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"An Individual-Oriented Model of a Wading Bird Nesting Colony"

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ABSTRACT

An individual-oriented model for a colony of nesting wading birds during a breeding season is described. The birds in the colony are modeled as an assemblage of individuals. Their behaviors, such as foraging, bioenergetics, interactions with conspecifics, and reproduction, as well as spatial movements, are modeled separately for each bird. The individual behavior of each bird is described by decision rules which specify what particular action the bird performs at any given time. The paper gives an overview of the most important behavioral rules used in the model and also briefly describes how the physical and resource environments are taken into account. Simulations of a breeding colony of wood storks (*Mycteria americana*) in a heterogeneous landscape and under a variety of environmental conditions (e.g., changes in standing water level and prey concentration through the breeding season) illustrate their effect on reproductive success of individuals in the colony.

1. INTRODUCTION

The Everglades, located at the southern tip of Florida, has experienced a 50% reduction in areal extent since the turn of the present century through drainage and associated agricultural and urban development. Remaining natural areas of the Everglades exist within an increasingly fragmented, human-dominated landscape. Spatial and temporal characteristics of these remaining natural areas, particularly the landscape composition, hydrological and salinity regimes have also been altered (Blake, 1980; Hefner, 1986; Kushlan, 1986, 1990).

Populations of higher-order consumers in the Everglades have declined concurrently with alterations in fundamental environmental characteristics.

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Consumer populations inhabiting the remaining natural areas are characterized by continuing low numbers, frequent reproductive failures, and increasing biotic instability. Characteristic indicator species, such as colonial wading birds (egrets, herons, ibises, and storks), have declined dramatically from predrainage conditions to significantly lower population levels (Robertson and Kushlan, 1974; Kushlan et al., 1975, 1984; Kushlan and White, 1977; Ogden, 1978; Ogden and Patty, 1981; Kushlan and Frohring, 1986; Frederick and Collopy, 1988; Fleming et al., 1993a).

Various hypotheses have been proposed to account for the decline in population numbers and reproductive success observed in wading birds and other populations in the Everglades as a result of an altered hydrological regime and associated changes in core habitat characteristics (Kushlan et al., 1975; Ogden et al., 1980; Frederick and Collopy, 1988; Fleming et al., 1993b). The rigorous way to test between these hypotheses would be through large-scale manipulations of water levels and other conditions in the Everglades during the nesting season. This method is impractical, however, and would require many years to produce enough data to reject the incorrect hypotheses. Simulation modeling provides an alternative approach for studying phenomena in a large natural system, such as the Everglades, where experimental testing of hypotheses is not possible. Development and use of a model helps in several ways: it

(1) forces one to focus one's ideas and assumptions and to quantify them,
(2) aids one in formulating hypotheses,
(3) reveals gaps in data, and
(4) provides the means to deduce, through mathematical analysis or computer simulations, the effects of the hypothesized causal chains, even when these are complex.

Individual-oriented models (IOM) offer a unique tool to incorporate a high degree of realism. In these models, the movements, foraging, bioenergetics and growth, mortality, interactions with conspecifics, and reproduction of individual organisms are followed simultaneously. One of the useful features of individual-oriented models is the ease with which they can be applied to populations in highly heterogeneous landscapes and where abiotic factors vary in time. In this paper, this feature is used in a model of a wading bird nesting colony during the breeding season. Below, the approach employed in developing this model is described and examples of the type of simulations and results that are possible are provided.

2. GENERAL DESCRIPTION OF "INDIVIDUAL-ORIENTED MODELING"

In individual-oriented models, and in the closely related individual-based models (IBM), which have been applied to a wide variety of ecological problems (Huston et al., 1988; Wolff, 1988; DeAngelis and Gross, 1992; for a distinction between IOM and IBM see Metz and de Roos, 1992), a population, or some specific subpopulation of interest, is modeled as an assemblage of individuals. Various behaviors, such as foraging, social, or reproductive behavior, as well as physiological conditions, are modeled separately for each individual in the population (or for each individual in a representative sample).

The IOM approach has a number of advantages over other, more traditional types of modeling techniques that consist of equations for total population size or density. For example, the logistic equation describes the dynamics of a population in terms of its intrinsic rate of increase, r, and the environmental carrying capacity, K. One weakness of such a model is that it is too coarse in structure to represent the complex ways in which the environment may affect reproduction. Even more complex models, such as Leslie matrix models which take into account the age structure of populations (e.g., Caswell, 1989), lack the detail to allow one to describe what happens within a given reproductive season. In individual-oriented models, differences in age and size of adult wading birds, as well as variations in weight and development of nestlings at any particular time through the year, are easily taken into account because each individual is simulated. This is an important advantage over models that consider only the average individual in a population, because frequently it is the atypical individual, the individual that succeeds where most others fail, that determines population recruitment.

Another advantage of the IOM approach is that short time scale environmental fluctuations and stochastic events affecting individuals can be modeled because the time step of IOM models is usually a day or less, e.g. in the nesting colony model a time step corresponds to 15 min. In addition, the decision-making facility of individuals can be included in a straightforward way in IOMs. The individual behavior of each member of the population is described by rules which specify what particular action an individual is going to perform at a given time. For example, individual pairs in a wading bird colony are allowed to assess the environment at each day and choose whether or not to initiate nesting. Spatial heterogeneity and movement of individuals can also be accommodated. Each individual bird moves spatially from location to location according to a set of rules that incorporate its needs and preferences. Rules particular to a wading bird species can be prescribed that, e.g., lead to patterns of movement that are similar to their real counterparts.

3. MODEL DESCRIPTION

The model of a wading bird nesting colony described in this paper consists of four major parts that spe [illegible]) the physiology, energetics and behavior of individual adult birds, (2) the energetics, growth, survival, and fledging of nestlings, (3) the physical environment, i.e. the landscape surrounding the colony site, and (4) the resource environment, in particular the prey available to the birds. Each part is described in more detail below.

The area considered in the model is the part of the landscape that is used by the birds from the colony. It is assumed to be a square of 40 km × 40 km which is divided into cells of 1/4 km × 1/4 km each, such that a total of 25600 cells make up the entire area (cf. Section 3.5, Fig. 2). Water depth and the availability of fish are defined on a cell-by-cell basis. A more detailed account of how the environment is modeled is given in the last two sections of the model description. Because the first implementation was written to be applicable to wood storks (*Mycteria americana*), some of the aspects of the model are designed for those wading birds in particular, but can be modified for other species.

3.1. The adult wood stork

Each adult bird's foraging, social, and reproductive behavior, as well as its physiology and energetics, are specified by rules. These rules define and specify the actions and the state of each simulated bird at a given time. In general, the behavioral choices and their outcome depend on the current state of the bird, but additional information such as time of day, actions of other birds, location and condition of foraging habit are frequently taken into account. These rules are expressed in the form of "if–then" statements. Often several such statements are necessary and must be chained together to reach a final decision. The following notational convention is used: whenever "stork" or "wood stork" is used in a rule, this particular rule is considered to be specific for wood storks; otherwise the same rule, or a very similar one, could apply to other wading bird species as well.

3.1.1. Energetics of adult wood storks

Mature wood storks weigh between 2 and 3 kg, with an average of about 2.5 kg. Kahl (1964) estimated that an adult, free-flying stork needs about 180 kcal/kg/day in energy intake and has an approximate energy assimilation efficiency of 79%. Thus an average stork of 2.5 kg must ingest about 570 kcal daily. For convenience in the model, all prey are assumed to be mosquito fish (*Gambusia affinis*). Mosquito fish are 3 cm in length and weigh about 1 g with a caloric value of about 1.1 kcal/g live weight (Kahl, 1964; Loftus and Kushlan, 1987).

Any food that a bird gathers above its own need is assumed to be carried back to the nest. Upon arrival at their nest, wood storks regurgitate food, which is then picked up by the nestlings. The maximal amount an adult

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stork can store in its throat or stomach and carry back to the nest is assumed to be 300 g. I am unaware of any data to corroborate the specific value of 300 g that seems to be a reasonable estimate (M. Coulter, pers. commun.). However, one can test the sensitivity of simulation results to this value. Anticipating some of the results presented later, a maximum load considerably less than 300 g does not enable the parents to provide nestlings with sufficient food to meet their energy requirements, even under optimal conditions. On the other hand, values considerably larger than 300 g often result in more food being carried to the nest than the nestlings can possibly utilize.

These estimates lead to the following rule for the food uptake of adult storks:

Each mature stork needs 500 g of food daily. In addition, up to 300 g can be stored and carried back to the nest. [1]

3.1.2. Cost of movement behavior

During the breeding season, wood storks often travel long distances in search for food (Kahl, 1964; Browder, 1984; Frederick and Collopy, 1988; Coulter, 1989). The total time spent for foraging, including travel, may be substantial, thereby limiting the number of foraging trips and the time available for other activities. The behavior of adults during each day is modeled in 15-min time steps, so individual flights and their duration can be simulated.

Flight time is determined by the distance flown and the speed at which wood storks travel. Storks can fly in excess of 50 km/h (Kahl, 1964). Nevertheless, storks rarely travel at maximum speed and it is unlikely that they will always choose a direct route to their final destination. Flight time is also affected by the type of flight used by the bird: flapping flight or soaring-gliding flight which takes advantage of thermal updrafts (Kahl, 1964; Browder, 1984; Coulter, 1989). Soaring flight only costs a tenth of the energy of flapping flight (A.L. Bryan and M.C. Coulter, pers. commun.) and is used whenever possible (Kahl, 1964), particularly for larger distances (Coulter, 1989). The average rate of travel, or cross country speed, has been estimated to be 25.6 km/h (Coulter, 1989 and pers. commun.). Similar values (23.9 km/h in 1986 and 27.4 km/h in 1987) were obtained by Frederick and Collopy (1988) for stork flights in the Everglades.

The rule specifying flights and flight time is as follows:

Wood storks fly directly from one location to another with a speed of 25

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[1] For technical reasons, adult birds are assumed to gather food in units of 50 g. The rule thus implies that a bird can carry a load between 50 g (1 unit) and 300 g (6 units).

km/h. The flight time is calculated from the ratio [2] direct distance/flying speed.

3.1.3. *Foraging behavior*

Adult wood stork legs are approximately 50 cm long. Usually storks do not feed in water deeper than that (Meyers, 1984) and most of their food is obtained from a water depth between 15 and 50 cm (Kahl, 1964; Coulter, 1989; G. Morales, pers. commun.). Other observations suggest that wood storks feed less successfully in deep water than shallow water, where foot-stirring is often used to drive prey concealed below submerged vegetation into the nearby open bill (Kahl, 1964). On the other hand, fish in deeper water might be larger than those in more shallow areas, such that the decrease in energy uptake may not be as large as suggested by the decrease in success rates (Coulter, 1989).

The locations where storks can forage are then specified as follows:

Wood storks forage only in shallow water areas, i.e. in cells with a water depth between 10 cm and 40 cm. Any cell in this depth class can be chosen for foraging.

The above rule merely defines the class of locations where a bird can forage. It does not specify how a particular location is chosen by a bird. Since a majority of their foraging trips are fairly direct (Coulter, 1989), it is reasonable to assume that foraging birds know the general areas in which conditions, particularly the water depth, will likely yield high concentrations of prey. Furthermore, the wood stork is gregarious while feeding as well as nesting (Audubon, 1840; Rand, 1954; Rechnitzer, 1956; Kahl, 1964; Ogden et al., 1978). Kushlan (1977, 1978) has suggested that wading birds forage more successfully in groups than singly.

It has yet to be specified how a bird chooses where to forage. The simplest rule is to have a bird pick a cell at random out of the foraging depth classes. Searching at random, however, does generally not lead to flocking behavior. If it is the conspicuous color of their plumage that attracts other birds, as Kushlan (1977) suggests, one might argue that the larger an existing flock the more often other birds are attracted to it. Not all birds, however, fly to sites that are already occupied by other birds. Observations have shown (Coulter, 1989) that usually less than half of the foraging trips end at sites used by other birds, although this low value might be due to the distribution of foraging sites in Georgia and may differ elsewhere.

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[2] The value calculated from this ratio is always rounded up to give the flight time in units of the 15-min time steps.

Furthermore, it is not at all obvious how a flock should be defined within the framework of the model because the positions of the birds are only specified on a cell-by-cell basis. Defining a flock as the set of adjacent cells where birds forage at any one time might be expected to give reasonable results in some situations, particularly when the birds are sufficiently clumped. But it also includes the somewhat unrealistic case where, e.g., two cells, far apart and each containing a large number of birds, are connected by a string of cells with only one bird in each of them. The less ambiguous convention is that birds searching for a site base their choice of final destination by assessing the local density of foraging birds. More specifically, it is assumed that a searching bird will assess the density of birds in all cells currently used for foraging. A particular cell is then chosen with a probability that is taken to be proportional to the local density of foraging birds, i.e. the number of birds currently foraging in this cell.

The rule by which a birds chooses a cell for foraging allows for random searching as well as flocking is as follows:

Before leaving on a foraging trip, a stork can choose between two different searching modes: random search and flocking. Random search is chosen with probability p and flocking with probability $(1-p)$. Using the latter, a bird chooses a cell where other birds forage already and, therefore, joins an already existing flock. The probability with which a particular cell is chosen out of the set of currently used cells is proportional to the number of birds already foraging in this cell.

For example: suppose there are a total of 10 birds foraging at 3 locations, 3 birds at the first, 5 birds at the second, and 2 birds at the third site. If another bird chooses to join one of these flocks instead of doing a random search it will fly to the first site with probability 3/10, the second site with probability 5/10, and the third site with probability 2/10.

This convention ensures that large aggregations of birds will grow even larger whereas cells with fewer birds are chosen less often. However, this only applies to the short-time behavior. Large flocks can rapidly deplete the fish available in their cells, after which birds start to leave in large numbers. Although searching birds might still be attracted by the large size of the flock, they will find the cell deprived of food and then fly away shortly after their arrival. The number of birds leaving quickly exceeds the number of bird arriving and, despite the particular form of the choosing rule, even large flocks will exist only as long as there is enough fish available for the birds to forage profitably.

Furthermore, the rule should not be seen as a description of how a stork actually chooses a site at which to forage. The probability with which flocks are chosen probably does not reflect the number of times a stork joins a flock or the rate at which flocks grow. Yet, in order for a large flock to exist for more than a couple of time steps, the storks flying away from a site must be replaced by others choosing that site. In other words, in order to obtain large flock sizes there must be a positive feedback between flock size and the number of storks joining the flock. In its current form the rule does just that and should by regarded as a first attempt to incorporate local flock enhancement in wading birds (Kushlan, 1977).

Foraging in flocks can have positive as well as negative effects. On the positive side, flocking is thought to increase the efficiency at which birds find good foraging grounds (Kushlan, 1978). In addition, birds will tend to stay longer in cells with a large abundance of fish thereby attracting other birds to forage in these cells as well. On the negative side, even cells with a very high abundance of fish can be depleted rapidly if too many birds choose to forage there.

After arriving at a site, a bird will stay at least long enough to assess the density of prey. If the density is so low that none or only a few catches could be made in a 15-min time span the bird will give up and fly to another cell. This behavior of leaving a site because of lack of foraging success has been observed in a number of bird species, e.g., the carrion crow, *Corvus corone* L. (Croze, 1970). Krebs (1974) has measured giving-up times of 11.5 min, for another wading bird, the great blue heron (*Ardea herodias* L.). After attracting wading birds to locations with low food availability using model birds, Kushlan (1977) observed that birds left the site shortly after arrival despite the presence of a great many other birds and only remained at a site when the feeding success was high. These observations suggest that a giving-up time rule (Krebs et al., 1974; Stephens and Krebs, 1986) is appropriate when a bird lands at a site where food availability is low. It is worth noting that a giving-up time rule does best when patches vary highly in quality and cannot be recognized beforehand (Iwasa et al., 1981). The giving-up time rule is specified as follows:

If a bird arrives at a cell where the available food is below a threshold, the bird loses one time step, i.e. 15 min, in assessing the local food availability, give up and leave this cell to try somewhere else.

This rule does not take into account that there might be some other good sites nearby. These cells would go undetected and the bird might lose time flying to a site further away. To account for this possibility, but also to incorporate some behavioral flexibility to the birds, a bird may explore nearby cells before flying to more distant cells:

When a bird leaves a cell, it may check a random sample of nearest and next-nearest neighboring cells. If it finds a cell with a water depth appropriate for foraging, it tries there. If a nearby cell is chosen a bird looses only one time step to get there.

Foraging trips generally take place between 10:00 and 16:00 (Kahl, 1964; Coulter, 1989). This is possibly due to the wood storks' preference for soaring flight (Kahl, 1964; Browder, 1984). Storks often wait until thermal updrafts have built up before leaving the colony and return before the thermals wane in the afternoon. If they miss the thermals in the afternoon, birds may sometimes stay at their foraging sites and return on thermal currents the next morning (Kahl, 1964). These behaviors are put into rule form as follows:

A day in the model corresponds to 24 time steps of 15 min each. If a bird forages at the end of a day, it decides whether to return to the colony or stay overnight. The bird returns if (a) it has gathered fish above its own need, and (b) its current position is not too far (in the current implementation a value of 10 km is used) from the rookery; otherwise it remains at its feeding site overnight and returns to the colony the next morning.

3.1.4. Feeding behavior and foraging efficiency

Wood storks are tactile foragers that grope with their bills as a feeding technique (Kahl and Peacock, 1963). Visual cues do not seem to play a role in prey detection and capture, although they seem to assist in prey handling (Kahl, 1964). Because tactile foraging is related to the rate of encounter between a bird's bill and prey items, it is more efficient at higher prey densities. The maximal capture rate (estimated from table 4 in Kahl (1964)) is about 200 catches in a 15-min time period. Using mosquito fish as a reference prey (see above), these 200 catches correspond to a total of 200 g of fish (live weight). Coulter (1989) reported considerably smaller success rates averaging only about 2 catches per 15-min time period, but his data also suggest that the average size of prey taken by wood storks in east-central Georgia is considerably larger than in the Everglades. Even lower capture rates averaging only 0.54 catches/h have been observed in the Venezuelan Llanos, but prey size was even larger than in Georgia, averaging about 15 cm (G. Morales, pers. commun.). Larger fish seem to be of minor importance in the diet of wood storks in the Everglades. Although wood storks are capable of eating fish in excess of 22 cm, consumed prey averaged only 4.6 cm (Ogden et al., 1976).

When a bird arrives at a feeding site, it first assesses the food availability there, and then makes a decision whether to give up and leave after one time unit or to stay and forage. The current prey density determines the success rate. The assumption is that the success rate increases with the amount of food available up to the maximal value. In addition to capturing more food, more successful birds are assumed to remain longer at their site. Thus, food availability also indirectly determines the amount of time a bird will remain and forage at its current feeding site.

This is modeled as follows:
A bird forages at the rate set by the current food availability in its cell. It forages until its storage capacity is reached, or the success rate drops below a certain threshold. The following values for success rates [3] were used:

food availability (% of maximal value)	food gathered/time step (g)	leave site after 1 time step
0– 20	0	yes
20– 40	50	yes
40– 60	75	no
60– 80	100	no
80–100	125	no

3.2. Nestlings

Nestlings are modeled in the same way as the adult storks. Simulating nestlings, however, is much simpler because their main activity consists of eating the food brought back by their parents and sleeping (Kahl, 1962). In particular, because the main interest is whether a nestling receives enough food to fledge successfully, it suffices to keep track only of their food intake.

Clutch sizes in wood stork nests range from two to five eggs, with three eggs being the most common (Kahl, 1964; Coulter, 1989). Incubation starts as soon as the first egg has been laid and lasts for about 30 days (Kahl, 1964). The eggs are laid several days apart and hatch in the order they have been laid.

Young storks are fed by regurgitation. Parents deposit the food on the nest floor from where it is picked up by the nestlings. Competition for food among the chicks in a nest is fierce. The method of feeding clearly favors the larger nestlings, which are able to obtain a larger fraction of the food. During periods of food shortage, the smallest nestling is often unable to obtain enough to survive. Asynchronous egg laying and hatching thus leads to a type of contest competition, as contrasted to a scramble competition (cf. Nicholson, 1954; Colinvaux, 1986) and seems to have evolved as an adaptation to an uncertain food supply (Kahl, 1964). Similar types of sibling rivalry occurs also in other wading bird species (Jenni, 1969; Mock, 1984a,b, 1985; Mock et al., 1987).

Kahl (1962) conducted a thorough study of the bioenergetics and growth in nestling wood storks. The pattern of maximal food intake can be divided into three 3-week stages (Fig. 1). During the first 3 weeks after hatching the nestlings' food intake increases linearly to a maximal value between 350 and 400 g per day. This value is maintained for the next 3 weeks. During the final 3 weeks the daily food intake decreases linearly to about 200 g per day. During the 60–65-day nestling period each young stork can ingest up to 16.5 kg live weight of fish. Over half of this is consumed during the second stage when the nestlings are between 22 and 45 days old.

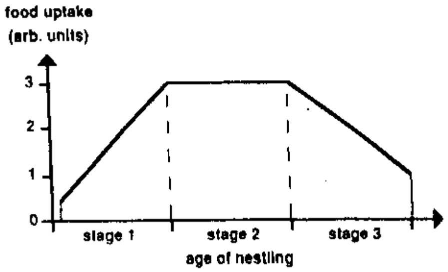

Fig. 1. Simplified pattern of maximal daily food intake of nestling wood storks.

To model the growth of the nestlings I assume that their relative sizes are solely determined by their individual total cumulative food intakes. Since one only has to know which nestlings are the larger ones, one does not have to model their growth explicitly. Total food intake, however, determines whether the nestlings have grown to a size enabling them to leave the nest, forage on their own and care for themselves.

On some days the parents might not be able to bring back enough food to fully satisfy the requirement of all of their nestlings. The smaller nestlings will be affected more than their larger mates, which might still be able to obtain a substantial fraction of what they need. A young stork can certainly endure one or a few days without food, without suffering too much damage. Extended periods of food shortage will, however, decrease a nestling's chance of survival. This is particularly true when larger nestmates have been able to obtain greater amounts and have outgrown the smaller ones. I shall therefore assume that the amount of food accumulated within 5 consecutive days must not fall below a certain threshold; if it does, the nestling will be assumed to have died.

The amount of food parents bring back to the nest is broken up into units of 25 g each. In the order of their decreasing size, i.e. also their hatching order, each nestling in turn receives one item until all items have been distributed. A difference in food intake occurs when one of the adults returns with a load that does not provide each of the nestlings with an equal share. This difference will then be enhanced and from then on the nestlings accumulate food at slightly different rates.

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[3] The rates given in the table are smaller than those calculated from Kahl's data and should be regarded as conservative estimates.

Another way to distribute the food is as follows (true 'contest' competition): all food is given to the largest nestling until its daily requirement has been satisfied; then the second largest one receives all it can ingest, and so on, until all the food brought back by the parent during this trip has been distributed. Distributing the food in this way, however, is so unfavorable to the smallest chick, that given the model's current parameter values, it does not survive the first weeks.

Starting 60 days after their day of hatching, each nestling is checked daily to determine whether its total food intake exceeds the amount required for successful fledging. A successfully fledged nestling leaves its nest but remains in the vicinity of the colony for an additional 25 days (Kahl, 1964). Young storks behave essentially according to the same rules as mature ones (see below).

Healthy fledglings when first leaving the nest can weigh as much or even more than adults (Kahl, 1962). I shall thus assume, that young fledging storks require the same amount of food per day as adults. On the other hand, a young stork is less experienced in catching fish and his success rates will correspondingly be lower than for mature storks (Recher and Recher, 1969; Bildstein, 1983, 1984). For simplicity, I shall assume that a young stork only has 75% of an adult bird's efficiency and thus has to forage longer to obtain the same amount as an adult bird.

To summarize, a nest and the nestlings are modeled by the following set of rules:

(1) Each nest contains three eggs initially which are laid 2 days apart.
(2) Each egg is incubated for 30 days before hatching.
(3) The amount of food each nestling can maximally ingest on a single day increases linearly to 400 g during the first 3 weeks after hatching. It remains at this value for the following 3 weeks and then decreases linearly to about 200 g per day during the final 3 weeks.
(4) The amount of food a nestling receives can fall below these values for some days, but the accumulated actual food intake for 5 days in a row must not fall below 50% of the accumulated maximal values; if it does, the nestling will be assumed to have starved.
(5) Each nestling must be provided with a total of 15.5 kg of food over the whole nestling period to be successfully fledged. This value corresponds to an average daily food intake of about 300 g during the second stage of highest food demand.
(6) Nestlings can fledge after 60 days and can stay up to 65 days in the nest.
(7) The relative size of the chicks in a nest is determined by their total cumulative food intake.
(8) Larger nestlings obtain more food than their smaller mates.

3.3. Nest initiation

What triggers the formation of colonies and the start of nesting is uncertain and may vary with the location of the colony. Kahl (1964) observed that nest initiation in the Corkscrew Swamp colony was timed to specific points in the decline of the water level, while Kushlan et al. (1975) found no such correlation for wood storks nesting in the Everglades. A rule for initiation of nesting must not simply rely on drydown and declining water levels. If it did and nesting commenced as soon as water levels fall to specific points, prey availability might be too low for survival of adults or their nestlings. Furthermore, the production of eggs may be dependent upon the female's ability to collect and store nutrients (Ankney and MacInnes, 1978; Winckler and Walters, 1983; Eldridge and Krapu, 1988; cf. also Gill, 1990). Delay in colony formation or, even worse, the failure to nest and to produce eggs at all, is then probably due to the female's inability to attain enough food, if food is the proximate stimulus in initiating nesting as Kahl (1964) suggests. In fact, in a number of bird species one can artificially advance breeding by supplementary feeding of the female (Drent and Daan, 1980). Yet, no study that I am aware of has related nesting in wood storks to factors besides water level decline and drydown (see, e.g., Ogden et al., 1980).

Despite this uncertainty, the decline of water levels is included in the rule to specify nest initiation. I assume that a pair may start nesting as soon as there are cells within a certain distance of the colony with a water depth appropriate for storks to forage in. As a first working hypothesis, I assume this range corresponds to a distance which birds can travel within 1/2 h of flying time. Since a bird does not know the availability of food in a cell without actually having foraged there and forgets this information as soon as it leaves the cell, the rule only includes water depth but not prey availability as a cue to nest initiation.

Lacking reliable information of the effect of prey availability on colony formation, I assume that the timing of nesting is also dependent upon the female's ability to acquire sufficient food to meet the additional energetic cost of egg production. This requirement is met when, for at least 3 days in row, the female has been able to obtain 25% more food than it normally needs in a day. I have checked that this particular value does not have a significant effect on the timing of nesting. Any value between 20 and 40% leads to nesting dates with a difference of less than a week.

To summarize, nest initiation is modeled as follows:

A pair starts a nest when two requirements are met:

(1) Cells with a water depth appropriate for foraging are within a 10-km radius of the colony.

(2) The female bird has obtained at least 600 g of food (i.e. more than 20% above its daily energy requirement) during 3 consecutive days.

In this form, the rule ensures that shallow water areas are close to the colony and that food is not only available, but also has been detected and is actually utilized by the birds. While the first condition has almost no effect on the timing of nesting when food conditions are right, the second can impose a severe restriction on timing when food return is low. In fact, the second condition is easily met when about half of the birds are able to forage at maximal rates for at least 1 h a day, and then it is only the location of shallow water areas and their distance to the colony that determines the onset of nesting. Depending on the spatial distribution of water depths, the onset of nesting may then correlate with either specific points in the decline of water level (Kahl, 1964) and/or with the evaporation rate at the beginning of the dry season (Kushlan et al., 1975).

3.4. *Nest desertion*

A multitude of factors is thought to be responsible for the abandonment of nests by wading birds. These include predation, low availability of food, and adverse weather conditions, such as heavy rainfall, severe storms, and extended periods of cold weather. Predation by mammals (e.g., racoons) or aves (e.g., crows) has frequently been implicated in the failure of wading bird nests (Dusi and Dusi, 1968; Jenni, 1969; Taylor and Michael, 1971; Pratt, 1972; Pratt and Winkler, 1985; Rodgers, 1987). However, Frederick and Collopy (1988, 1989) found little evidence for predation. Mammalian predation, in particular, was noted only after the area around a colony had dried out, leading to the conclusion that large expanses of shallowly inundated grassland is an effective barrier against mammalian predation. Raids by racoons can cause the disruption and abandonment of entire colonies, often through excess killing (Lopinot, 1951; Coulter, 1987; Rodgers, 1987; Post, 1990). Such catastrophic events can be modeled by a deterministic rule like

if: condition for the occurrence of a catastrophic event is fulfilled
then: all nestlings still in nests are killed

or a probabilistic one, where the colony fails with a specified probability given fulfilment of some conditions. Because such events lead to synchronous and complete abandonment of all nests in the colony, the process does not need to be explicitly simulated. The cause and effect relationship is explicitly included with a rule like the one above and nothing additional can be learned from a simulation, except whether a condition has been fulfilled or not. To find out whether this is the case, particularly for conditions that are solely triggered by external events, one does not have to go through a full simulation of a wading bird colony because these conditions are fulfilled or not, independently of what the birds have done.

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Non-catastrophic events, which lead to the abandonment of only a fraction of the nests, are a completely different matter. One way to include such events is to include a (daily) failure rate for each nest. Another is to externally specify some instance in time at which some nests are deserted. For the time being, such possibilities are neglected and only conditions that are brought about by the birds themselves are taken into account. This is not to say that, e.g., predation is unimportant and can be always neglected, but neglecting it for the moment will provide baseline data against which the effect of predation can be compared.

Rather than have such events lead directly to the desertion of some nests in the colony, each pair in the model makes its own decision whether to leave the colony or to stay. In the model a pair will desert its nest for only two reasons. First, the adults might not be able to find enough food to satisfy their own needs and the needs of their young (if they have any). I shall assume that when both parents are unable to satisfy their own requirements for 3 consecutive days, they will abandon their nest (and nestlings). Second, a nest may be deserted when the parents are capable of finding enough for themselves but do not find sufficient food to feed their young. In this case, the nestlings will eventually starve, starting with the smallest one. If all nestlings in a nest have perished, the parents will desert the nest.

The corresponding rule is then formulated as follows:

A pair gives up their nest when one of the following two conditions is met:

(1) The birds have not been able to satisfy their own energy requirements for at least 3 consecutive days.

(2) All of their nestlings have perished.

It should be noted that as a consequence of the rules described previously, the parents will not leave the colony after one or more of their nestlings have fledged and left the nest, but will rather stay at the colony together with their offspring. Depending on how far the breeding season has progressed, a nest may be deserted and not restarted for the remainder of the breeding season, or it may be restarted later, when conditions have become favorable again.

3.5. *The physical environment*

The area that is considered in the model is the part of the landscape that birds from the colony use for foraging. Adult wood storks may fly as far as 40 km from the rookery to their feeding grounds (Kahl, 1964), but a

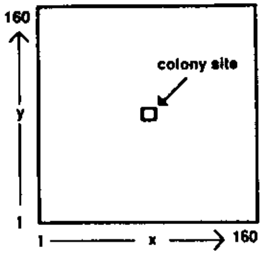

Fig. 2. A schematic representation of the landscape surrounding a wading bird colony. The entire area is divided into 160 cells × 160 cells.

distance of less than 20 km is most common (Kahl, 1964; Coulter, 1989; see also Frederick and Collopy, 1988). Browder (1984) has observed wood storks feeding as far as 97 km from the rookery. However, foraging at these great distances coincided with the occurrence of strong thermal updrafts making it easier for the storks to travel that far, and only occurred at the beginning of the breeding season before the eggs were laid and near the very end of the season when the nestling were already very large or had fledged. The storks worked nearer to the rookery during the other stages of the season, in particular during incubation and the early stages of raising young. The area considered in the model is thus restricted to a square region of 40 km × 40 km and for the moment assume the colony to be in the center of the square, although this is not a necessary requirement in the model.

To account for spatial heterogeneity, the landscape is divided into cells of 1/4 km × 1/4 km each, such that the entire area consists of 160 cells × 160 cells, or 25600 cells in total (Fig. 2). Topographic details within each cell, e.g. ponds, alligator holes, vegetation cover of ponds, are not explicitly considered. Rather, it is assumed that average conditions specify the character of a cell. In particular, each cell is given an average elevation, which taken together form the topography of the landscape.

Very flat terrain is characteristic of a number of wetlands where wading birds feed and nest. For example, the Everglades in southern Florida is a vast, almost treeless, marsh extending over more than 160 km with an average slope of only 3 cm/km (Parker et al., 1955; Parker, 1974; Kushlan, 1991). Seasonal rainfall, one of the most distinctive climatic features of such wetlands, results in seasonal variations of water levels with a periodic drying and reflooding during the alternation of the dry and wet season. The hydrological pattern which results from the temporal distribution of rainfall on the foraging area and the inflow and outflow of water is a very important factor in the model.

Perhaps the most simple topography one may envision to represent flat terrains is a tilted plane with an elevation gradient along increasing values of x and y. Elevations are measured relative to some arbitrary value and the elevation h of a cell with coordinates (x,y) is then given by

$$h(x,y) = a \cdot x + b \cdot y, \tag{1}$$

where a and b are the average slopes in the horizontal and vertical direction, respectively. In this special case, the origin (0,0) serves as a reference level, $h(0,0) = 0$, and the highest elevation is reached by the cell with coordinates [4] (159,159). If $a = b = 3$ cm/km are taken as the value for the slopes, the highest elevation is then given by

$$h(159,159) = 2 \cdot 159 \cdot 0.75 \text{ cm} = 238.5 \text{ cm}. \tag{2}$$

The water level (measured relative to some arbitrary mark, e.g. sea level) is taken to be uniform across the entire landscape. While this may be a reasonable assumption for flat terrains like the one just described, this may not necessarily be the case for a more complicated topography. Nevertheless, I shall use it as first working hypothesis. Since cells may have different elevations, the water depth changes from cell to cell and is determined by [5]

$$\text{water depth} = \text{water level} - h(x,y). \tag{3}$$

The depth changes according to the pattern of water level change and cells may dry out or become reflooded accordingly.

In general, evaporation will make the water level fall during the dry season and rainfall during the wet season will make it rise again. Assuming a constant daily drying rate of δ cm/day, a reflooding rate of ρ cm/day, and neglecting rainfall, the pattern of water level change is thus given by

$$W(t) = \begin{cases} W_0 - \delta \cdot t, & t \leq t_0 \text{ (``dry season'')} \\ W(t_0) + \rho(t - t_0), & t > t_0 \text{ (``wet season'').} \end{cases} \tag{4}$$

Here the time t is measured in days, t_0 denotes the end of the dry season and the beginning of the wet season, and W_0 is the initial water level at the start of the simulation.

For the tilted-plane example mentioned above the boundary separating submerged cells from cells above the current water level $W(t)$ is given by the straight line calculated from $h(x,y) = W(t)$ or

$$y = (1/b)(W(t) - ax), \tag{5}$$

which moves across the landscape corresponding to the change in water level.

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[4] Cells are numbered from 0 to 159 in horizontal and vertical directions, respectively.

[5] Negative water depth is equivalent to a cell being *above* the current water level.

Rainfall can temporarily disrupt the decline or enhance the rise of water levels during the two seasons. To capture the basic features of the climatic and hydrological patterns, several simplifying assumptions are made. First, all rainfall is evenly distributed across the entire landscape. Thus each cell receives the same amount of rainfall on a given day. Second, rainfall raises the water level by an appropriate amount, but has no effect otherwise. For example, no runoff from cells above the current water level is taken into account, i.e., rain falling on dry cells is instantly and completely absorbed and as a consequence neglected in the model. The change in water level during 1 day is thus the change calculated from Eq. 4 plus the amount of rain (measured in cm) that has fallen onto the entire landscape during that day.

3.6. The resource environment

Fish is the major food of the wood stork (Kahl, 1964; Ogden et al., 1978), and water level fluctuation is a principal factor affecting fish populations (Kushlan, 1980). Wood storks are tactile foragers and depend on high densities of prey for successful foraging and reproductive success. These densities vary both spatially and temporarily. During the dry season, the lowering of water levels concentrates aquatic prey, whereas fishes move out of these dry-season refugia when water levels increase (Kushlan, 1978, 1980).

Heterogeneity in fish density is explicitly taken into account and each cell in the model has a temporal history of fish density. Fish density is usually highest at the beginning of the dry season and is determined by the characteristic conditions within each cell during the wet season, such as vegetation and soil characteristics, along with water depth. Changes in the water level of each cell (usually declining depths) cause changes in the densities of fish within a cell and, possibly, movement of fish from one cell to another. Foraging by birds reduces the fish abundance in the cells through time. Furthermore, reproduction by fish and invertebrates may continue through the dry season. The heterogeneity within each cell is not explicitly taken into account. The model rather attempts to capture average conditions in a cell and to represent in an average sense what the concentrations of fish would be in a cell based on the average water depth within the cell.

It is difficult to find accurate data about the prey availability for wood storks. Kushlan (1980) examined prey availability for the white ibis (*Eudocimus albus*) in southern Florida. Although his data might not be directly applicable to wood storks, they give at least an idea how much food is available and where. Energy content of food available for ibis in primary feeding habitat was in the range of about 6 kcal/m^2 (with a high of 120 kcal/m^2 in marsh ponds) with an energy content of about 6.5 kcal/g or 1 g/m^2. The cells measure 250 m × 250 m, i.e. 62500 m^2, yielding a maximum of 62 kg of fish per cell. Given the microtopography within a cell this estimate should probably be regarded as being too high for an average value and a maximal value of 30 kg of fish within a cell is used as a first assumption.

Although the physical and resource environments were introduced in two separate sections, they are, of course, not independent of each other. Naturally, fish can only live in cells which are under water. Whenever a submerged cell dries, the fish density in it is immediately set to zero. Even when such a cell is reflooded again, it will be assumed to contain no food that is available for storks. The major effect of rainfall and of water level reversals is thus a decrease in the number of cells that are in the appropriate depth class and contain prey. It is fairly easy to produce rainfall patterns such that there will be shallow water areas but none of the cells in these areas contains any food (see Section 4.3).

Compared to drydown, which can wipe out all fish in a cell, foraging by birds only reduces the amount of fish in its cell. At every time step the amount of fish each bird has gathered is subtracted from the total amount of fish in the cell. When large aggregates of birds develop, they may deplete the fish available in a cell within just a few time steps.

3.7. Some final remarks

In the preceding sections, I gave an overview of the most important rules in a model that is used to simulate the individual actions of single birds, their interactions with conspecifics and with their environment. I have also briefly commented on how the physical and resource environments are taken into account. It should be noted, however, that this overview does not contain a full description of all rules. For instance, the rules that describe foraging behavior and movement between feeding sites at night are similar to the ones during daylight hours presented above. In its current implementation the model uses more than 100 behavioral rules for a single bird, most of which are variations of or similar to the ones considered above, but a full description would be beyond the scope of this work.

Although the model could be formulated in greater generality to encompass other species of wading birds, the description was, for sake of brevity, confined to wood storks. Nevertheless, an extension to other wading birds species, e.g. spoonbills, blue herons or ibis, is not only possible but requires only minor modifications of the program code – an advantage of decision-based models and object-oriented programming languages (Saarenma et al., 1988; Folse et al., 1989) which have been used in constructing the model. Parameters, on the other hand, are usually specific to each wading bird species and must be changed accordingly. The same remarks hold for the underlying landscape. In fact, the model has been used already to assess recent changes in the Everglades landscape and their effect on wading bird reproduction (Fleming et al., 1993b).

4. SOME SAMPLE RESULTS

Rather than begin immediately with simulating specific real-world situations with all their details, three sample simulations with typical parameter values are presented to illustrate the types of output the model generates. More detailed investigations will be presented in future work. The simulations are of three scenarios:

(1) A breeding season where external conditions, particularly the extent and location of shallow water areas, ensure a high food availability at feeding sites close to the rookery. Parameters are chosen such that nestlings are provided with sufficient food to survive the nestling period and fledge successfully.
(2) A borderline case where the maximal load that parents can bring back to their nest is smaller and the starvation threshold for the nestlings is larger than in the first scenario, while all other parameters and conditions are the same. The nestlings will thus receive less food and, in addition, are more sensitive to variations in the amount of food they receive.
(3) A breeding season that starts off as in the first scenario but where the drydown is disrupted by several water level reversals resulting from rainfall during the last weeks of the nest attendance period.

In all three scenarios, a small colony of 50 breeding pairs was simulated. This colony size is well below the carrying capacity of the environment, which, given the current parameter values and choices for elevation pattern and fish availability, could support a colony of 250 pairs. The colony was deliberately made small to avoid additional effects originating from density dependence and competition among the birds resulting in a too rapid depletion of their resources. Nevertheless, 50 pairs are sufficient to pick up most of the interesting features that are prevalent for larger colonies.

As soon as conditions become suitable, nesting commences and each female can lay 3 eggs, which gives a total of up to 150 nestlings if all eggs hatch and no nest is deserted. Most parameters have the values specified in model description section (Section 3). The only exceptions are the following:

(i) In the first and third scenario, the threshold in the rule specifying when a nestling starves was decreased from 50% to 25% of what a nestling can maximally ingest.
(ii) The total amount of food a nestling must have received to fledge successfully is decreased to 14 kg. This value corresponds to an average daily food intake of about 300 g during the second stage of the nestling period when the food requirement is highest (cf. Section 3.2).
(iii) The probability with which birds join an existing flock was set to 0.45. Thus birds select a site at random with a probability of 0.55.
(iv) The length of the incubation period was reduced to 20 days (instead of 30 days). This change does not affect any of the following results. Doing so increases the more interesting period of time when nestlings are present in the colony.

External conditions were such that a high food availability was ensured under optimal conditions, i.e. no water level reversals disrupt the food supply (scenario 1). Specifically, the amount of fish in the cells comprising the shallow water areas was assigned at random, independent of their location and distance to the colony site, with two thirds of the cells containing the maximal amount of 30 kg per cell, while the remaining third contained just 10 kg. A distribution such as this one with a high variation between different locations seems to be typical for the Everglades at the beginning of the dry season (W.F. Loftus, pers. commun.). It should be kept in mind, especially for the third scenario, that cells that were dry and became reflooded after periods of rainfall do not contain fish available to the birds.

Special elevation profiles, such as the tilted plane, implicitly impose patterns on the location and, more importantly, on the extent of shallow water areas in which birds forage. This creates an additional factor which must be accounted for when analyzing how well the birds in the colony reproduce. To exclude the influence of the extent of feeding areas, one may choose an elevation pattern in which, at any given time, approximately the same number of cells have a water depth appropriate for foraging. If, in addition, the availability of food at the feeding sites is distributed randomly, as in the prescription outlined above, the total amount of food which becomes newly available to the birds on each day is constant and does not change in time.

One way to create such a neutral landscape model (Gardner and O'Neill, 1991) is to randomly assign elevations to cells using a uniform distribution. One drawback of a random assignment is that the resulting pattern shows less contagion between sites than is often observed for actual landscapes (cf. e.g., Gardner and O'Neill, 1991). Foraging birds take advantage of contagiously distributed feeding sites (cf. Section 3.1.2).

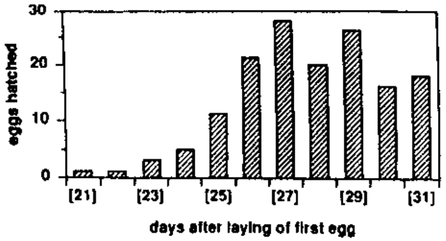

Fig. 3. Scenario 1: The number of eggs hatching in the colony. The first egg was laid on day 0 of the simulation.

Fortunately, a hierarchical algorithm (R.H. Gardner, pers. commun.) creates elevation patterns that, in general, have greater contagion between sites than a simple random assignment. A description of hierarchically generated elevation patterns is given in the appendix.

4.1. *Scenario 1: a successful breeding season*

Nesting commences when conditions, such as location and extent of shallow water areas, availability of prey, and food obtained by the birds, are right (cf. Section 3.3). Eggs are laid 1 week after a pair has initiated their nest. Other pairs will follow according to the rules described earlier. Eggs are incubated for 20 days and hence the first egg hatches [6] on day 21 and after that, all other eggs hatch in the order in which they were laid. The last eggs hatch on day 31, 10 days after the first one. Because each individual pair decides when to commence nesting, laying dates are spread out and asynchronous and, thus, so are hatching dates (Fig. 3). After 32 days all eggs have hatched and each nest contains a brood of three nestlings, such that the total number of nestlings in the colony reaches its maximal value of 150 (Fig. 4). All results presented in this section start with the day the first egg in the colony is laid.

External conditions, particularly the extent and location of shallow water areas, the absence of water level reversals, as well as the parameter values chosen in this scenario, lead to a successful breeding season. All nestlings receive enough food and survive the nestling period. No brood reduction occurs (Fig. 4) and all adults remain at the colony until all nestlings have fledged. All but one nestling fledged successfully when they reached the appropriate age or size and the single unsuccessful nestling had received only one unit of food (25 g) less than was required by the threshold for successful fledging.

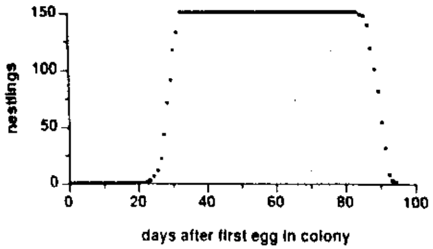

Fig. 4. Scenario 1: The number of nestlings in colony during the entire breeding season. The first nestling appears on day 22 and the last one fledges after 94 days.

The distribution of the accumulated food intake of each fledgling is shown in Fig. 5. Despite favorable conditions, the distribution shows a large variation amongst the nestlings, although somewhat less between the various nests (average: 14.28 kg in both cases; s.d.: 0.26 vs. 0.2 kg). The large variation, particularly the distribution being skewed to low values, indicates that the number of successfully fledged nestlings is sensitive to the threshold value used in the rule determining whether or not a nestling has fledged successfully. For instance, a threshold of 14.3 kg, instead of 14 kg as used here, would result in over half the nestlings being considered unsuccessful. Lacking reliable information on how much food a nestling really needs to fledge, the distribution of cumulative food intake is a much better indicator in this model of potential nesting success, than is the number of fledglings determined by indifferent application of the success rule.

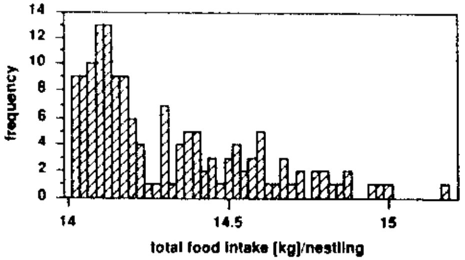

Fig. 5. Scenario 1: Distribution of total food intake of the nestlings at the time of their fledging.

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[6] In the current implementation, laying and hatching of eggs occur at the end of a day.

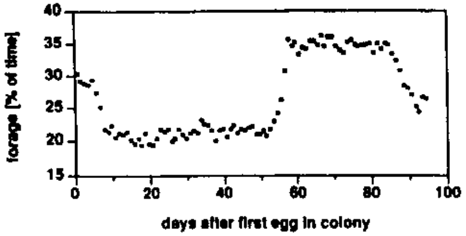

Fig. 6. Scenario 1: Average fraction of time each bird has been foraging.

After nest attendance all 100 birds can leave the colony on foraging trips and the time spent on foraging increases from about one fifth of the daylight hours to more than 35% (Fig. 6). On the other hand, the average daily rate of success decreases slightly compared to the earlier values (Fig. 7). This decrease was not because the prey base became depauperate, but resulted from larger congregations of birds gathering at feeding sites. According to the rules specifying foraging behavior and the selection of feeding sites, the birds do not know beforehand how much fish a cell contains. They rather base their choice on the number of birds foraging at a particular site. On average, flocks are about twice as large when all birds forage simultaneously, leading to a more rapid depletion of food at feeding sites which in turn results in a decrease in the overall foraging rate. Yet, more time now is available for foraging which provides ample compensation and the average amount of fish caught by each bird during a single day increases from about 600 g to more than 900 g.

This change is also reflected in the amount of food brought back to the nests and fed to the nestlings (Fig. 8). During nest attendance, each nestling receives about 150 g, which given the current parameter values seems to represent an upper limit of how much a single bird can supply.

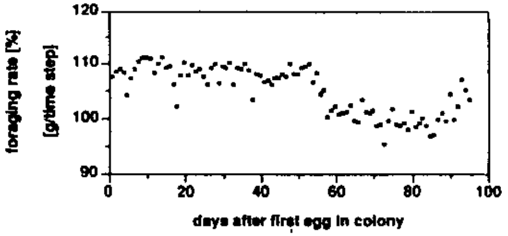

Fig. 7. Scenario 1: Daily foraging rate (average over all adult birds in the colony). The vertical units are g of fish obtained per 15 min foraged.

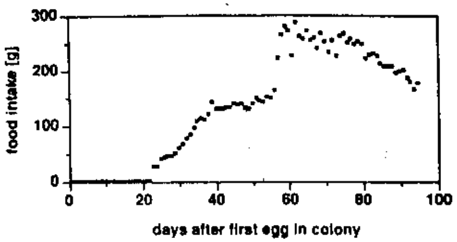

Fig. 8. Scenario 1: Average daily amount of food received by each nestling.

After nest attendance, nestlings are fed almost twice as much, about 275 g, still much less than the 400 g they can ingest in a day.

4.2. Scenario 2: reduced load and higher starvation threshold

In the second scenario, two parameters have been changed to make it more difficult for the birds to successfully raise their young. The value for the maximal load has been decreased from 300 g to 250 g for each trip. As mentioned already in Section 3.1.1, the maximal load that adult storks can carry to their nest when returning from a foraging trip critically affects the chances of survival of their young. Although I shall not present a detailed sensitivity analysis, the following results corroborate that a value of 250 g represents a borderline value, below which nestling survival is greatly decreased or not possible at all. The situation is made even worse by increasing the threshold value for starvation of nestlings. If a chick receives less than half of the maximal amount it can ingest during 5 consecutive days, it will have starved at the end of the fifth day.

These two parameter changes only affect the survival of the nestlings, everything else remains unaffected. In particular, the timing of nesting and egg laying, and thus the days on which the eggs hatch, are the same as in the previous scenario. All eggs hatch and the number of chicks reaches the maximal value of 3 per nest, or 150 in the colony, on day 32 (Fig. 9). Nevertheless, because parents bring back less food when returning from their foraging trips and starvation is more likely, some of the nestlings die eventually. Very young nestlings with low energy requirements can still be provided with enough food, but their demand soon surpasses the capabilities of the parents to supply food. Nestlings will subsequently starve starting with the youngest in each nest (cf. Section 3.2).

The sharp decrease in the number of nestlings and the constant value thereafter indicates that starvation and brood reduction occurred only during a short interval and is not spread out over the nestling period. The

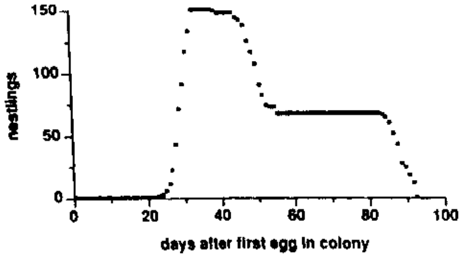

Fig. 9. Scenario 2: The number of nestlings in colony during the entire breeding season. The first nestling appears on day 22 and the last egg hatches on the 31st day. After brood reduction between day 38 and 55 the number of nestlings stabilizes at 66 and decreases late in the season when nestlings fledge.

age distribution of the 84 starved nestlings at the time of their death is shown in Fig. 10. The majority of these nestlings died between the ages of 17 and 23 days (average 19.82 ± 2.76 (s.d.)). At this time, the nestlings have almost reached their highest food demand (cf. Fig. 1). This also coincides with the final week of nest attendance. The new set of parameters made it impossible for one bird alone to provide all of its young with enough food and thus some of the young starved: 9 pairs lost all their offspring, then deserted the nest and left the colony (see the rules specifying nest desertion in Section 3.4); 16 pairs lost 2 of their 3 nestlings, while the remaining 25 pairs lost only one chick each. The average brood size dropped from 3 nestlings to 1.6 nestlings. All of the remaining 66 nestlings survived and fledged successfully after reaching the fledgling age.

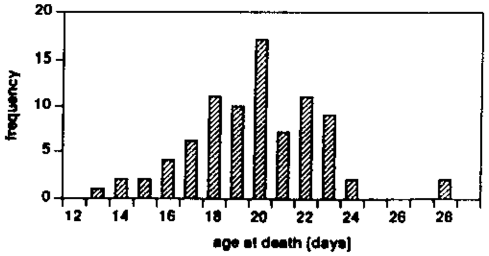

Fig. 10. Scenario 2: Age distribution of starved nestlings at the time of their death.

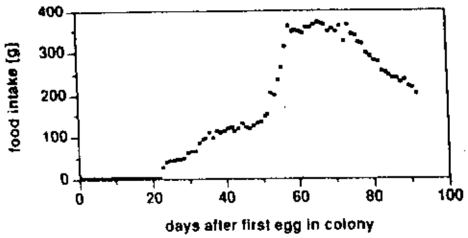

Fig. 11. Scenario 2: Average daily amount of food received by each nestling.

Except when triggered by large water level reversals, brood reduction occurs most severely during the last week of nest attendance, i.e. between the 17th and 25th day after the first egg has hatched. Then the oldest chick has almost reached the second stage where food demand is highest. The two other nestlings are only a few days younger and require less food than their older sibling. Nevertheless, the overall requirement of the young places a severe load on the parents. Using a maximal food intake of 400 g and 20 days for the duration of the first stage (cf. Section 3.2), the maximal amount all three nestlings can consume on a single day increases from about 650 g on day 17 to nearly 1100 g on day 25. As long as only one parent at a time is foraging, the parents are barely able to provide sufficient food during this period to avoid starvation of their young.

The higher starvation threshold, which renders nestlings more sensitive to fluctuations in the amount of food supplied by their parents, and the smaller load adult birds can carry back to the colony amplify the criticality of the short period of brood reduction. Initially, the amount fed to each nestling increases as in the first scenario but levels off sooner at about 125 g (Fig. 11) versus 150 g (Fig. 8). Given the different maximal loads in the two scenarios, these values seems to represent the upper limits of how much can be supplied by a breeding pair during nest attendance. Since the time budgets in the two scenarios at this time are very similar, both values corresponds to about 3 completed foraging trips within a 2-day time period. Closer inspection of the individual actions of all 100 birds in the colony revealed that pairs followed roughly the same pattern: one of the parents leaves in the morning and returns early afternoon to remain at the nest feeding the young; its mate leaves to forage and returns late the following morning; a second switch occurs and the other parent leaves and returns late in the afternoon or early the next morning.

The difference in the amount that was fed to the chicks seems insignificant at first sight, but is indeed sufficient to induce starvation of younger nestlings. If nothing else, this shows how critical the situation is during the final stages of nest attendance. Concurrently with the termination of nest attendance, the amount supplied to each nestling jumps to over 375 g each day, nearly the maximum a nestling can ingest on a single day and about 100 g more than was fed in the previous, baseline scenario.

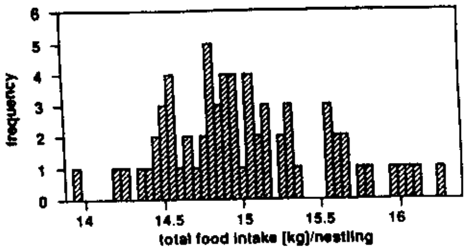

Fig. 12. Scenario 2: Distribution of total food intake of the nestlings at the time of their fledging.

The increase in food supplied to the nestlings during the later stages of their development made up for what was missed earlier. At the time of fledging, nestlings have, in general, received more food than in the previous case, with most of them safely surpassing the fledging threshold by more than 500 g (Fig. 12). The distribution of the accumulated food intake for the surviving 66 nestlings at the time of fledging is more symmetrical and less skewed to lower values than in the first scenario where no brood reduction had occurred (cf. Fig. 6). Furthermore, the average cumulative food intake is higher (15.5 kg vs. 14.4 kg), but the variability is almost twice as large (3.8% vs. 1.9%). Although fewer nestlings fledged successfully, their overall condition, as measured by their cumulative food intake, seems to have improved. This feature appears to be generic to the model and has been observed in all simulations so far. Whenever brood reduction occurred, the successful fledglings, although often fewer in number, had consistently received more food than nestlings in comparable situations where brood reduction had not occurred. The alternatives seem to be many, but lean, or few, but fat fledglings.

The general pattern of how the birds allocate their time among the various activities is the same as in the previous case. Nevertheless, there are a few subtle differences which are worth noting. For one, because starvation has reduced the number of nestlings, the task of providing food for the young has been greatly alleviated. The fraction of time allocated to foraging can thus be smaller and the decrease in foraging rates is not as pronounced because fewer birds compete with each other and each bird needs to take less food (Figs. 13, 14 vs. Figs. 6, 7). A rough estimate yields a total of about 64 kg of fish taken each day as compared to more than 90 kg in the previous scenario with no brood reduction.

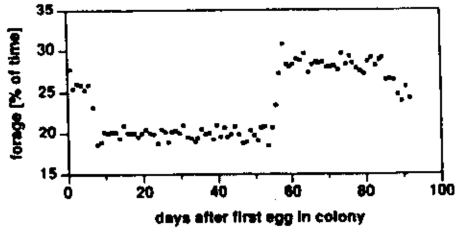

Fig. 13. Scenario 2: Average fraction of time each bird has been foraging.

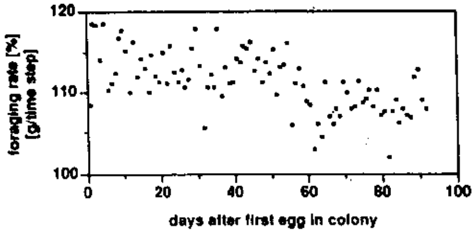

Fig. 14. Scenario 2: Daily foraging rate (average over all adult birds in the colony). The vertical units are g of fish obtained per 15 min foraged.

4.3. Scenario 3: a breeding season with flooding

The last scenario is a breeding season with the same baseline conditions as in the first scenario. However, the drydown is disrupted by heavy rainfall during the critical last stages of nest attendance, when the food demand of the nestlings approaches its highest value. It should be kept in mind that, according to the rules in Section 3.5, the amount of rainfall is directly converted into a change of water levels, i.e. the water depth of submerged cells. Note also that reflooded cells do not contain any food available to the birds.

The rainfall pattern in the third scenario is divided into three stages (Fig. 15). The first reversal occurs between day 35 and 39 after the first egg was laid with 2 cm of rain each day. There is no rainfall during the next 3 days and the water falls by 1.5 cm. A second period of rainfall occurs on day 43 and 44 with 4.5 cm and 3.25 cm, respectively. During the next 3 days the water level falls again by 1.5 cm. The strongest reversal occurs between day 48 and 50 with a daily precipitation of 4.5 cm.

Time budgets (Figs. 16, 17) and foraging success (Fig. 18) are little affected by the first period of rain after which one third of the depth classes in the shallow water areas below the maximal foraging depth of 40 cm consist of reflooded sites. Cells in these depth classes, however, are not

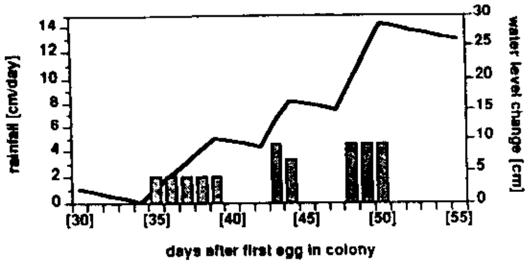

Fig. 15. Scenario 3: Daily rainfall and water level change between days 30 and 55.

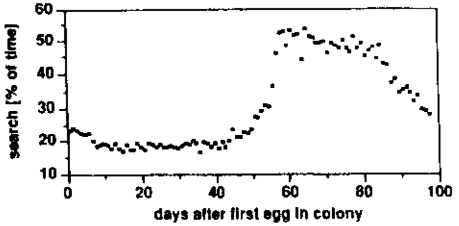

Fig. 16. Scenario 3: Average fraction of time each bird spent on searching flights.

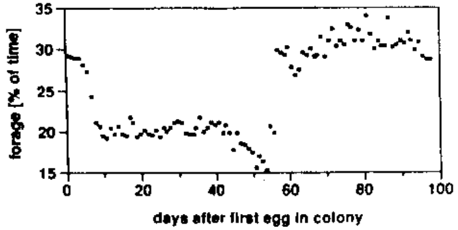

Fig. 17. Scenario 3: Average fraction of time each bird has been foraging.

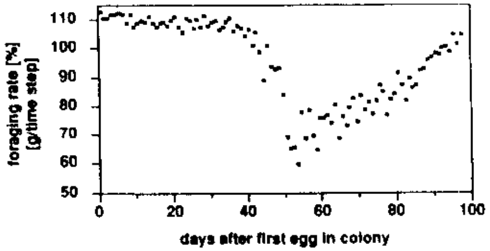

Fig. 18. Scenario 3: Daily foraging rate (average over all adult birds in the colony). The vertical units are g of fish obtained per 15 min foraged.

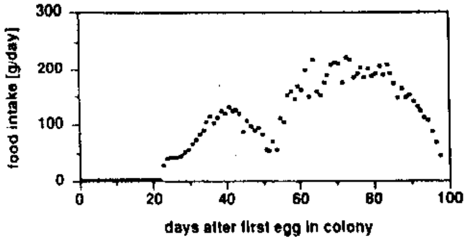

Fig. 19. Scenario 3: Average daily amount of food received by each nestling.

utilized for foraging anyhow (cf. Section 3.1.3) and the only effect of this first reversal is to stipulate birds to forage at sites which have already been in the proper foraging depth class before and, therefore, might have experienced some exploitation earlier on. Nevertheless, the extent of the shallow water areas is large enough to prevent resource depletion have more than a minor effect on foraging rates.

The second reversal leads to a water level rise of 16.25 cm relative to day 34. Cells which were being used for foraging became either reflooded, and thus do not contain prey, or have been foraged at continuously since nesting has started and thus might have been depleted of food already. Reflooded cells are not recognized as such beforehand and birds have to assess these sites, i.e. forage without success, before leaving and trying elsewhere. Although foraging rates decrease (Fig. 18), the amount of food returned to the nests at this time is still sufficient to satisfy the demands of nestlings (Fig. 19).

The situation is completely changed by the last and strongest period of rainfall. Besides creating the largest water level rise, it also coincides with the critical period of the nestling stage. After this last period of rainfall, water has risen by 27.5 cm (relative to day 34) and thus most of the cells that birds can forage in were previously dry and became reflooded.

Following this last reversal, the birds must spend an increasing amount of time on searching flights finding one of the few remaining sites that still contain prey (Fig. 16). Consequently, the time left for foraging decreases (Fig. 17). Furthermore, birds will tend to congregate at what few sites remain and which thus become heavily exploited. Overexploitation and unsuccessful foraging at reflooded sites add up to a decrease in success rates to only half their pre-reversal values (Fig. 18). Although foraging rates start to rise again after the reversal is over, its effects are seen for the next 50 days. Repercussions of water level reversals generally depend on the degree of water level rise and the drying rate. As a rough estimate, the number of days one or several reversals effect foraging rates can be obtained from

$$\frac{\text{total water level rise after the last reversal (cm)}}{\text{drying rate (cm/day)}}$$

The different extent to which reversals affected the colony is also manifest in the amount fed to each nestling (Fig. 19). During and after the first reversal, the values do not differ from the first, baseline scenario (Fig. 8). During the second reversal, which starts on day 43, foraging rates start to decline and nestlings receive less. Foraging rates continue to decline, even after the rainfall is over, because it takes several days before the additional water on the shallow areas has evaporated. The third reversal accelerates the decline even more, and nestlings now receive so little food that some of them starve. Immediately after the reversal, the surviving nestlings are much better fed because the average rate of foraging has increased, the average brood size has dropped to 2.25 nestlings (see below) such that the food brought back by the parents is shared among fewer siblings, and, most important, nest attendance has ceased so both parents are foraging simultaneously.

Immediately following the last reversal more than half (26, i.e. 52%) of the initial 50 nests were given up by the birds and the number of nestlings in the colony dropped from its peak value of 150 to 54 within the 6 days following the last incident of heavy rainfall (Fig. 20). Twenty-three breeding pairs lost their entire brood due to starvation and then left the colony. Still the majority of these perished nestlings had received more than 75% of their requirements during the last 5 days before their death (Fig. 21). Some nests were deserted because the parents could not find enough food to satisfy their own energy requirements. These birds left their nest and the colony despite their nestlings having received sufficient amounts to overcome the period of food shortage. One pair had lost two of its nestlings and then deserted the remaining one 2 days later. Two pairs abandoned their entire brood of three nestlings although one nest contained chicks which had received considerably more food than required by the threshold in the starvation rule (112, 125, and 128% of the threshold value; cf. Fig. 21).

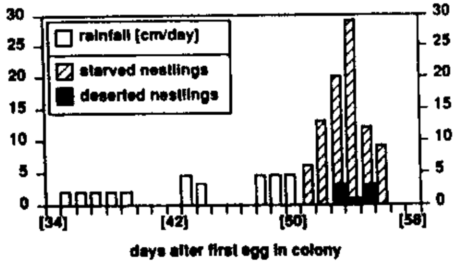

Fig. 20. Scenario 3: Number of starved and deserted nestlings relative to the periods of rainfall.

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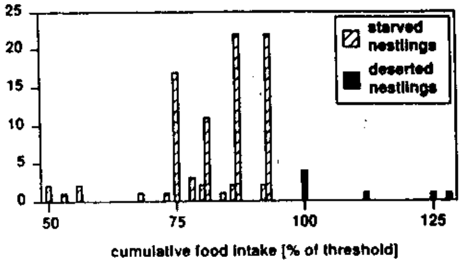

Fig. 21. Scenario 3: Distribution of the total food intake during the final 5 days before a nestling had starved or was deserted by its parents. The horizontal units are in percent of the age-dependent threshold in the starvation criterion.

The timing of the last reversal relative to the nest attendance period plays a crucial role in whether a nest is lost or not. Early nesters, which laid their eggs during the initial days of nesting, had their first egg hatch between day 22 and 25. Nest attendance only lasts for 25 days, so these 8 pairs could cease attending their nest during or right after the rainfall. Only 5 out of 24 (21%) nestlings starved. One pair lost its entire brood, another pair lost 2 of its 3 nestlings. Of the 42 remaining pairs which started to nest later, 25 (59%) lost their entire brood or deserted their nest and 91 out of 126 (72%) nestlings were lost. The chances of escaping the reversals without losing too many of their young are thus markedly different for the early and late nesters (Fig. 22) and most of the nests that were started early remained intact. Late nesters, on the other hand, had little

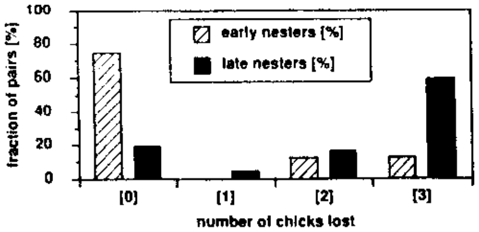

Fig. 22. Scenario 3: Fraction of pairs (8 early nesters and 42 late nesters) which lost one or more (1, 2, 3) of their chicks after the last period of rainfall or lost none of their young (0).

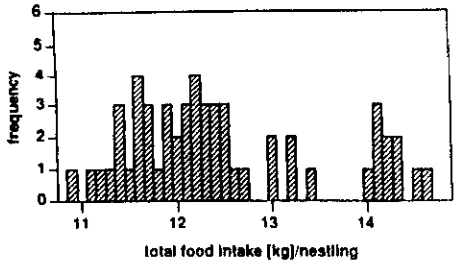

Fig. 23. Scenario 3: Distribution of total food intake of the nestlings that survived all three reversals either at the time of fledging or at the age of 65 days. The threshold for fledging was 14 kg.

chance to overcome the reversals, but, despite the detrimental conditions, all nestlings in 8 of the 42 nests (19%) survived the entire nestling period, although only 2 surpassed the threshold for fledging at an age of 65 days.

After having disturbed the system to such a high degree it is no surprise that only 9 out of the initial 150 nestlings accumulated enough food to exceed the threshold for fledging successfully (Fig. 23). Most nestlings remained well below the threshold, even after they had been allowed to extend their stay in the nest and the period of being fed by their parents to 65 days. Still, 9 nestlings managed to exceed the threshold for successful fledging, all but one originating from late-nesting pairs and 2 nestlings came out of the same nest – an illustration for the assertion in Section 2 that it is frequently the atypical pair, the pair that succeeds where most others fail, that determines population recruitment.

5. CONCLUDING REMARKS

I have given an overview of what could be described as a first step in the development of an individual-oriented model of a colony of nesting wading birds. This approach, which simulates a population as a collection of individual organisms, incorporates a high degree of realism and explicit information about the spatial and temporal heterogeneity of the environment, both of which seem mandatory for highly fragmented landscapes such as those in southern Florida and in east-central Georgia.

In the first part of this work the main components comprising the model were described, i.e. the rules which attempt to mimic the behavior of individual birds and the interaction among themselves and their surroundings, as well as the physical and the resource environment. Some of these rules and a few parameter values are specific to wood storks. With relatively little effort, however, the model can be adapted to other wading bird species and, in fact, an adaptation to a rookery of great blue herons is under way.

In the second part of this work, the results of three sample scenarios were presented. These simulations are not intended to model a particular real situation, but rather were designed to illustrate the potential of an individual-oriented approach. This allowed the use of an artificial, but conceptually simple environment with well-defined statistical properties, namely a neutral landscape model with some degree of contagion between sites and a random assignment of resources to potential feeding sites. Already, these simple cases provide a wealth of information on the determinants of a nesting colony, the mutual interdependencies of the various components, and the importance of different behavioral patterns of the birds.

The need for detailed information about individuals may appear as a drawback of individual-oriented models. However, information on individuals is often easier to obtain than on populations or entire colonies. Yet, although wood storks have been studied extensively the existing data base does not contain all the data needed in the model. The main data gaps are:

(1) The foraging efficiency of storks depending on prey availability and/or other characteristics of a feeding site (Section 3.1.4).

(2) The energy requirements of the adult storks depending on their size and activities (Section 3.1.1): while the basic metabolic rates have been measured (Kahl, 1964), additional energy requirements, e.g. due to long-distance flights, are not known (for white ibis, cf. Pennycuick and de Santo, 1989).

(3) The energetic cost of egg production (Section 3.3): I assumed in Section 3.3 that colony formation, i.e. nest initiation, and egg laying depends on the females' ability to acquire sufficient food to meet the additional energetic cost of egg production. Data on how much energy is needed to produce eggs are lacking for storks (and, to my knowledge, for any other wading bird species as well).

(4) The subsistence level and starvation threshold of the wood stork chicks (Section 3.4): in the feeding experiments by Kahl (1962) wood stork chicks have been fed ad libitum yielding only the maximum amount of food chicks can eat and digest.

APPENDIX

The elevation pattern is generated hierarchically as follows. The entire 40×40-km landscape is structured into three levels. In the first level the landscape is divided into 16 equally sized areas of 10×10 km, each of which is assigned a number $e_1 = 1$ with probability p_1 and $e_1 = 0$ otherwise.

In the second level of the hierarchy these parts are subdivided again, this time into 25 areas of 2 × 2 km and each part is again assigned a number $e_2 = 1$ with probability p_2 and $e_2 = 0$ otherwise. In the third step the remaining 2 × 2-km areas are broken up into single cells with a corresponding probability p_3 for $e_3 = 1$ and $e_3 = 0$ otherwise. Every cell can thus be characterized by a set of three numbers $\{e_1, e_2, e_3\}$ and an associated probability of occurrence. In the model, the probabilities are chosen as $p_1 = 0.4$ and $p_2 = p_3 = 0.1$. Then a cell with a set $\{0,0,0\}$, for instance, has an associated probability of $P_{0,0,0} = (1 - p_1) \cdot (1 - p_2) \cdot (1 - p_3) = 0.6 \cdot (0.9)^2 = 0.486$.

The (relative) elevation of each cell is then established as follows: the cumulative probabilities, $F_1 = P_{0,0,0}$, $F_2 = F_1 + P_{0,0,1}$, $F_3 = F_2 + P_{0,1,0}$, …, divide the unit interval $(0,1]$ into subintervals $(0,F_1]$, $(F_1,F_2]$, …, of different widths $d_i = F_{i+1} - F_i$, which are equal to the probabilities of occurrence of the sets. Each cell is associated with a set $\{e_1, e_2, e_3\}$ and its corresponding probability, and therefore with an interval $(F_i,F_{i+1}]$. The elevation of a specific cell is then taken to be a random number uniformly drawn from its interval and scaled by the maximal elevation value, i.e. scaled by 300 (cm). For example, a cell with a set $\{0,0,0\}$ and a probability $P_{0,0,0} = 0.486$ can have an elevation ranging anywhere from 0 cm to 145 cm, a cell with $\{0,0,1\}$ and $P_{0,0,1} = 0.054$ has an elevation between 146 cm and 162 cm, and so forth.

The frequency distribution of the realized elevations is uniform with approximately $25\,600/300 \approx 85$ cells for every possible value, the same as one would obtain from a random uniform distribution. Indeed, choosing all probabilities p_i, $i = 1,2,3$, to be equal and either 0 or 1, the elevations would be randomly distributed. In general, however, the elevation pattern generated hierarchically shows greater contagion. If, for simplicity, "patch" denotes the parts of the landscape generated within the second level of the hierarchy, i.e. an area of 8 × 8 cells leading to a total of 400 patches, the number of different values within a patch is directly proportional to its probability of occurrence. If a patch has an associated set $\{1,0\}$, say, and thus occurs with a probability $0.4 \cdot 0.9 = 0.36$, all 64 cells have elevations between 108 cm and 288 cm; for a patch with $\{1,1\}$, the probability is $0.4 \cdot 0.1 = 0.04$ and the elevations of its 64 cells fluctuate only between 288 cm and 300 cm. Since only about 1100 cells are expected to be in this range all such cells are confined to 16 patches (4% of 400 patches) of 8 × 8 cells each, rather than being scattered across the entire landscape.

ACKNOWLEDGEMENT

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