Recovery of the Snail Kite in Florida: Beyond a Reductionist Paradigm

Robert E. Bennetts and Wiley M. Kitchens
Florida Cooperative Fish and Wildlife Research Unit
Gainesville, Florida

Donald L. DeAngelis
U.S. Geological Survey, Biological Resources Division
and University of Miami
Coral Gables, Florida

Introduction

In science and problem-solving in general, it is easiest to seek a simple explanation for an observed phenomenon. In a book on the psychology of understanding and managing complex systems, Doerner (1996) illustrates through many examples how great the temptation is to use simple although sometimes erroneous hypotheses, or to push a correct one far beyond the limits of its validity. Doerner describes experiments in which subjects were presented with artificial, but realistically complex ecological and economic systems. The subjects were charged with running these systems over a period of time, with the goal of maintaining their viability, by making decisions, observing the consequences, making further decisions and so forth. Time and again, the subjects grasped at a single simple hypothesis or factor that resulted in a failure of the system they were charged with managing. Scientific practice, heeding Ockham’s razor, encourages a reductionist approach that is often successful when the scope of inference is limited. However, the initial success of an hypothesis that reduces a phenomenon to one or a small number of factors may blind one to other factors that may be important or become important later, particularly if inferences are extended beyond their original scope. Too often in science, reductive approaches are used in the hope of avoiding having to deal with the complexity of such systems.

Doerner’s conclusions have been repeatedly exemplified in resource management. A recent review of 23 case histories of resource management that were considered failures indicated that the type of reductionist approach described by Doerner was a common pathology that contributed to these failures (Holling 1995, Holling and Meffe 1996). In these cases, the emphasis was placed on finding a target variable and attempting to stabilize that variable such that

normal fluctuation would not impose a threat to the resource of interest. The result was that key elements of these systems changed over time. These changes, however, generally either occurred so slowly as to escape detection, or they were not considered of major concern because the resource problem was narrowly defined in such a way as not to encompass these changing elements. The net result of this reductionist approach was that, over time, these ecosystems tended to become more spatially homogenous and, consequently, were less resilient to disturbance. Here, we present a case history of endangered species management for the snail kite (Rostrhamus sociabilis) in Florida that we believe strongly parallels this type of pathology, which we refer to as the "reductionist paradigm."

The Reductionist Paradigm for Snail Kites

An Historical Perspective Leading to the Paradigm

Descriptive accounts of snail kite populations during the late 1800s and early 1900s indicated that snail kites were relatively abundant in Florida, at least at some locations. Scott (1881) described snail kites as being "abundant" at Lake Panasofkee. Bailey (1884) quotes from a letter he received from an egg collector, Mr. E.W. Montreuil, describing snail kites as being "found in numbers in the Everglades." Wayne (1895) described kites as "exceedingly common" on the Wascissa River in the Florida Panhandle. Later, Howell (1932) described "scattered flocks of a hundred or more" birds frequently having been found.

By the 1920s and continuing through the 1950s, virtually all reports began to describe snail kites in Florida as declining or rare (Howell 1932, Sprunt 1945, Wachenfeld 1956). These declines were attributed primarily to widespread drainage that occurred throughout Florida (Howell 1932, Sprunt 1945, Sykes 1983a, Bennett et al. 1994). Since that time, snail kite numbers have rebounded from what was considered to be a low of about 50 to 100 birds (Sprunt 1945) to a current estimate of approximately 1,500 birds (V.J. Dreitz unpublished data). This rebound has been largely attributed to the creation of several water conservation areas, whose primary purpose was flood protection and water storage, but which also provided long-hydroperiod marshes in areas where they had been substantially reduced by drainage (e.g., Sykes 1983b).

Snail kites in Florida have been monitored since 1969 via an annual statewide survey (Sykes 1979, Rodgers et al. 1988, Bennett et al. 1994). Several authors have viewed the survey as a census of population size, thus, enabling inferences to be made about changes in population size, particularly in response to water levels (e.g., Sykes 1979, 1983a, Snyder et al. 1989, Beissinger

Snail Kite Recovery in Florida 487
1995). For example, the difference between the 1980 and 1981 surveys has been widely cited as an estimate of mortality during a widespread drought in 1981 (e.g., Beissinger and Takekawa 1983, Beissinger 1986, Takekawa and Beissinger 1989).

Reproductive success also has been reported to be influenced by water levels. For example, Snyder et al. (1989) presented a summary of nesting data over an 18-year period and concluded that nest success was lower during years of low water. This effect was largely due to nest collapse resulting from the use of less stable herbaceous nest substrates during low-water years when drying increased access of woody substrates to potential predators. Beissinger (1986) also reported that a large proportion of snail kites did not attempt to nest during a drought in 1981, and that nest success was low both in 1981 and 1982.

More recently, Beissinger (1995) presented a population viability analysis (PVA) for snail kites. This model used the annual survey as a primary basis for verification and as a source of data for its most sensitive parameter, survival during drought years. The model focused on the occurrence of droughts as the primary environmental effect for predicting changes in population size. Projections from the model indicated that the Florida population of snail kites would not be viable unless the interval between successive droughts exceeded 4.3 years.

**The Resulting Paradigm**

The cumulative effect of these observations, regardless of the validity of specific approaches, was a perception of water levels being the primary influence on the Florida snail kite population (Beissinger and Takekawa 1983, Sykes 1983a, 1983b, Takekawa and Beissinger 1989). In particular, droughts have been portrayed as demographic catastrophes in which both survival and reproduction plummet (Takekawa and Beissinger 1989, Beissinger 1986, 1995). Management recommendations under the existing paradigm have focused primarily on increasing the interval between droughts and maintaining permanent water levels (e.g., Stieglitz and Thompson 1967, Martin and Doebel 1973, Beissinger 1983, 1995), although a need for refugia during droughts also has been recognized (Sykes 1983a, Takekawa and Beissinger 1989).

We suggest that this management paradigm closely parallels the pathology described above for failed resource management in other ecosystems. A target variable was identified, in this case water levels. The proposed solution for maintaining viable populations of snail kites was then to minimize the occurrence of droughts. Thus, stabilization of water levels was intended to buffer the population from potential demographic consequences of hydrologic variability. However, as in other systems, this approach has ignored effects beyond the species of interest, particularly plant communities, and hence the long-term indirect effects on the snail kite through other changes to the ecosystem.

Conflicts and Limitations of the Existing Paradigm

There are a number of conflicts inherent in the existing paradigm that warrant consideration. For example, under the existing paradigm, conflicts have been perceived among species with differing hydrologic requirements. Suitable conditions for snail kites have been portrayed as being in conflict with species such as wood storks (Mycteria americana) (Graham 1990) or white-tailed deer (Odocoileus virginianus) (Beissinger 1983), even though these species have coexisted with kites for centuries. Management recommendations under the existing paradigm also have largely overlooked the influence of stabilizing water levels on other species within central and southern Florida, and even on habitat quality for snail kites beyond a limited time frame. Recent assessments (e.g., Beissinger 1995) have merely assumed that habitat quality will not change in response to stabilizing water levels despite substantial evidence to the contrary. These assessments have focused only on a lower limit of drying frequencies, which implies that an upper limit does not exist, or that it is of relatively little concern. In contrast, there is a considerable body of evidence regarding the tolerances of the plant species that comprise suitable habitat to prolonged inundation (e.g., Craighead 1971, U.S. Department of Interior 1972, McPherson 1973, Worth 1983, Gunderson 1994). Similarly, the occurrence of drying events is often the only hydrologic effect considered, when substantial evidence suggests that other factors such as water depth also are important (e.g., Steiglitz and Thompson 1967, Sykes 1987, Bennetts et al. 1988). Assessments of the effects of drought (e.g., Snyder et al. 1989, Beissinger 1995) also have made no distinction regarding the spatial extent or severity of a given drought, even though the effect on survival or reproduction of kites probably depends greatly on the spatial extent of the drought (Bennetts and Kitchens 1997a, 1997b).

Beyond the Current Paradigm

The Importance of Spatial and Temporal Scales

One of the possible reasons for failures in resource management is a lack of attention to all of the spatial and temporal scales that are relevant to a problem. There is a substantial body of ecological literature describing the linkages between patterns and processes and how these linkages are related to scale (e.g., Wiens 1989a, Holling 1992). We suggest that a lack of consideration of some relevant scales has been an inherent feature of the reductionist paradigm of snail kite management. Recommendations have focused on stabilizing the conditions that seem most suitable for kites at a given time, while ignoring the

Snail Kite Recovery in Florida 489
consequences of that action over longer time scales. Similarly, management recommendations have focused on a limited spatial scale by considering the impacts of management to individual wetlands (e.g., Bennetts et al. 1988), while ignoring the spatial and temporal dynamics those wetlands contribute to the functioning of the whole network of habitats used by kites. We suggest that explicit incorporation of scale can, at least conceptually, resolve many of the conflicts and limitations of the existing paradigm. We further suggest a conceptual framework, described below, that goes beyond the limitations of the existing paradigm to enable a more comprehensive evaluation of snail kite population dynamics. This framework involves the interaction between spatial and temporal scales of snail kite habitat and population dynamics, and the long-term persistence of kites in a fluctuating environment. Although many of the features we describe in this conceptual model have a strong empirical basis, our intention here is to represent our ideas as hypotheses to be tested, rather than as a verified model.

The Dynamic Landscape Hypothesis

We agree with proponents of the current paradigm that water levels are a critical component of snail kite habitat and viability. However, we argue that favorable habitat for the snail kite depends on at least three different aspects of hydrology that can be related to different temporal scales. When these temporally explicit hydrologic factors are considered across a broad spatial scale, a dynamic pattern emerges that we call the “dynamic landscape hypothesis.” The first scale is that of current water levels (depth). The empirical relationship between snail kite use of a given habitat and water depth has been well recognized and has been illustrated by the distribution of nests or foraging birds with respect to water depth (e.g., Steiglitz and Thompson 1967, Sykes 1987, Bennetts et al. 1988, Bennetts and Kitchens 1997a). The response of snail kites to changing water depth also can be seen in shifts in spatial distribution. For example, the spatial distribution of nesting kites within Water Conservation Area (WCA) 3A, a 237,000-hectare impoundment used extensively for nesting during the past three decades, was similar for 1992, 1993 and 1994 (Figure 1). During the 1995 breeding season, water depths were at record-high levels throughout the Everglades as a result of tropical storm Gordon the previous fall (Bennetts and Kitchens 1997a). The distribution of nesting kites within WCA-3A shifted dramatically to the north during 1995, to an area of higher elevation. When water levels receded the following year, the distribution of nesting birds shifted back to the south where they had been prior to the high water. Similar shifts also have been observed in other areas.

Figure 1. The distribution of snail kite nests in Water Conservation Area 3A during each year from 1992 through 1996. During 1995, this area experienced exceptionally high water levels as a result of Tropical Storm Gordon, and the distribution of nesting kites shifted to higher elevations.

Water depth probably is important for snail kites because of how it affects their primary food source, apple snails (Pomacea paludosa), particularly with respect to snail behavior. Shallow water depths may restrict the movement of snails, as submergent vegetation becomes densely compacted within the water column (Darby et al. 1997). Shallow water during certain seasons also may result in water temperatures rising above the tolerance level of snails (Darby et al. 1997). Conversely, water that is too deep may lack sufficient oxygen to support apple snails (Hanning 1978) and/or lack sufficient vegetation that would enable snails to climb near the surface, where they are available to kites (Darby et al. 1997).

The second hydrologic factor is the time since a dry-down at a given location. This factor affects both apple snail population dynamics and the plant communities comprising snail kite habitat. Florida apple snails are aquatic and
have a limited capacity to survive dry conditions (Little 1968), although the
timing of drying may be as if not more important to the overall population
dynamics than just the occurrence of drying (Darby et al. 1997). Drying events
result in periodic reductions in the availability of snail kite food resources
regardless of whether there is a substantial effect on the snail population. At the
present time, no data exist on how quickly apple snail populations recover fol-
lowing a drying event. However, we compared the number of snail kites counted
during the annual survey before and after drying events in several wetlands to
provide an indication of how quickly snail kite numbers recovered following a
drying event. We found the number of kites counted during the year following a
dry year averaged about 50 percent of the number counted the year prior to
drying. The percentage increased to 85 percent two years following and had
exceeded 100 percent after three years. However, there could be a lag time be-
tween apple snail recovery and the return time of kites. The speed at which
recovery occurs also probably depends considerably on the severity (i.e., mag-
nitude and duration) and timing of a given drying event (Darby et al. 1997).
Apple snails are capable of surviving dry conditions for at least 12 weeks, al-
though survival may depend on age and reproductive status (Darby et al. 1997).
Drying that occurs after peak snail reproduction (April to May) that does not
persist for an extended time (e.g., more than one month) may require little time
for recovery. Conversely, drying that occurs before peak snail reproduction and
persists for an extended period may require more time for recovery.

Although the occurrence of drying events may affect apple snail popu-
lations, the absence of drying results in changes in plant communities. Snail
kites tend to select woody vegetation as a nest substrate if it is available (Bennetts
et al. 1988), and nest success tends to be substantially higher when woody sub-
strates are used compared with herbaceous substrates (Snyder et al. 1989). Thus,
esting habitat is usually comprised of a mixture of woody shrubs and stands of
sawgrass that are interspersed among foraging habitats (Bennetts et al. 1988,
1994, Sykes et al. 1995). Foraging habitat is generally comprised of wet prairie
or slough communities (Loveless 1959) with sufficient emergent vegetation to
allow apple snails to surface where they are available to kites (Bennetts et al.
1994, Bennetts and Kitchens 1997a). Observable changes in these plant com-
munities, including the loss of both woody and herbaceous species, in the ab-
sence of drying occurs after about five to six years (Ager and Kerce 1970, U.S.
Department of the Interior 1972), and some plant communities comprising kite
habitat can be replaced by other communities in as little as 9 to 10 years (Milleson
1987). Thus, the relationship between relative habitat quality for snail kites and
time since a drying event can be shown using a conceptual model (Figure 2).
Figure 2. Conceptual model of relative habitat quality in relation to the time since a drying event at a given location. In the absence of a drying event (A), habitat quality initially increases as the apple snail population recovers, but declines after five to six years as the plant communities comprising nesting and foraging habitat begin degradation. If drying events occur too frequently (B), the apple snail population will not have recovered to its full potential. If drying events occur at longer intervals (C), then a cumulative process of slow and incremental degradation will occur as plant communities undergo transition.

Snail Kite Recovery in Florida  ♦  493
The third hydrologic factor is a cumulative effect of drying patterns over a longer time scale. In particular, the frequency of drying events is expressed as a "hydrologic regime" and is measured as long-term hydroperiod (the proportion of time an area is inundated). This long-term pattern is the primary hydrologic scale at which plant communities are regulated, although vegetation may also be regulated by still slower processes that affect climatic regimes and sea-level rise (Gunderson 1994). Although rapid degradation of kite habitat occurs if a site is kept inundated, most sites experience drying at intervals less than that which would result in a direct transition of a plant community (Bennetts et al. 1988, Bennetts and Kitchens 1997a). Habitat changes often occur slowly and incrementally, with periods of at least partial rejuvenation resulting from periodic drying. The response of snail kites to habitat changes at this scale also can be illustrated by changes in their spatial distribution over longer time scales (Figure 3).

Available evidence suggests that suitable conditions at each of these hydrologic scales is necessary, but none is sufficient by itself to constitute suitable habitat for snail kites. The hydrology at each of these scales regulates a different aspect of the environment important to snail kites. In combination, these factors regulate: 1) the behavior of apple snails and, consequently, their availability to kites; 2) apple snail population dynamics; and 3) plant community change. Thus, if a given location has the appropriate water depth, but has experienced a drying event within the past few months, the apple snail population may be too low to be used by kites. Similarly, if a location has been inundated for a suitable period of time, but water depth is too high or low, the availability of prey may be unsuitable for kites, and so on. Thus, we hypothesize that an indication of overall habitat quality can be determined as an alignment of suitable conditions at each of these three scales. This alignment can be viewed as a dynamic "window" of hydrologic conditions at a given point in time and space in which snail kites occur (Bennetts and Kitchens 1997a).

Persistence of Snail Kites in a Dynamic Landscape

The second element of our dynamic landscape hypothesis was initially described (Bennetts and Kitchens 1997a, 1997b) and is based on the concept that persistence of the Florida population of snail kites is enhanced more by spatial extent of suitable habitat than by prolonging local inundation. We agree with Beissinger (1995) that there is a threshold mean periodicity of droughts below which kite populations will not be sustained. However, this applies more to droughts that affect the full extent of the kite's range in Florida than to localized drying affecting a small number of wetlands. In fact, periodic disturbance events such as fire, hurricanes, and local and regional droughts are integral parts
Figure 3. The reported nesting distribution of nesting snail kites (shaded) in Water Conservation Area 3A (WCA3A) from 1965 to present showing the shift in distribution from areas of longer hydroperiod (i.e., lower elevation) to shorter hydroperiod over a period of several decades. Birds nesting in southeastern WCA3A during the 1992 to 1996 period were foraging primarily in Everglades National Park and the "Pocket" between the L-67A and L-67C levees, both of which have shorter hydroperiods than the nesting area.

of southern Florida's landscape patterns (Davis et al. 1994). In virtually every ecosystem where disturbance processes have been markedly reduced, there has been a subsequent realization of their ecological importance (Pickett and White 1985). In southern and central Florida droughts occur at periodic intervals of

Snail Kite Recovery in Florida  •  495
about 5 to 10 years (Thomas 1974, Beissinger 1986, Duever et al. 1994). However, like most disturbance processes, the frequency and spatial extent of such events are not independent (Delcourt et al. 1983). Rainfall patterns across Florida are quite variable and localized drying events occur at a relatively high frequency, while widespread droughts that encompass all or most of the snail kite's range in Florida occur much less frequently (McVicar and Lin 1984, Duever et al. 1994, Bennetts and Kitchens 1997a, 1997b). It is these widespread droughts that have the greatest impact on the snail kite population. When a localized drying event affects only a limited portion of the kite's range (e.g., the "drought" of 1985), kites may be able to escape its effect by moving to another location. However, during a widespread drought, refugia are less available (Takekawa and Beissinger 1989), and a numeric response (i.e., change in survival and/or reproduction) becomes increasingly likely (Bennetts and Kitchens 1997a, 1997b). Thus, periodic local drying, necessary to maintain plant communities and, thus, kite habitat, occurs without catastrophic effects on the snail kite population. These local drying events, at natural frequencies, should be considered as an essential component of a functioning ecosystem, rather than as catastrophic events requiring stabilization. Stabilization results in a slow but steady conversion of wetlands to a more homogeneous aquatic state, degrading their habitat value for snail kites.

The heterogeneity of rainfall patterns throughout the kite's range plays a crucial role in enabling snail kites to persist in a dynamic environment. Because of the ability of kites to escape the effects of local drying events by moving, demographic consequences of most such events are buffered. Consequently, conservation of habitat over a broad spatial extent (e.g., in several watersheds) that encompasses natural heterogeneity of rainfall patterns is essential if refugia are expected to be available during droughts. Reducing the spatial extent of habitat thus reduces the mechanism for resilience of the population to local drying events. Others have recognized a need for drought refugia (e.g., Sykes 1983a, 1983b, Takekawa and Beissinger 1989), but the importance of the spatial pattern of such refugia has been largely overlooked.

Conclusions

We are not arguing for a more spatially and temporally complex view of snail kite dynamics purely for the sake of complexity. Rather, we find that this framework is essential to understand kite population and movement dynamics and to make long-term predictions and prudent management decisions. The principle of parsimony suggests that a model should contain enough factors to describe the system of interest and to eliminate excessive parameters that do

not significantly contribute to an understanding of that system (Burnham and Anderson 1992, Lebreton et al. 1992). It is our belief that the existing reductionist paradigm goes beyond parsimony and has resulted in an inadequate understanding of snail kite habitat and population dynamics by virtue of its narrow view of spatial and temporal time scales. Inferences derived from studies of very limited spatial or temporal scope should not be expected to enable reliable predictions of systemwide behaviors over long periods of time. This limitation on scope of inference is a basic principle of research design that often is overlooked when managers are seeking solutions to guide their management actions. It is easy to overlook subtle but critical vegetation changes that occur at a temporal scale of one or two decades, when one is looking at year-to-year changes in kite numbers. Reversing some of the negative effects of stabilization also may be extremely difficult and require up to several decades.

Hydrologic variability, both temporal and spatial, is and always has been an intrinsic feature of the environment of snail kites in southern and central Florida. Temporal variation in the hydrology of the individual wetlands that make up the range of the snail kite likewise is an intrinsic feature and is not in itself a danger to this species. In fact, it is this variability that likely enables the coexistence of species (e.g., snail kites and wood storks) with seemingly different hydrologic requirements. These species merely don't tend to occur at the same location at the same time. Thus, we believe that the reduction of natural variability, through the reduction of natural fluctuations in water level or hydroperiods, will ultimately erode the landscape and biotic diversity, and will ultimately reduce the value of individual wetlands as habitat for snail kites. The temptation to “freeze” in place snail kite habitat through artificial ponding may be stimulated by a narrow reductionist view of the wetlands in southern and central Florida that focuses on the temporal frequency of droughts without considering spatial extent and heterogeneity, and the snail kite’s adaptation to a spatially and temporally varying environment. Under a historical pattern of localized droughts, snail kites have been able to persist through movements among habitats as local conditions changed. Snail kites are behaviorally adapted to this mechanism of individual survival and can quickly recolonize habitats that they abandoned because of temporarily bad conditions when local conditions change for the better.

This concept of snail kite adaptation to a spatially and temporally varying environment (or a “dynamic landscape”) is well substantiated by data on its natural history (Bennetts et al. 1988, Sykes et al. 1995, Bennetts and Kitchens 1997a). It is also consistent with theory that has been developed for many other species (den Boer 1981, Delcourt et al. 1983, Wiens 1989a, 1989b, Holling 1992). Management policies are beginning to recognize the ecological importance of natural variability instead of trying to create a static environment. For
instance, regeneration of habitat through fire is now part of the long-term environmental management in many ecosystems. A similar perspective is now needed for natural hydrologic disturbance processes that can be incorporated into management of the snail kite and other wetland-adapted species of southern and central Florida.

There are at least two crucial management implications of the dynamic landscape view for the snail kite. The first is that artificial attempts to create stable habitat by reducing hydrologic variability will be harmful in the long run. The second is that the focus of management should be on maintaining the existence of as much as possible of the diverse and geographically extensive network of wetland habitat areas for the snail kite. The primary danger to the snail kite is from severe systemwide droughts. Droughts that affect the entire range of the snail kite are rare (about once every 10 to 20 years), because climatic conditions are not usually homogeneous over such a large area (Bennetts and Kitchens 1997a). However, any reduction in the range of the snail kite would increase the probability of droughts affecting the entire range. Thus, the management emphasis, in our view, should be oriented strongly to conserving suitable wetlands across a wide geographic area of southern and central Florida, rather than managing individual wetlands for short-term habitat values.

Acknowledgments

We appreciate the helpful comments of Peter Frederick. Victoria Dreitz generously allowed access to her data on 1996 nesting distribution. This paper represents Florida Agricultural Experiment Station Journal Series No. R-06408.

References


Snail Kite Recovery in Florida  499


