss to urban and agricultural development continues to occur, even within the current spatial extent of the habitat network. Habitat quality may be deteriorating as a result of increasing nutrients (Bennetts *et al.* 1994). Drying events also may be increasing above naturally occurring frequencies as a result of water management (Beissinger 1986).

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