Exploring the effect of drought extent and interval on the Florida snail kite: interplay between spatial and temporal scales

Wolf M. Mooij a,*, Robert E. Bennett b, Wiley M. Kitchens c, Donald L. DeAngelis d

a Netherlands Institute of Ecology, Centre for Limnology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands
b Florida Cooperative Fish and Wildlife Research Unit, Department of Wildlife Ecology and Conservation, University of Florida, P.O. Box 110450, Gainesville, FL 32611-0450, USA
c Florida Cooperative Fish and Wildlife Research Unit, US Geological Survey/Biological Resources Division, University of Florida, P.O. Box 110450, Gainesville, FL 32611-0450, USA
d US Geological Survey/Biological Resources Division, Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, FL 33124, USA

Abstract

The paper aims at exploring the viability of the Florida snail kite population under various drought regimes in its wetland habitat. The population dynamics of snail kites are strongly linked with the hydrology of the system due to the dependence of this bird species on one exclusive prey species, the apple snail, which is negatively affected by a drying out of habitat. Based on empirical evidence, it has been hypothesised that the viability of the snail kite population critically depends not only on the time interval between droughts, but also on the spatial extent of these droughts. A system wide drought is likely to result in reduced reproduction and increased mortality, whereas the birds can respond to local droughts by moving to sites where conditions are still favourable. This paper explores the implications of this hypothesis by means of a spatially-explicit individual-based model. The specific aim of the model is to study in a factorial design the dynamics of the kite population in relation to two scale parameters, the temporal interval between droughts and the spatial correlation between droughts. In the model high drought frequencies led to reduced numbers of kites. Also, habitat degradation due to prolonged periods of inundation led to lower predicted numbers of kites. Another main result was that when the spatial correlation between droughts was low, the model showed little variability in the predicted numbers of kites. But when droughts occurred mostly on a system wide level, environmental stochasticity strongly increased the stochasticity in kite numbers and in the worst case the viability of the kite population was seriously threatened. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Conservation; Everglades; Rostrhamus sociabilis; Spatially explicit individual based model; Habitat quality; Hydrology; Inundation; Succession

* Corresponding author. Tel.: +31-294-239352; fax: +31-294-232224. E-mail address: mooij@cl.nioo.knaw.nl (W.M. Mooij).
1. Introduction

The snail kite (Rostrhamus sociabilis plumbeus Ridgway) is a raptor whose distribution in the United States is limited to the freshwater marshes of southern and central Florida, including the Everglades (Sykes et al., 1995). It is listed as an endangered species in the United States, although its numbers appear to have increased in recent years. Because of its endangered status, the snail kite is among the species being given specific attention in the ongoing Everglades restoration project (Bennetts et al., 1994; Davis and Ogden, 1994). To evaluate the viability of the whole Everglades ecosystem under a range of future hydrological scenarios a large model called Across Trophic Level System Simulation (DeAngelis et al., 1998, 2002) is currently being developed and a spatially-explicit individual-based model for the snail kite will be included in ATLSS. It is the aim of this paper to describe an exploratory model that can be used as a baseline for the detailed model that is to be included in ATLSS.

Because the snail kite feeds almost exclusively on the apple snail (Pomacea paludosa), it is subject to changes in hydrology that affect apple snail dynamics and, therefore, the availability of apple snails to snail kites. Apple snails occur in areas of extended inundation (Kushlan, 1975) and their availability to kites is greatly reduced during droughts. Thus, snail kite population-dynamics are strongly linked with the hydrology of the system (Beissinger, 1986). Within southern and central Florida snail kites are highly mobile and may escape local drought conditions through movement, provided that suitable refugia are available (Sykes, 1983; Takekawa and Beissinger, 1989).

On the basis of an extensive field study, Bennetts and Kitchens (1997a) postulated that the viability of the Florida snail kite population depends on the time interval and spatial correlation between droughts. They hypothesised that droughts of low intensity and spatial extent are more likely to produce a behavioural response (i.e. birds move to a new location), but do not necessarily have a numerical response (i.e. change in survival and/or reproduction; Bennetts and Kitchens, 1997b). As the severity of the drought increases, the probability of a numerical response also increases because birds become unable to ‘behaviourally’ escape the effects of the drought.

Although drought in a particular wetland has a direct negative effect on snail kite reproduction and survival in that wetland, prolonged inundation is hypothesised to lead to long-term degradation of the habitat from the viewpoint of foraging by the snail kites. For this reason, occasional droughts that dry the wetland appear to be essential for its stability as snail kite habitat.

This paper reports on a model investigation of the effects of droughts, both their temporal frequency and spatial correlation, on snail kite dynamics. Because the above hypotheses focus on the effects of a spatially heterogeneous and temporally varying landscape on an animal that has a complex life-history, that moves frequently, and that occurs in low numbers, development of a spatially-explicit individual-based seems to be necessary (DeAngelis and Gross, 1992; Mooij and DeAngelis, 1999a).

Individual-based models are often alleged to lack transparency, to have data demands that cannot be met, and to be prone to error propagation (e.g. Wennergren et al., 1995; Ruckelshaus et al., 1997; but see also Mooij and DeAngelis, 1999b). Therefore, mathematically more straightforward approaches like matrix models are sometimes suggested as a better alternative (Caswell, 2001). Because of the complexities of the problem described above, however, a matrix model does not seem to provide a convenient format so we used the individual-based approach. Great care was taken to keep the model as simple and straightforward as possible, to minimise data demands and maximise transparency. Error propagation is not a significant factor, since is not the aim of this paper to make accurate predictions of kite numbers.

Instead, the aim of this paper is to identify the major components of a spatially-explicit individual-based snail kite model that allow for the evaluation of the postulated relation between the spatial extent of a drought and the response of the kites. The model presented here should thus be
seen as an exploratory prototype of a detailed snail kite model. Studying the behaviour of the exploratory model is useful in itself because it allows for an evaluation of some of the general aspects of the snail kite dynamics. These general aspects may be obscured in later versions of the model due to the high level of system-dependent detail that will be included at that stage. So, whereas these later versions may have an increased predictive power, their power in generating insights may decrease (see for a discussion on this subject Mooij and Boersma, 1996).

The predicted average number of kites is a key component in an analysis of the viability of the kite population. However, the variability in kite numbers should also be given attention, as this variability, which is caused by environmental and demographic stochasticity, is an inherent property of the system, not under control of management practices. Therefore, this paper specifically concentrates on the effects of both drought interval and spatial correlation between droughts on the average number of snail kites and on the variability in these average numbers in multiple runs of the model. Knowledge about this variability allows for the definition of the worst case for a given management scenario. In the present study different values of the time interval between droughts and different values of the spatial correlation between droughts were analysed in a factorial design, given some simple assumptions on the spatial structure of the system, the development of habitat quality after a drought, and the behavioural and population-dynamical responses of the kites to varying habitat quality.

In a more general context we can relate our work to other theoretical discussions of spatial scale and species interactions in the literature, much of which relates to species richness at different scales (e.g. Wright et al., 1993; Cornell and Karlson, 1997; Ritchie and Olff, 1999; Waide et al., 1999) and the effects of spatial scale on processes and stability (e.g. Turner, 1989; Levin, 1992; Pascual and Levin, 1999). Our study of the effects of drought on the snail kite relates closely to question of effects of spatial scale on population stability. The fact that the apple snail is the almost exclusive prey of the snail kite should in principle lead to tight coupling between the populations. Although the relatively low numbers of snail kites probably limit the overexploitation of the snail population on a wide scale, climate induced fluctuations in the apple snail abundance could potentially have major effects on the snail kite. However, such fluctuations in apple snails are usually localised and to lead only to a functional response (movement) by the snail kites, not a numerical one. Therefore, the chance of strong dynamic interactions is relatively small. Current literature has emphasised that mechanisms leading to weak trophic interactions are an important stabilising effect on ecological communities (see McCann, 2000 for a review). Spatial scale and heterogeneity, plus the behaviour response of the snail kite to droughts, appears to be a mechanism that weakens the effective interaction strength between the apple snail and snail kite populations.

2. Methods

2.1. General model structure

The model was structured using the OSIRIS framework (Mooij and Boersma, 1996; Mooij and DeAngelis, 1999a). This framework defines a set of basic entities that have to be specified for each particular model. The general idea behind OSIRIS (see Fig. 2 in Mooij and DeAngelis, 1999a) is that for each ecological model one has to define a spatial structure (here the network of wetlands), and for each spatial unit one must define the interacting conditions (droughts), resources (snails) and populations (kites). Finally the temporal structure, which determines how the different processes are integrated, should be defined. Each of these aspects will be discussed below.

2.2. Spatial structure

One of the first choices to be made during development of the model was how to represent the spatial structure of kite habitat in southern and central Florida. Within ATLSS, southern Florida is modelled as a grid with a cell size of
500 × 500 m and future versions of the model will even use a 100 × 100 m grid. These grids, however, seemed too detailed for the kites, which cover many cells during their daily flights. Therefore, a representation of southern and central Florida as a system of discrete major wetland units was chosen instead. Besides a reduction in the computational overhead, this approach has the advantage reducing the problems with the absence of detailed hydrological data for the northern part of the range of the kites in Florida.

Following Bennetts and Kitchens (1997a), we identified 14 major wetlands in southern and central Florida as suitable kite habitat: Everglades National Park, Big Cypress National Preserve, Water Conservation Area 1 (Loxahatchee NWR), 2A, 2B, 3A, and 3B, Loxahatchee Slough, Lake Okeechobee, Upper Saint Johns March, Lake Kissimmee, Kissimmee Chain of Lakes, Lake Tohopekaliga and East Lake Tohopekaliga (Fig. 1). A 15th spatial compartment was added to the model, representing the scattered pieces of peripheral habitats. This aggregate of peripheral habitat acts as a refugium for the kites during system wide droughts (Takekawa and Beissinger, 1989; Bennetts and Kitchens, 1997a).

2.3. Spatial drought generator

The occurrence of droughts in southern and central Florida was modelled as a stochastic process. In a predictive snail kite model this component of the model will be replaced by a link to a hydrological model. The probability of a drought was defined as $1/\tau_i$, where $\tau_i$ is the average time interval between droughts (for an explanation of the symbols used in this paper see also Table 1). Two types of droughts were distinguished, local and global droughts (Bennetts and Kitchens, 1997b). Global droughts affected all wetlands and local droughts affected wetlands individually. The proportion of global versus local droughts was modelled using:

$$F_{\text{gbl}} = \frac{\rho_d}{\tau_i}$$

$$F_{\text{loc}} = \frac{1 - \rho_d}{\tau_i(1 - F_{\text{gbl}})}$$

in which $F_{\text{gbl}}$ is the frequency of a global drought, $F_{\text{loc}}$ is the frequency of local droughts, and parameter $\rho_d$ describes the proportion of global droughts. Note the term $(1 - F_{\text{gbl}})$ in the denominator of the equation for local drought frequencies (Eq. (1b)). This term is necessary because in the model global droughts take precedence over local droughts and local droughts would therefore be underrepresented without a correction for the frequency of global droughts.

To evaluate the effect of different values of the drought interval ($\tau_i$) and the spatial correlation between droughts ($\rho_d$) on kite behaviour and population-dynamics, the model was run for 11 values of $\tau_i$ (2–12 years) and five values of $\rho_d$ (0.0, 0.25, 0.5, 0.75 and 1.0) in a factorial design. These ranges were chosen such that they
Table 1
List of variables and parameters used in this study

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_{glob}$</td>
<td>Frequency of global droughts</td>
</tr>
<tr>
<td>$F_{loc}$</td>
<td>Frequency of local droughts</td>
</tr>
<tr>
<td>$S_t$</td>
<td>Apple snail recovery at time $t$</td>
</tr>
<tr>
<td>$Q_t$</td>
<td>Structural habitat quality at time $t$</td>
</tr>
<tr>
<td>$K_t$</td>
<td>Carrying capacity at time $t$</td>
</tr>
<tr>
<td>$N_t$</td>
<td>Number of kites at time $t$</td>
</tr>
<tr>
<td>$B_{adult}$</td>
<td>Average fecundity after age 1</td>
</tr>
<tr>
<td>$D_{adult}$</td>
<td>Probability of dying after age 1 (per year)</td>
</tr>
<tr>
<td>$B_{yearling}$</td>
<td>Average fecundity at age 1</td>
</tr>
<tr>
<td>$D_{yearling}$</td>
<td>Probability of dying up to age 1 (per year)</td>
</tr>
</tbody>
</table>

Parameters that were estimated a priori

- $\tau_s$ Time after a drought necessary for full snail recovery (2 years)
- $\tau_{q1}$ Time after a drought with constant structural habitat quality (4 years)
- $\tau_{q2}$ Time after a drought necessary for full habitat degradation (20 years)
- $\alpha$ Fractional improvement of structural habitat quality per drought ($1/8$)
- $K_{max}$ Maximum carrying capacity per wetland (ranging from 30 to 470, see Fig. 4)
- $\beta_{adult}$ Probability of migration after age 1 (0.25 per month)
- $\beta_{yearling}$ Probability of migration up to age 1 (0.25 per month)
- $\beta_{adult}$ Average fecundity after age 1 under optimal conditions (2.0)
- $\beta_{yearling}$ Average fecundity at age 1 under optimal conditions (0.67)
- $\delta_{adult}$ Probability of dying after age 1 under optimal conditions (0.07 per year)
- $\delta_{yearling}$ Probability of dying up to age 1 under optimal conditions (0.21 per year)

Parameters of which the effect was analysed

- $\tau_1$ Time interval between droughts (2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12 years)
- $\rho_d$ Spatial correlation between droughts (0, 0.25, 0.5, 0.75, 1.0)

2.4. Temporal habitat quality dynamics

There is little question that the drying of an area results in apple snail prey being unavailable to snail kites; thus, temporarily resulting in extremely low habitat quality (i.e. Beissinger, 1995). But also prolonged inundation may have negative effects, as postulated by Bennetts et al. (1998). To cope with both effects, the temporal changes in habitat quality due to periodic droughts were modelled by a combination of two processes. The first mimics the recovery of the snail population after a drought and the second describes the degradation of structural aspects of the habitat under prolonged inundation. It was assumed that, after a drought, it takes the apple snails a period of time $\tau_s$ to recover. During this period the variable describing snail recovery, $S_t$, was assumed to increase linearly from zero to one and to stay at that level thereafter (Fig. 2).

Structural habitat quality $Q_t$ was assumed to remain constant after a drought for $\tau_{q1}$ years but, after that, was assumed to gradually decrease until it reached a value of zero at $\tau_{q2}$ years after the last drought (Fig. 3). Droughts were assumed to improve structural habitat quality. This was modelled by adding a fixed amount, $\alpha$, to the structural habitat quality at the occurrence of each drought (to a maximum of one, representing optimal structural quality). This new value determined the new plateau level in structural habitat quality for the next $\tau_{q1}$ years. Following Bennetts et al. (1998), the parameter $\tau_{q1}$, denoting the time period after which structural habitat quality starts to decrease, was fixed at a value of 4 years. For parameters $\tau_{q2}$ and $\alpha$ no good empirical data were available and they were arbitrarily set to 20 years and $1/8$, respectively. The latter parameter implies that it would take at least eight droughts to regenerate a fully degraded wetland back to optimal quality. For an average drought interval of 5 years this would thus take at least several decades. Note that the product of the functions describing snail recovery $S_t$ and structural habitat quality $Q_t$ mimics the development of habitat quality after a drought, as postulated by Bennetts et al. (1998) in their Fig. 2.
2.5. Carrying capacity

A stage structured snail kite model was developed by Beissinger (1995) and applied to data from the snail kite annual count that was started in 1970. Beissinger’s model does not take density dependent limitations of the population into account. In its application to historical records for the snail kite in the 1970s and 1980s this did not cause a problem, since kite numbers were relatively low during that period. In the exploratory model presented here that attempts to project into the future, however, the absence of density dependence can result in unrealistically high values of tens of thousands of kites under randomised series of the hydrological conditions. This problem of unrealistic high-predicted numbers of kites was solved by introducing some form of density de-
dependence in the model. This approach raised another problem, however, because the existing data on density dependence are still scarce (but see Dreitz, 2000).

To solve this second problem we took a pragmatic approach by defining the highest number of kites observed in a given wetland during 1970–1994 (Bennetts and Kitchens, 1997a) as an estimate of the carrying capacity of that wetland under optimal hydrological conditions (Fig. 4). This resulted in an estimate of the total carrying capacity of the system of 1513 birds. In the absence of a good argument for the absolute values of the carrying capacity of the wetlands of southern and central Florida for kites, these values should only be interpreted as relative estimates of the importance of the different wetlands for kites. The effects of different estimates of the total carrying capacity of the system on the output of the model can easily be approximated by re-scaling the numbers in the output afterwards. The carrying capacity of a wetland for kites, $K_t$, at a given moment in time $t$ was calculated by multiplying the maximum carrying capacity of that wetland under optimal condition ($K_{\text{max}}$) with snail recovery $S_t$ and structural habitat quality $Q_t$ at that moment in time:

$$K_t = K_{\text{max}} \times S_t \times Q_t$$  (2)

2.6. Behavioural response of the kites

The behavioural response of the kites to varying conditions in each of the 14 wetlands of southern and central Florida was implemented by allowing the model kites to make periodic comparisons between wetlands. At the beginning of each month, each kite has, depending on its age, a probability of $\mu_{\text{yearling}}$ or $\mu_{\text{adult}}$ that it will make an excursion to one randomly chosen wetland. The kite then compares the ratio between the number of kites and the current habitat quality ($N_t/K_t$) in the visited wetland with that ratio for the wetland in which it is currently living. If the conditions in the visited wetland are better ($N_t/K_t$ smaller) the kite migrates; otherwise it stays in its initial wetland.

During this procedure, a kite also checks whether conditions have deteriorated so much that it makes sense to move into peripheral habitat. It does so if both the wetland in which it is currently living and the visited wetland have a ratio of $N_t/K_t$ higher than 2.0. In peripheral habitat no density dependence is assumed and a fixed value for the ratio between $N_t/K_t$ of 2.0 is used always, irrespective of the number of kites in this spatial refugium. After conditions in the 14 major wetlands have improved ($N_t/K_t < 2.0$), birds living in peripheral habitat can migrate back, again with a
monthly probability of $\mu_{\text{yearling}}$ or $\mu_{\text{adult}}$. In the current implementation yearling birds (up to 1 year) were assumed to have an equal probability of migration as adult birds and both probabilities were fixed at a value of 0.25 per month (Bennetts and Kitchens, 2000).

2.7. Population-dynamical response of the kites

The population-dynamical response of the kites was also modelled on basis of the ratio between the actual number of kites and the current carrying capacity of the wetland in which it is living ($N_t/K_t$). By definition, birth and death rates should be chosen such that they balance when $N_t$ equals $K_t$. Moreover, a physiological maximum had to be set to the birth rate of the kites under optimal conditions ($N_t/K_t = 0$). It also was assumed that birth rates are more sensitive to changing conditions than mortality rates. Finally, under the conditions in which the birds move into peripheral habitat ($N_t/K_t > 2.0$) birth rate should be low or zero, whereas the mortality rate should not be unrealistically high. All these constraints lead to the following equations for the average fecundity and probability of dying of birds older than 1 year, as a function of the ratio $N_t/K_t$ (Fig. 5):

$$B_{\text{adult}} = \beta_{\text{adult}} \times 2^{-2N_t/K_t}$$  \hspace{1cm} (3a)

$$D_{\text{adult}} = \delta_{\text{adult}} \times 2^{2N_t/K_t}$$  \hspace{1cm} (3b)

Parameters $\beta_{\text{adult}}$ and $\delta_{\text{adult}}$, describing the birth and mortality rate of adult birds under optimal conditions ($N_t/K_t = 0$) were set to values 2.0 and 0.07, respectively (Bennetts and Kitchens, 1997a). Because the model is individual-based, average fecundity had to be transformed in a series of integer values, with a long-term average equal to $\beta_{\text{adult}}$. Yearling birds (up to 1 year) were assumed to have an increased probability of dying and a reduced fecundity during their first breeding season:

$$B_{\text{yearling}} = \beta_{\text{yearling}} \times 2^{-2N_t/K_t}$$  \hspace{1cm} (4a)

$$D_{\text{yearling}} = \delta_{\text{yearling}} \times 2^{2N_t/K_t}$$  \hspace{1cm} (4b)

Parameters $\beta_{\text{yearling}}$ and $\delta_{\text{yearling}}$, were set to values 0.67 and 0.21, respectively. Thus yearling birth rate is a factor three lower than adult birth rate and yearling mortality rate is a factor three higher than adult mortality rate.

The resulting maximum population increase (under optimal conditions) and maximum population decrease (in peripheral habitat) were analysed with a cohort life-table (Begon et al., 1990), and compared with the observed population changes.

![Fig. 5. Hypothesised relations (dashed lines) between the instantaneous birth and death rates of the kites under varying relative densities, expressed as the number of kites divided by the carrying capacity. The resulting instantaneous population growth rate (solid line) is also shown.](image)
from year-to-year during 1970–1994. In both cases the modelled instantaneous rates were well within the range of observed population changes (Fig. 6), but these modelled rates could not account for the extreme changes in numbers observed in the 1980–1981 snail kite annual count data. These extreme changes in the empirical observations are likely due, in part, to an artefact in the counting procedure. The birds probably moved into peripheral habitat due to the 1981 drought and, therefore, did not show up in the annual count, as no effort was made to count birds in those areas. This could have mistakenly been interpreted as a numerical change in the population. Consequently, they may not represent a true population-dynamical response (Bennetts et al., 1999), and probably do not represent a discrepancy with the model.

2.8. Initial conditions

The model was started a year after a global drought. The initial structural habitat quality was set to 0.5 in all 14 wetlands. Each of the wetlands and the peripheral habitat was initiated with a population of eight birds (one yearling male, three adult males, one yearling female and three adult females). This total number of 120 birds is about equal to the number of birds that were observed during the annual count in the early 1970s (Sykes et al., 1995). At birth birds were given a sex ratio of 1:1.

2.9. Handling of time

All simulations lasted for 30 years, a period which is equal to the focal period in ATLSS (1965–1995) and which is about equal to the period covered by the annual count (1970–1994). Droughts could occur at most once a year, in the first week of April. Snail recovery, structural habitat quality and the resulting carrying capacity were updated weekly. Carrying capacity and the number of snail kites were monitored four times a year, in the last week of February, May, August and November. Kites were allowed to migrate monthly, in the last week of each month. Mortality of each kite was evaluated monthly, again in the last week of each month after migration. Reproduction took only place in the first week of April, after the possible occurrence of a drought.
3. Results

Due to the stochastic nature of the model each run looks different. A typical example of the development of the carrying capacity of the system over time is shown in Fig. 7. The parameter settings of this specific run were a drought interval ($\tau_i$) of 5 years and a spatial correlation between droughts ($\rho_d$) of 0.5 (this is of the same order as what happened in the Everglades in the period 1970–1994). This specific run with this scenario resulted in three global (system wide) droughts, in years 10, 20 and 28. In the wetland with the highest carrying capacity, water conservation area 3A (WCA3A), three local droughts occurred in years 12, 14 and 16. Fig. 7 shows that a scattered pattern of carrying capacity in the 14 wetlands of the system developed after a global drought due to local droughts. This pattern was again synchronised by the next global drought. For WCA3A the combination of snail recovery (Fig. 2) and the development of structural habitat quality (Fig. 3) is clearly visible: after each drought carrying capacity recovered in 2 years, after which it reached a plateau that was higher than the carrying capacity just before the drought. This is due to the beneficial effect of droughts on structural habitat quality. After 4 years, however, structural habitat quality started to decline, until the next drought, or, in the absence of droughts, until a wetland would have become totally lost as kite habitat.

The scattered pattern of carrying capacities is reflected in the widely varying numbers of kites in the different wetlands (Fig. 8, showing the same run as Fig. 7). Overall, the number of birds in each wetland tends to increase over time, due to the small initial number of birds (120) relative to the estimated carrying capacity of the system (1513). The range of values over which the number of modelled birds fluctuates, however, is lower than the range of the carrying capacities. This reduced variability in the number of birds is due to the buffering mechanism of the behavioural response. In case of a local drought, kites can escape to other wetlands where conditions are still favourable. During a global drought (year 10, 20 and 28) the peripheral habitat acts as a buffer. Although the birth rate of the kites in this spatial refugium is almost equal to zero, the mortality rate is low enough to keep a considerable fraction of the population alive. These surviving birds can then re-colonise the major wetlands after conditions have improved.

Fig. 7. Example of a hypothetical development of the carrying capacity in the 14 major wetlands of southern and central Florida during a 30 years period. The solid line and the thin lines show the carrying capacity in water conservation area 3A and the other 14 wetlands, respectively. See also Figs. 2 and 3.
Fig. 8. Example of a hypothetical development of the kite population in the 14 major wetlands of southern and central Florida during a 30 years period. The solid line and the thin lines show the number of kites in water conservation area 3A and the other 14 wetlands, respectively. The dashed line shows the number of kites in peripheral habitat.

Fig. 9. Total carrying capacity (dashed line) and total number of birds (solid line) for the run shown in Figs. 7 and 8. 'Counted' number of kites (lower solid line during system wide droughts) does not include the birds in peripheral habitat.

The global behaviour of the model becomes clearer if we only look at the total carrying capacity and the total number of birds summed over all wetlands (Fig. 9, showing the same run as Figs. 7 and 8). At the global level, the variability in the carrying capacity is dominated by the effects of system wide droughts, because the effects of local droughts cancels out. Still, a local drought in one of the major wetlands, such as WCA3A in year 12, may have a considerable effect on the total carrying capacity of the system. In between system wide drought events, the number of kites shows a steady increase. Only during a global drought do these numbers drop. The graph also shows that the kites use the peripheral habitat as a refugium during these extensive droughts. The
number of birds in the major wetlands, which was taken into account during the annual count ('counted' number of birds), shows considerably lower values during a global drought than the values that would be reached if the peripheral habitat would have been included in the snail kite annual count or census (total number of birds).

Plots of the carrying capacity (Fig. 7) and number of kites (Fig. 8) in a specific run illustrate the internal dynamics of the model. Because of its stochasticity, however, the overall behaviour of the model can only be analysed after re-running the model many times for each combination of the parameters that are to be analysed. In the present study, these parameters are the mean interval between droughts (\(\tau_i\)) and the spatial correlation between droughts (\(\rho_d\)). Fig. 10 shows a summary of 2750 runs with the model with 11 values of \(\tau_i\) (2–12), five values of \(\rho_d\) (0.0, 0.25, 0.5, 0.75, 1.0) and 50 repetitions of each run. Shown are the average numbers of kites during the 30 modelled years for each combination of the drought interval and the correlation between droughts. These averages clearly show the reduced numbers of kites at drought intervals (\(\tau_i\)) shorter than 4 years. But also long periods between droughts lead to lower numbers of kites, as a result of degradation of structural habitat quality.

Fig. 10 also shows the variation (± 2 S.D.) in the average number of kites derived from multiple runs with the same parameter settings of \(\tau_i\) and \(\rho_d\). This variability should not be confused with the variability of the number of kites during one run, although the two are related. The variation shown represents the unpredictability of the average number of kites during a period of 30 years due to the stochasticity of the environment. It is, therefore, a measure of the (un)predictability of the viability of the kite population. This predictability clearly decreases with an increased spatial correlation between droughts. Knowledge of this variation allows for judgement in making management decisions based not only in terms of the average effects of a scenario on the kites but also on what would happen in the worst case.

4. Discussion

The model of the snail kite presented in this paper was specifically designed to contain the bare

![Fig. 10. Summary results of 2750 runs with the model, showing the average number of kites during 30 years. The model was run for five values of the spatial correlation between droughts (0.0, 0.25, 0.5, 0.75 and 1.0) and for 11 values of the time interval between droughts (2–12). Runs for each of these 55 scenarios were repeated 50 times. Bars represent two times the S.D. in the average number of kites per run.](image-url)
minimum of detail necessary for a spatially explicit individual-based based description of the dynamics of this species. After definition of the spatial structure of the model, five modules had to defined (1) the spatial drought generator, (2) the habitat quality dynamics, (3) the carrying capacity, (4) the behavioural response of the kites, and (5) the population-dynamical response of the kites. Finally, the temporal structure of the model was chosen by defining the order of evaluation of these processes. The results show that this chain of modules allows for the evaluation of hypotheses formulated by Bennetts and Kitchens (1997a) of the dependency of kite behavioural and population-dynamical response on the frequency and spatial extent of droughts. Not only can the model predict average numbers of kites under different hydrological scenarios but also the variability in these predictions due to environmental, behavioural and demographic stochasticity.

The current model has 13 parameters in total (Table 1) of which two relate to drought generation ($\tau_i$ and $\rho_d$), four to habitat quality ($\tau_e$, $\tau_{q1}$, $\tau_{q2}$, $\lambda$), one to the carrying capacity ($K_{max}$, estimated per wetland), two to the behavioural response ($\beta_{adult}$, $\beta_{yearling}$) and finally four to the population-dynamical response ($\beta_{adult}$, $\beta_{yearling}$, $\delta_{adult}$, $\delta_{yearling}$). Because of the structure of the model and analysis of its general behaviour for different values of $\tau_i$ and $\rho_d$ is the target of this paper, only crude estimates of the remaining eight parameters were made. Of these, four act as scaling factors ($\tau_e$, $\tau_{q1}$, $\tau_{q2}$, and $K_{max}$), and within a reasonable range of values their effects on the outcome of the model can be predicted a priori. This does not hold for the six biological parameters ($\mu_{adult}$, $\mu_{yearling}$, $\beta_{adult}$, $\beta_{yearling}$, $\delta_{adult}$, $\delta_{yearling}$) and a further sensitivity analysis with the current model for these parameters seems a useful enterprise.

The results show that high drought frequencies lead to reduced numbers of kites (Fig. 10). Under the current parameterisation of the model, an average drought interval below 4 years results in reduced average numbers of kites over the modelled period. This drop in average numbers reflects the stress put on the apple snail population, which lacks sufficient time to recover at such high drought frequencies. This result is fully in accordance with the literature on the strong relation between droughts and kite numbers (i.e. Beissinger, 1995). However, the results were also consistent with the hypothesis of Bennetts and Kitchens (1997b) that it is system-wide droughts, rather than local droughts, that are primarily responsible for changes in numbers of kites at the population scale (Fig. 9). In addition, prolonged periods without droughts also resulted in lower average numbers of kites. This is the result of the negative effect of prolonged inundation on structural aspects of the kites’ habitat. Prolonged inundation reduces the availability of woody vegetation used as nesting substrates, and can reduce emergent vegetation that enables snails to climb near the surface where they are vulnerable as prey (Bennetts et al., 1998; Kitchens et al., 2002).

Bennetts and Kitchens (1997b) also postulated that a high spatial correlation between droughts should have a negative numerical impact on the kites. Indeed, an increased proportion of system-wide droughts relative to the numbers of local droughts (keeping the drought interval and thus the average number of droughts equal), resulted in somewhat reduced numbers of kites (Fig. 10). Unexpectedly, however, the largest impact of increased spatial correlation was a corresponding increase in variability of the number of kites. With increased correlation, model runs sometimes resulted in very low or very high numbers of kites, depending on the proportion of system-wide droughts and the chance occurrence of exceptionally long or short drought intervals. Thus, the effect of environmental stochasticity is much stronger when droughts are spatially correlated, resulting in a high stochasticity in kite numbers.

Besides being a tool for the analysis of the basic properties of a spatially-explicit individual-based model of the snail kite, the current model can serve as a baseline for the detailed snail kite models that aim at predicting kite dynamics for specific hydrological scenarios. The exploratory model described here covers the whole range of dynamics from hydrology to kite numbers and it is likely that the general structure of the detailed model will be the same as that of the current
model. This allows for a one by one replacement of the simple modules by their more complex counterparts. To move from the exploratory model to a predictive model, the simple drought generator has to be replaced by the output of a hydrological model for the watersheds of southern and central Florida. The habitat quality generator could be replaced by an algorithm that estimates habitat quality on basis of the detailed information on the interaction of water levels, vegetation and the snail population.

Having a full dynamical apple snail model would be optimal, because this would allow for the inclusion of bio-energetical details in modules describing the snail kites. Also, having a snail model could eventually provide a mechanistic basis for wetland carrying capacity. As long as the habitat quality approach is used, however, estimates of the carrying capacity have to be made, in absence of good data on density-dependence kite population-dynamics. Because this parameter merely acts as a scaling factor, this should not be a problem, however. The detailed versions of the behaviour module and the population-dynamical module can fully benefit from the wealth of data collected on snail kites during 1970–1994, but especially during the last few years (Bennetts and Kitchens, 1997a). It is tempting to include already some more detail in these modules in the current model. However, this would create an unbalanced model (for a discussion on the balance in details of models see Starfield and Bleloch, 1986) with, due to the increasing numbers of parameters, reduced possibilities for a good understanding of the basic properties of the model.

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