

This article was downloaded by: [McGill University Library]

On: 02 January 2013, At: 17:17

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Ethology Ecology & Evolution

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tee20>

Adapting foraging to habitat heterogeneity and climate change: an individual-based model for wading birds

Y.G. Matsinos^a, W.F. Wolff^b & A. Moustakas^c

^a Biodiversity Conservation Laboratory, Department of Environmental Studies, University of the Aegean, Mytilene, 81100, Greece

^b IBG-2: Plant Sciences, Forschungszentrum Jülich, 52425, Jülich, Germany

^c Institute of Integrative & Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK
Version of record first published: 14 Dec 2011.

To cite this article: Y.G. Matsinos, W.F. Wolff & A. Moustakas (2012): Adapting foraging to habitat heterogeneity and climate change: an individual-based model for wading birds, *Ethology Ecology & Evolution*, 24:3, 209-229

To link to this article: <http://dx.doi.org/10.1080/03949370.2011.601762>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Adapting foraging to habitat heterogeneity and climate change: an individual-based model for wading birds

Y.G. MATSINOS¹, W.F. WOLFF² and A. MOUSTAKAS^{3,4}

¹ Biodiversity Conservation Laboratory, Department of Environmental Studies, University of the Aegean, Mytilene 81100, Greece

² IBG-2: Plant Sciences, Forschungszentrum Jülich, 52425 Jülich, Germany

³ Institute of Integrative & Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

Received 22 February 2011, accepted 23 June 2011

In an effort to assess the role of adaptive foraging behaviour to the spatial and temporal heterogeneity as a factor determining the success of the colony, we used single-colony individual-based spatial models for a visual foraging, the Great Blue Heron and a tactile foraging bird, the Wood Stork. The model followed simultaneously daily activities of individuals, their spatial movements, foraging efficiency, bioenergetics and growth of the nestlings during a nesting season. For each colony we used two scenarios; in the first, that depicted a normal nesting season, the extent and distribution of feeding sites led to successful reproduction for both species. In the second, we simulated increased precipitation regimes resulting in reversals in water depth (i.e. increases in depth during the dry season when water levels are normally falling). The results reveal that Wood Storks were significantly more adversely affected than Great Blue Herons by the prey dilution caused by the reversals in water depth. In the latter scenario where resources became scarce, resource predictability decreased. The foraging birds that foraged in groups exhibited low foraging success, resulting in poor reproductive performance. This result was more pronounced in the case of storks that foraged in groups than for herons foraging in groups. Concluding, increased variance in precipitation regimes is more likely to affect tactile rather than visual foraging bird species. Further, in harsh climatic conditions (increased precipitation and water level regimes) solitary foraging was more beneficial for wading birds than group foraging.

KEY WORDS: tactile-visual foraging, group-solitary foraging, increased precipitation, *Ardea herodias*, *Mycteria americana*, Everglades, habitat fragmentation.

⁴ Corresponding author: Aristides (Aris) Moustakas, Institute of Integrative & Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK (E-mail: arismoustakas@gmail.com).

INTRODUCTION

Group versus solitary foraging behaviour is a highly debated topic in behavioural ecology in general and birds in particular (SMITH 1995; CRESSMAN & GARAY 2011; ZOU et al. 2011). It has been claimed that birds departing without prior knowledge of profitable foraging grounds may reduce their search time and gain advantage by following other birds to foraging grounds (WARD & ZAHAVI 1973). On the other hand, it has been debated that given the unpredictability of patchily distributed prey, group foraging increases efficiency because individual birds can follow active flight lines or search commonly exploited areas and locate currently profitable patches of foraging habitat by cueing on the presence of other birds (KUSHLAN 1977).

Wetlands are among the most productive ecosystems in the world, hosting a large variety of species (MITSCH et al. 2009). Species composition, abundance, and ultimately survival depends upon hydrological cycles (water levels) that are formed by climate and landscape structure (MITSCH et al. 2009). Wading birds are dependent on wetlands that are under increasing pressure worldwide (HAFNER 1997). Understanding their ecology is a critical requirement of their conservation strategies (HAFNER 1997). Due to fluctuating weather conditions, nesting populations of many species of wading birds are highly variable (PADGHAM 2011). The nesting colonies of most species of wading birds are often concentrated in mangrove-coastal marsh areas, supporting abundant populations of small fish that wading birds depend on for food. The natural hydrological cycle of wet season rains and dry-downs functions to first expand fish populations and then concentrate them into shallow waters and isolated pools. This facilitates successful foraging by wading birds during the late winter-early spring nesting season, when energetic demands are the highest. Different species have somewhat different hydroperiod and habitat requirements, and therefore differ to some degree in the location and the timing of nesting and foraging activities.

Gradual recess on water levels causes fish to become concentrated in isolated depressions throughout the marsh. Birds effectively exploit these concentrations, usually to depletion. Over the course of the pre-nesting and nesting season, a recruitment and replacement dynamic mosaic of these fish concentrations must form as the fish populations of these ephemeral pools are depleted (KATZIR et al. 1989). To make these pools available, a nearly continuous recession of water levels must occur from December through May. Major reversals in this recession, due to heavy rainfall, cause water levels to rise, making efficient foraging by wading birds more difficult (TORRES et al. 2010). Stalls in the recession allow wading birds to fish out pools that are at optimal water depths but prevent the formation of new pools. Depending on the persistence of stalls or reversals nest failures and colony abandonment may occur (FREDERICK & COLLOPY 1988). Thus, habitat fragmentation and/or habitat loss plays a key role for fish abundance (both in terms of total abundance as well as abundance throughout the year), which in turn is a key factor for bird feeding and nesting and thus population dynamics.

Long-legged wading birds need water depths 10–40 cm for successful foraging (CUSTER & OSBORN 1978; POWELL 1987). Thus, for long-legged feeders water levels must be within a fairly narrow boundary to allow successful foraging. According to the Intergovernmental Panel on Climatic Change (IPCC) predictions for climatic change, precipitation variance is predicted to increase (IPCC 2007). In addition, habitat loss and fragmentation modifies water flow and thus water level. The combined effects of altered precipitation regimes and habitat fragmentation are highly likely to influence water levels and thus the population of long-legged feeders (KIRBY et al. 2008).

Wood Storks (*Mycteria americana*) and Blue Herons (*Ardea herodias*) were used as case study species of long-legged feeders using different foraging techniques. The critical difference between the foraging behaviour of the two species is that Wood Storks use tactile (DEPKIN et al. 2005) while Blue Heron use visual techniques (CUSTER et al. 2004). Both foraging behaviours are efficient in effect as both bird species are dominant and may co-exist in several areas. Wading birds' foraging behaviour is likely to be affected by climatic change and in specific increased water levels, reducing the likelihood of locating prey.

While in effect both solitary and group foraging is observed within most wading bird species, it remains unknown whether there is a climatically enforced behavioural advantage where one of the two foraging strategies becomes more effective. In an effort to identify species-specific responses to variable and unpredictable environments regarding resources, we used individual-based models (e.g. MATSINOS et al. 2000; MOUSTAKAS & SILVERT 2011) to simulate nesting cycles of two wading bird species using different foraging techniques. Habitat heterogeneity via water depth and prey size and abundance was explicitly incorporated in the model. Our main objective was to compare tactile (Wood Stork) and visual (Great Blue Heron) foraging modes of wading birds, under normal weather conditions (Scenario 1), and also under reversals (i.e. rapid inundation of feeding sites) caused by heavy rainfall (Scenario 2). We specifically sought to quantify the following questions: (1) What is the foraging strategy (tactile vs visual) least affected by the altered precipitation. (2) What is the optimal foraging behaviour (solitary vs grouping) when environmental conditions are getting harsh.

METHODS

In the current work we aim to follow responses of foraging behaviour strategies to climatic change and habitat heterogeneity. Since it was hypothesised that species with similar life characteristics, differing though in behavioural traits could be used as case studies for environmental variability, we selected for our modelling study two wading bird species. The model keeps track of a number of distinct individuals on a 15-min step for the whole nesting season. That includes the individual's foraging rate in grams/time step, and the fraction of time each bird spends for its daily activities, namely flying, searching for food, feeding, and feeding its nestlings. Detailed information is provided in the results for nestlings. Their daily food levels are given, their growth is kept track of, and the day for each nestling achieving the threshold for fledging is also recorded.

Description of the study area

For our simulations we used a landscape pattern indicative of the topography surrounding colony sites in the Everglades, Florida, USA. The colony is located in the middle of a long-hydroperiod marsh (interior wetland or central slough) surrounded by peripheral wetland areas, which are short-hydroperiod wetlands, areas that due to early drying provide wading birds with sufficient resources in the early nesting period.

Florida's average monthly rainfall increases dramatically in May, peaking in August and September, and then drops rapidly until November. Precipitation then remains steady between 5 and 7.5 cm a month for the 6-month period from November through April. The "Wet Season" rainfall (May–October) is dominated by daily solar radiation-induced sea breeze thunderstorms. During the "Dry Season" (November–April) there is not enough solar radiation

and available low level moisture to produce daily cycles of rainfall. We used precipitation data from 2002–2010 updated every 15 min available online at (<http://sofia.usgs.gov/eden/nexrad.php>) by the USGS for the Everglades for scenario 1; Mean Annual Precipitation (MAP) was 1409.4 mm/year (SD = 122.76). For scenario 2 we used MAP values of years in which MAP was ~10% higher than the long-term average. That resulted in MAP = 1573.44 mm/year (SD = 141.96). The assumption of 10% MAP increase for the area is a feasible future scenario according to climatic models (IPCC 2007). Rainfall was introduced on a daily basis based upon the long-term daily meteorological data.

All parameter values used during simulation scenarios are explicitly listed in Table 1. Parameter values for the two scenarios are identical except rainfall and grid scale. In all simulations we started with 50 pairs of conspecifics forming a colony and modelled their whole nesting season. The model is updated with a time step of 15-min intervals. The time step is chosen to be in agreement with the duration of many discrete activities of the birds, like time required bringing food in the nest, feed nestlings, etc. (STEPHENS et al. 2003). The model was based on published data on colony size of the study species or the mean foraging group size. Specifically mean colony size for Wood Storks in Florida (1991–2005) was 116.2 nests, SD = 209.5 (FREDERICK & MEYER 2008). Number of nests for Great Blue Herons is highly variable, ranging from 2 to 80 nests per colony (GIBBS 1991). The mean number of pairs in colonies for Blue Herons was 45.3, SD = 89.20 (BUTLER et al. 1995).

Model description

We used individual-based simulation models (WOLFF 1994; MATSINOS et al. 2000; MOUSTAKAS & SILVERT 2011) to simulate wading birds population dynamics during their breeding season. A bird's foraging, social and reproductive behaviour, as well as its physiology and energetics, are specified by rules that define and specify the actions and the state of each individual at a given time. These rules are expressed in the form of "if-then" statements (decision trees). In this study, we gave an overview of the new rules introduced followed by examples, if necessary. It should be noted, however, that this overview does not contain a full description of all rules. In its current implementation the model uses 120 behavioural rules for a single bird; a full description would be beyond the scope of this work. The modelling approach used has been described in detail in WOLFF (1994). A schematic model description is provided in Fig. 1.

The colony model for Wood Storks has been used as a baseline for developing the colony model for the Great Blue Heron. It uses the above structure and is modified in order to include differences in behavioural rules (e.g. foraging) and also in model parameters relating to life history. The model consists of the following sub-models: (i) a spatially explicit landscape sub-model, taking into account the hydrological cycles, so cells are characterised by changing water depth; (ii) a sub-model for prey resources, temporally and spatially dynamic; (iii) sub-models accounting for the energetics and behaviour of nesting adults; and (iv) sub-models for the growth and energetics of the nestlings, until fledging. The model was implemented in C++ on a Macintosh platform. Simulation time for each simulation run did not exceed 45 sec using a standard state-of-the-art desktop.

Landscape sub-model

The landscape structure was simulated to approximate the one of the Everglades, and followed the implementation of WOLFF (1994) that used an average elevation structure without explicit consideration of vegetation cover types (see WOLFF 1994). Landscape heterogeneity is taken into account by subdividing the area surrounding the colony into contiguous square cells, each with its own elevation and water level, so that the main attributes of topography and hydrology are included for the foraging areas. Further details for each cell, such as vegetation type or alligator holes, are not considered. The grain for the above landscape is not the same for the two

Table 1.
List of model parameters used for each bird species.

Model parameter	Wood Stork	Great Blue Heron	References
Weight (kg)	2–3	3–3.5	PALMER (1962)
Basal metabolism (kcal/day)	147	160	KAHL (1964)
Free flying metabolism	450	510	KAHL (1964), estimated
Assimilation efficiency	79%	75%	KAHL (1964)
Maximum distance (km)	15	8	Estimated
Nest initiation threshold (kcal/week)	545	600	Estimated
Number of eggs	3	3	PALMER (1962), KUSHLAN (1978)
Incubation period (days)	30	28	PALMER (1962)
Total food for fledging (kg)	14	15	KAHL (1964), KUSHLAN (1978)
Maximum food in cell (kg)	30	5	Estimated
Days before young leave colony	65	60	COULTER (1989)
Daily food requirement (g)	500	600	KAHL (1964)
Maximum food a bird can bring to nest (g)	300	320	COULTER (pers. comm.), estimated
Effective flying speed (km/hr)	25	22	SIMPSON (1984), COULTER (1989)
Minimum depth for foraging (cm)	5	5	PALMER (1962), KUSHLAN (1978)
Maximum depth for foraging (cm)	40	44	PALMER (1962), KUSHLAN (1978)
Probability of solitary foraging	0.5	0.7	KREBS (1974), estimated
Drying rate (cm/day)	0.50	0.50	Estimated
Fledging feeding efficiency	75%	Linear, increasing with age	Estimated
Patch giving up time (min)	60	60	Estimated
Starvation period for abandonment (days)	3	3	Estimated

models; for wood storks the size of the cell is taken to be 250×250 m, and for herons it is reduced to 50×50 m. This was due to the fact that feeding aggregations of Great Blue Heron only build up when the prey density is high and birds that forage in groups gain more food simply because flocks form when food is abundant. Solitarily foraging herons quite often establish and defend feeding territories. We changed the cell size to 50×50 m to account for the fact that visual feeders spend more time searching neighbouring sites walking slowly and for the apparent scarcity of large prey

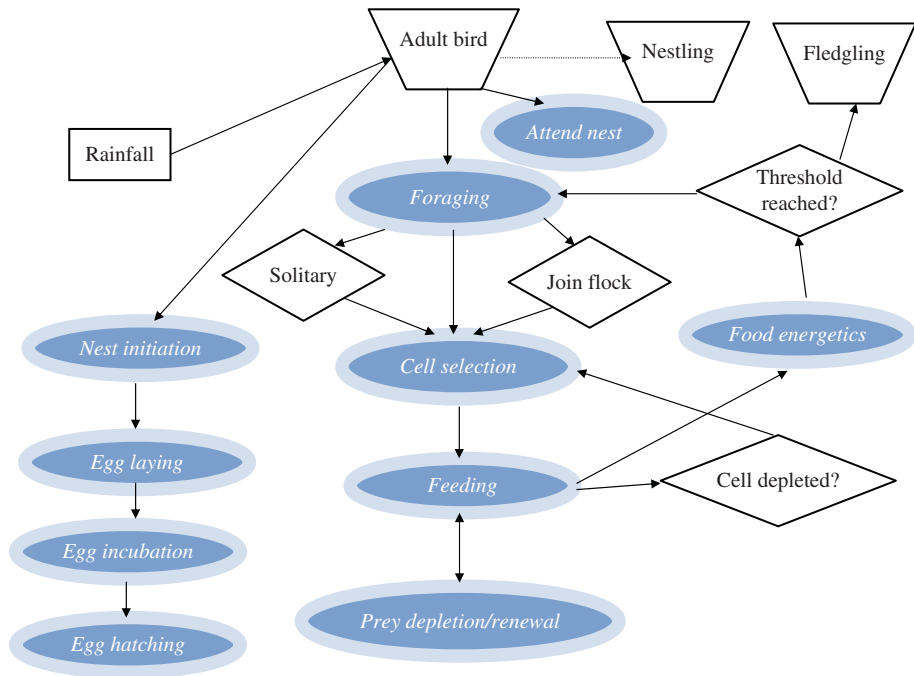


Fig. 1. — A schematic representation of the model. Ellipses depict actions, diamonds decisions, and trapezoids individuals.

items by increasing the resolution (KREBS 1974; KUSHLAN 1976). Water levels are updated daily in the model.

Prey base sub-model

Both models assume fish and aquatic macroinvertebrates as the main food item of wading birds in the Everglades. In the beginning of the simulation (near the end of the wet season) fish biomass values typical for the hydrological conditions being simulated are assigned to all wet cells throughout the landscape. The prey base assigned to each cell is assumed to be accessible to the birds only if water levels are suitable for wading (minimum and maximum depth for foraging, Table 1). Since the same resources are exploited by other birds than those simulated, often non-breeding overwintering birds, we have discounted the actual prey base to account for the background competition. Since data on prey availability are quite scarce and not always accurate, cells have been assigned fish densities from different distributions with parameters (means, etc.) estimated from field data. Thus, prey availability was distributed over cells using a Monte Carlo approach with an average of 70 kg/cell (KUSHLAN 1980). For the Wood Stork model all prey is assumed to occur in the form of Cyprinodontoid and Centrarchid fishes, with an average weight of 1.73 g (OGDEN 1994). However, visually feeding long-legged waders, like Great Blue Heron, exhibit a much broader range of sizes of consumed prey (KUSHLAN 1978). Field data suggest that larger fish like *Lepomis punctatus* and smaller like *Poecilia latipinna* constitute its diet. The prey base sub-model accounts for this. The unit of prey is 20 g and the foraging bird can handle prey items of 1–5 units at a time. The choice of 20 g as a unit is rather of practical value from a modelling

viewpoint. The idea is that within a cell we can specify the size distribution of fish based on the unit as, for example, 20% of size 1 (1 unit), 30% of size 2, 15% of size 3, 15% of size 4, and 20% of size 5. Based on these abundances a foraging bird will encounter a fish of size 1 (20 g) with a probability of 0.2, a fish of size 2 (40 g) with a probability of 0.3, and so forth. It is often the case, especially during the dry season, that prey is quickly depleted within a cell when a flock is formed at the cell. If a cell dries out it is assumed not to be replenished with fish if it becomes wet later in the breeding season. It follows then that the effect of rainfall is to reduce the number of the cells with resources. Prey distribution is updated on a daily basis following rainfall events. The model uses a negative exponential relationship between prey size and frequency in order to assign prey units to each cell. The model assumes no competition with other wading bird species for prey. Prey availability is not related to water levels or flooding but to seasonality so long as water levels are within the min and max depth for foraging. Also fish migration among cells is not implemented.

Behaviour and energetics of adult

Rules pertaining to the Wood Stork model. The very first of the choices that the birds have to make is when to begin nesting. The Wood Stork model assumes that if a female is able to forage sufficiently for a week, with resources being able to satisfy a foraging threshold (20% more than its requirement), during the late wet season, nesting will start. Eggs are laid asynchronously, and both parents take turns incubating. Adult Wood Storks are simulated between 10:00 and 16:00, since foraging trips generally take place between these hours. This is possibly due to the preference Wood Storks show for soaring flight (KAHL 1964), since they wait to use the thermal updrafts from the colony to the foraging sites and back.

One of the decisions a bird must make before foraging is where and how to forage. A bird selects a cell based on its water depth – only cells with water depth between min and max water depth for foraging (Table 1) are desirable for foraging. When the cell's water level is outside the min-max foraging depth interval, the bird continues to another cell. It is assumed to have some partial information about the landscape, so it knows where cells with appropriate water depths are and will move to cells with the appropriate water level for foraging; but it is assumed ignorant of the prey levels in them, so sampling of the cell is required. This is implemented using a Monte Carlo approach to select candidate cells to forage. The foraging bird can either forage by itself or join a flock already formed. This decision is made based on a weekly memory of the bird regarding selected foraging mode in order to fulfil the fraction of time foraging solitary (probability of solitary foraging, Table 1). Decisions about solitary-group foraging are taken every 15 min. The (weekly enforced) probability of solitary foraging is fixed throughout the simulations in both scenarios. If the individual is set as "flocking" according to the probability it will join a flock, but if there is no flock in the vicinity it will continue solitary foraging until there is a flock or another individual to form a flock. A bird will search the adjacent cells if the prey abundance in the cell that it is currently in is not adequate until it satisfies the daily energetic needs (daily food requirement, Table 1). The latter is based upon the parameters basal metabolism, free flying metabolism, assimilation efficiency, and maximum distance (Table 1), with formulas explained in detail in WOLFF (1994). The model assumes that if more than one flock exists in the vicinity of an adult that could potentially join, the decision regarding which flock to join is weighted by the size of the flocks. For example, if three flocks, one with five, one with three and one with two birds exist, a bird will choose the first with a probability of 0.5, the second with 0.3, and the third with 0.2. Usually the presence of a flock is an indication of high food density; however, since depletion by the flock takes a short time, the benefits for a late joining bird are minimal.

Rules pertaining to the Great Blue Heron model. The initiation of the nest is governed by rules identical to those in the wood stork model. Adult great blue herons are also followed between 10:00 and 16:00. A threshold of 600 kcal for a week is the required energy that a female must obtain in order to start a nest. Visually feeding long-legged waders exhibit a much broader range of sizes of consumed prey. So it was necessary to change the prey base sub-model from that used for Wood Storks. The unit of prey is 20 g and the foraging bird can handle prey items of 1–5 units at a time. Size of prey determines handling time. Large prey items require more handling, and

time increases exponentially with size (KUSHLAN 1978). Pausing of foraging also correlates with size, longer pausing with larger prey items. Thus a bird foraging at a cell will remain at the cell as long as food is available or has fulfilled its daily cumulative energetic needs.

A bird, after selecting a certain cell, will update its feeding capabilities based on (i) the depth of the cell, (ii) the actual prey resources of the cell, (iii) the time of the day, and (iv) whether the bird is an adult or a fledgling.

Territoriality rule

If resources are abundant then territoriality breaks down and additional birds are allowed to join. This is modelled by the following rule: an adult heron samples a cell. If during the first day it has satisfied all of its energetic needs while in the cell it will return the next day. If this happens for more than 1 day, other birds searching can join in the cell.

Searching patch rule

Birds are left to forage for a period of 1 week. Then an instance variable (*weekly food*), keeping track of accumulated feeding performance, is used at the end of the week for comparison. The birds that fall below the minimum feeding performance are then able to use the upper 20% of the successful birds as information targets. Before an unsuccessful bird chooses a patch to forage next day, it will decide, based on a probability, whether it will join other birds already foraging. Then again it will choose whether it will join the “marked” successful birds based on their distance from the bird.

Giving up patch rule

After an adult bird chooses a patch to forage it will stay and feed at the location as long as it is profitable for the bird. If the yield is not sufficient the bird must change feeding locations. The model uses the following rule to determine when a bird will give up its patch: assume a bird is at a particular cell for time T . The last feeding occurred before time t . Then the probability of giving up its patch will be: $P(\text{give up}) = \frac{t}{T}$

Energetics and growth of the nestlings

Wood Stork model. Adult birds, after satisfying their own energetic needs, must obtain resources for their hatchlings. They regurgitate boluses of the food brought back in the nest, and the nestlings compete for it. The model assumes variability in allocation of food resources among the nestlings. Usually the oldest chick has a competitive advantage over its siblings, so after it has satisfied its needs the others share the remaining (if any) resources. From experimental measurements, it is known that a nestling must attain a certain threshold level of accumulated food throughout the pre-fledging period in order to fledge successfully. If the adults are not able to provide adequate food supplies before the wet season starts and their foraging efficiency declines, their nestlings are assumed to die. In addition, the model assumes that nestlings should not be subject to starvation for a prolonged time (3–4 days); otherwise they perish. Nest abandonment is also a possibility in the model, if adults are not able to satisfy their own energetic needs; that is failure to feed for 3 consecutive days. The model assumes that the minimum total amount of food a nestling wood stork must receive in order to fledge successfully is 14 kg over the nesting period (total food for fledging, Table 1). Both resource availability and total distances travelled are crucial as they influence energetics but eventually nest abandonment depends on the 3-days-rule described above.

Great Blue Heron model. Every nesting pair lays three eggs (number of eggs, Table 1) asynchronously, with a period of 2 days between eggs. Each egg is incubated (incubation period, Table 1) for 28 days before hatching (PALMER 1962). A nestling fed at the maximal rate can grow at the rate of 40 g/day, reaching a weight of 400 g within 10 days and a maximal weight in $\sim 3\frac{1}{2}$ weeks (OWEN 1960), and remains at the maximum for the next 2 weeks, finally decreasing its daily demands linearly to 150 g at the final period in the nest.

Each nestling fledges successfully after 60 days from hatching, if it has accumulated a total of 15 kg of food throughout that period, assuming it has not starved i.e. receiving food less than 50% of the accumulated values for a period of 5 consecutive days (total food for fledging, Table 1).

Example: feeding of the nestlings rule. In herons the laying of the eggs is asynchronous, and it enhances asynchronous hatching too. So, on average there is at least a week of age difference between the older and the youngest sibs. That has an effect in partitioning of resources during the nestling stage. So it is assumed that older sibs have a competitive advantage over younger ones during feeding from their parents. This is modelled as follows: depending on the size of the prey that parents bring back to the nest we have the following options: (a) if the adult parent has captured a number of small fish the simulation allocates equal shares for every nestling (scramble competition); and (b) if the catch is one or two larger prey items, the simulation will allocate the daily energetic requirement to the oldest chick first, and if food remains the next offspring will also feed. Since the maximum food that herons can bring back to the nest does not exceed 320 g, the youngest nestling will necessarily go without food (at least for that particular feeding episode). Thus the model assumes contest competition in the case of larger prey items. Siblicide has not been incorporated in the model.

Uncertainty-sensitivity to parameter values, statistical analysis

A total of 100 simulations for each of the two simulation scenarios were performed, and all the results presented here are averaged over 100. We used analysis of variance (ANOVA) to explore the relative contribution of each factor to the variation of successful fledglings within each simulation scenario. In an effort to assess the sensitivity of the parameters used in both models in relation to the model output we varied the parameters for the two models. Parameters from Table 1 were allowed to vary (up to $\pm 2\%$) and the resulting variance in the output was measured. The output variable was total number of successful fledglings. For each parameter a total of 100 simulations were performed using Latin hypercube sampling. For all parameters a range of possible values was given (resulting from the literature) and simulations were performed under two scenarios with values from a uniform distribution with the same range. A detailed description of all the parameters used in sensitivity and uncertainty analysis is given in Supplement 1 (available online only).

RESULTS

Scenario 1: a successful breeding season

In this scenario both colony models start with favourable water conditions for early nesting. Eggs are laid asynchronously a week after the first pair initiated their nest. Early nesting was commenced before the wet season began (which was approximately 150 days since the birds arrived at the colony). Food availability was adequate and all nestlings received enough to fledge successfully. After the hatching period, which lasted from day 28 to day 32, all nests produced three nestlings, so for each species we attain the maximum number of offspring (150) during days 31–88 (Fig. 2). Both species fledgling recruitment curve was linearly increasing, and reaching a stable number of around 130 fledglings (Fig. 2), with the only difference in the actual duration of incubation, which lasts on average 2 days longer in the case of Wood Storks. Most birds of both species fledged successfully; however, the distribution of the accumulated

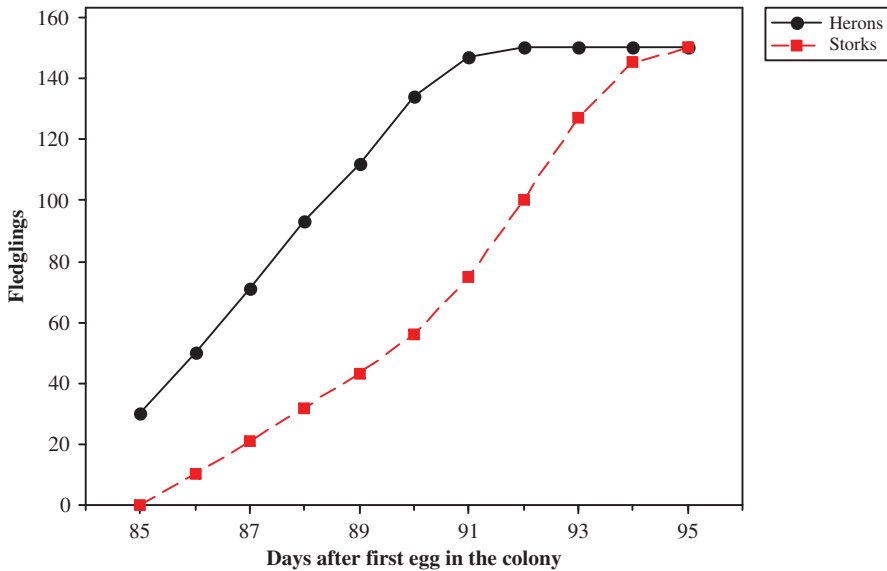


Fig. 2. — Scenario 1. The number of fledglings in each colony during the breeding season. Both species exhibit a constant rate of producing fledglings. The duration of incubation lasts on average 2 days longer in the case of Wood Storks.

food intake showed enough variation among the nestlings to alert us about possible threshold effects concerning our choice of the value that guarantees successful fledging (results not shown here). To this end, the actual distribution of cumulative food intake (rather than just the number of fledglings) may be an alternative indicator of the colony performance (Supplement 2a–b; available online only).

Although the energetic requirements for herons were higher than those for the storks, herons were the first (by an actual difference of 2 days) to reach the fledging stage. That is explained by their per capita foraging success. Herons tend to spend more time foraging than storks (Fig. 3a–b); that compensates for their lower feeding rates compared to storks that spend less time foraging. After the herons' nest attendance started, adult birds increased their time foraging by more than 15% on average (Fig. 3a). This is the high-demand period for parents, since the nestlings have hatched and food has to be carried back at the nest. As a result of intensive foraging, storks, in particular, tend to form aggregations, thus exploiting resources rapidly and lowering their per capita gain (Figs 3b and 6a). Successful fledglings per nest were higher for storks foraging in groups than solitary (Fig. 6a), while in herons, group or solitary foraging resulted in equally successful fledglings per nest (Fig. 6b). Overall, for both species both solitary and group foraging resulted in successful fledglings, with most bird individuals achieving a minimum of at least one (Fig. 6a–b).

Scenario 2: a breeding season disrupted by reversals

In this scenario the nesting season starts as in the previous scenario, but there is heavy rainfall during the critical last stages of nest attendance, when the demands

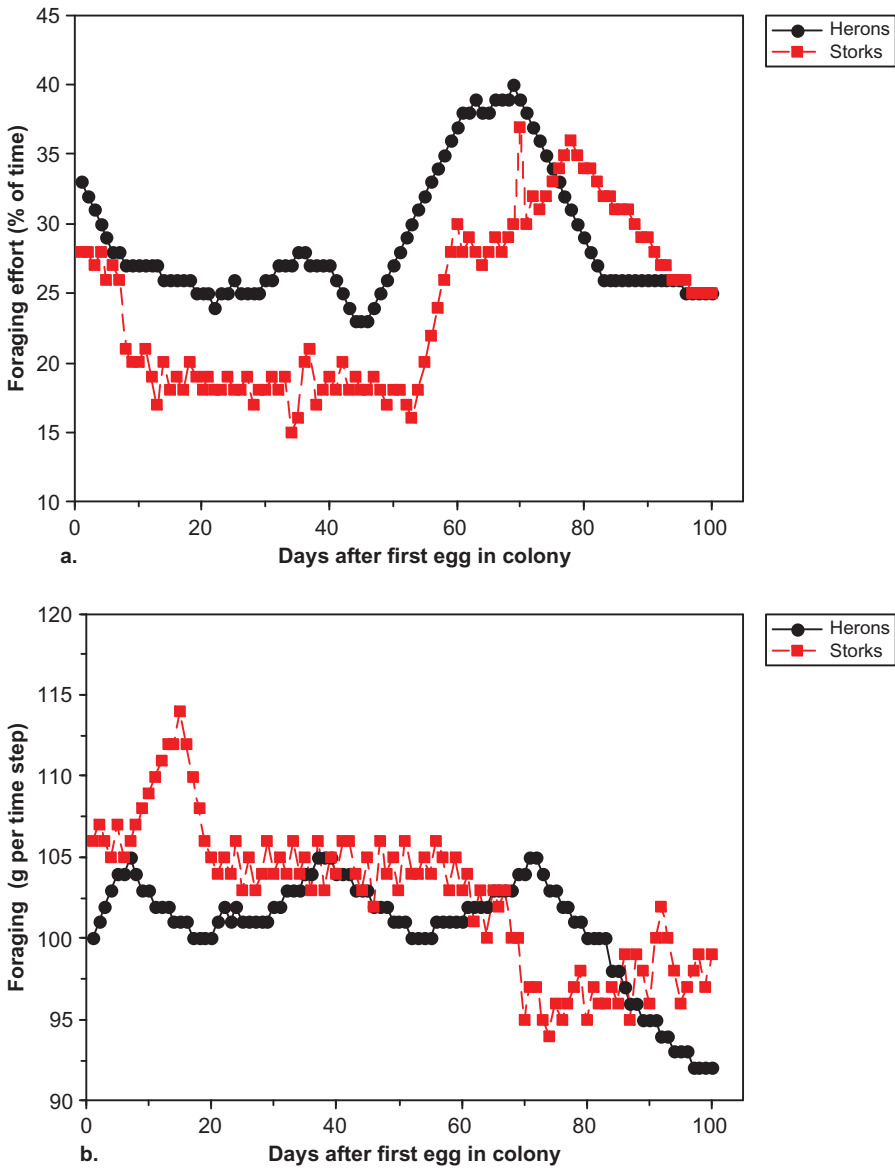


Fig. 3. — a: Scenario 1. Average fraction of time each bird has been foraging. Notice that the peak activity occurs around days 60–70 when the energetic requirements of nestlings are high. b: Daily foraging rate (average over all adults). Vertical units: grams of fish obtained per 15 min foraged.

for food at the nest reach the highest values. The model allows the implementation of rainfall events; the water level of the cells rises by the amount of daily rainfall. The rainfall pattern is divided into three stages (Fig. 4). The first reversal occurs between days 35 and 38 after the first egg was laid, with 2 cm of rain each day. It is followed

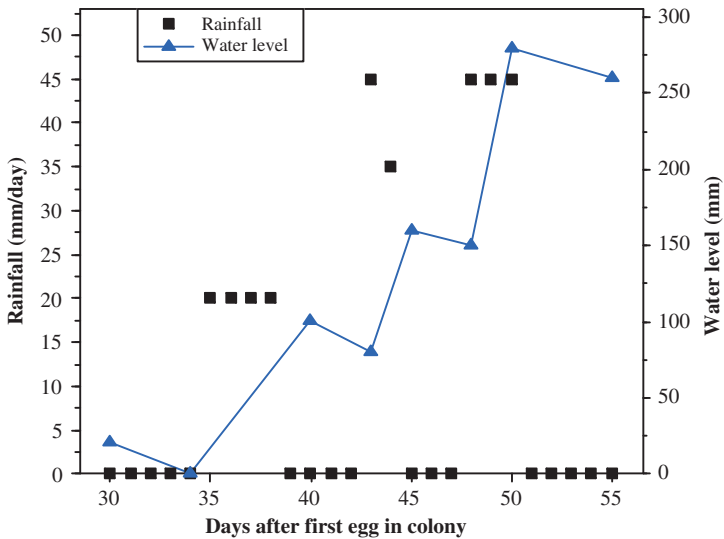


Fig. 4. — Scenario 2. A simulated reversal episode. Daily rainfall (left axis) and water level change (right axis) between day 30 and 55. Black squares depict rainfall in mm/day. Solid line depicts resulting water level change in mm.

by a period of 3 days when drying occurs, then another mild rainfall event for 2 days (day 43 and 44) with a 3 day drying period. Finally, a heavy rainfall occurs for the next 3 days, with a total rainfall of 13.5 cm (Fig. 4). According to our results, almost half of the stork nestlings failed to fledge successfully (Supplement 2c; available online only), whereas herons were able to raise almost two fledglings per nest (Supplement 2d; available online only).

The response of the birds to the early reversals is not as severe as to the last and more drastic where water levels have risen by 28 cm since day 34 (Fig. 5a-b). That last reversal coincides with the period of the high energetic demands of the nestlings. After the last reversal the birds must spend an increasing amount of time searching, so their time for foraging is less. Pronounced depletion of prey base during that stage occurs and with rainfall increasing the likelihood of a chosen cell being unprofitable adds up to a decrease in foraging success rates (Fig. 5a-b). Foraging rates increase after the reversal; however, it takes about 40–45 days to reach 20% lower levels than the pre-reversal. As the model assumes a steady and adequate food supply for successful fledging, reversals lead to poor reproductive performance (Figs 4–5a-b). The poor reproductive success of storks can be attributed to their tendency to form flocks (Fig. 6c). According to our simulation results, almost 80% of the birds foraging in flocks failed to raise a single fledgling; the only successful ones were the solitary (Fig. 6c). Foraging in flocks is not beneficial for herons either (Fig. 6d). All of the solitary herons were successful.

Analysis of variance

For both models nearly the total variance (> 80%) in number of successful fledglings observed was due to four parameters: total food required for fledging,

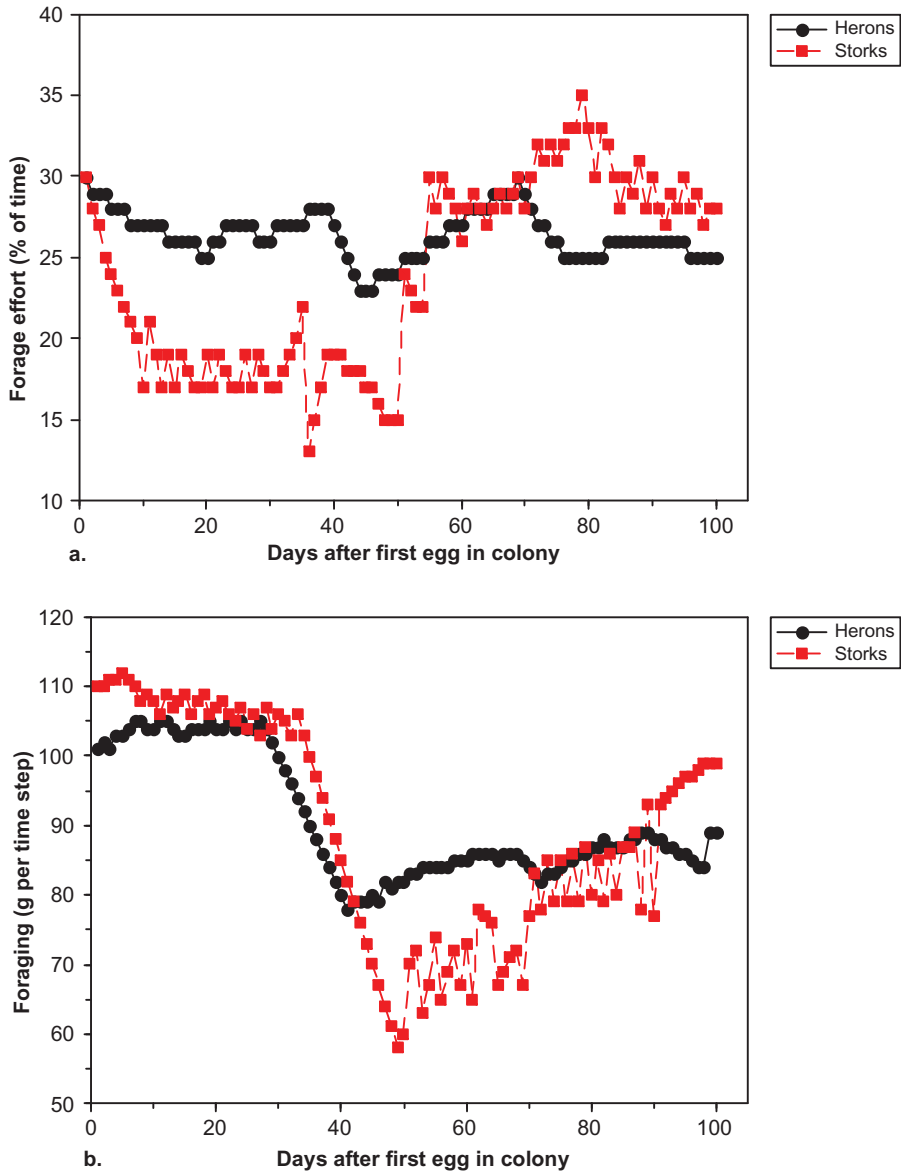
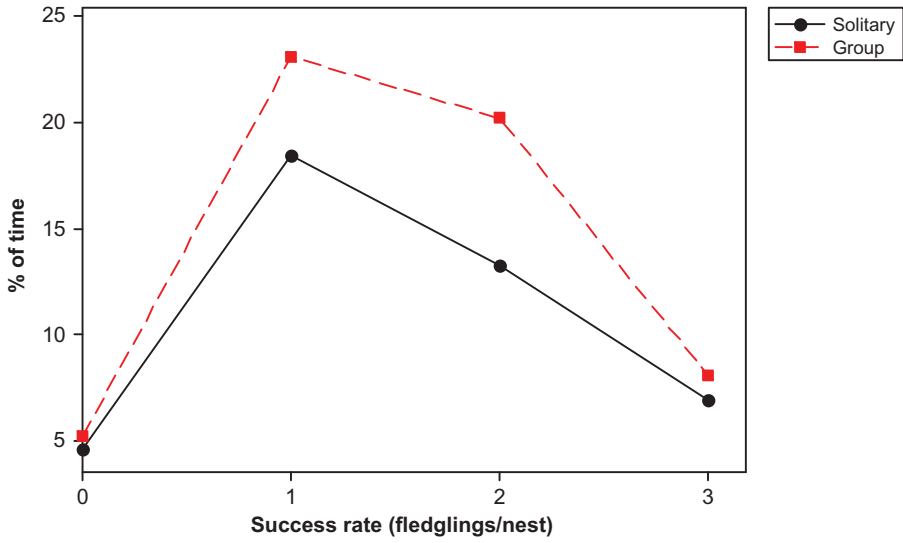


Fig. 5. — a: Scenario 2. Average fraction of time each bird has been foraging. b: Daily foraging rate (average over all adults). Vertical units: grams of fish obtained per 15 min foraged.

maximum food brought back to the nest, daily food requirement, and starvation threshold for fledging (Fig. 7). For the stork model the threshold to reach fledging was most important (34%) (Fig. 7). In the heron model it was of high importance too (29%), with maximum food brought back also important (26%) (Fig. 7).

a. Wood Stork foraging modes as related to colony success, Scenario 1



b. Blue heron foraging modes as related to colony success, Scenario 1

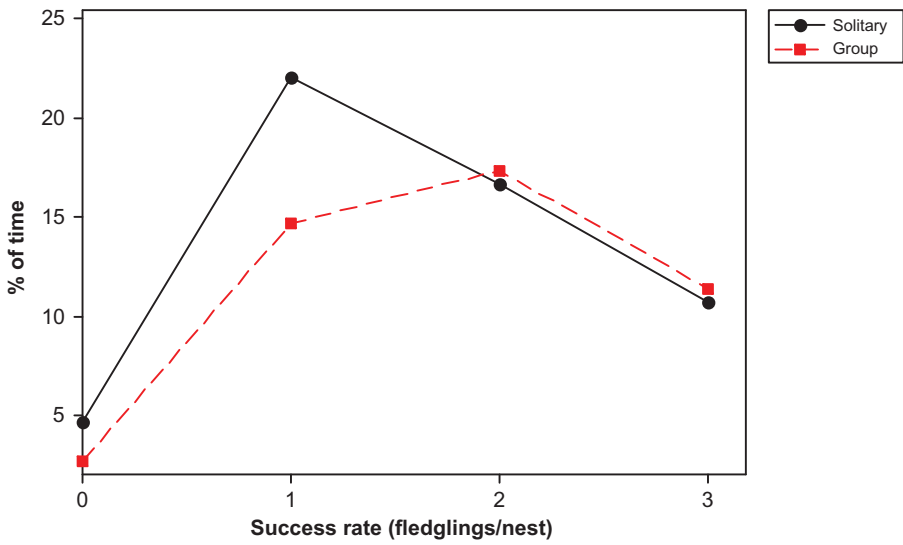
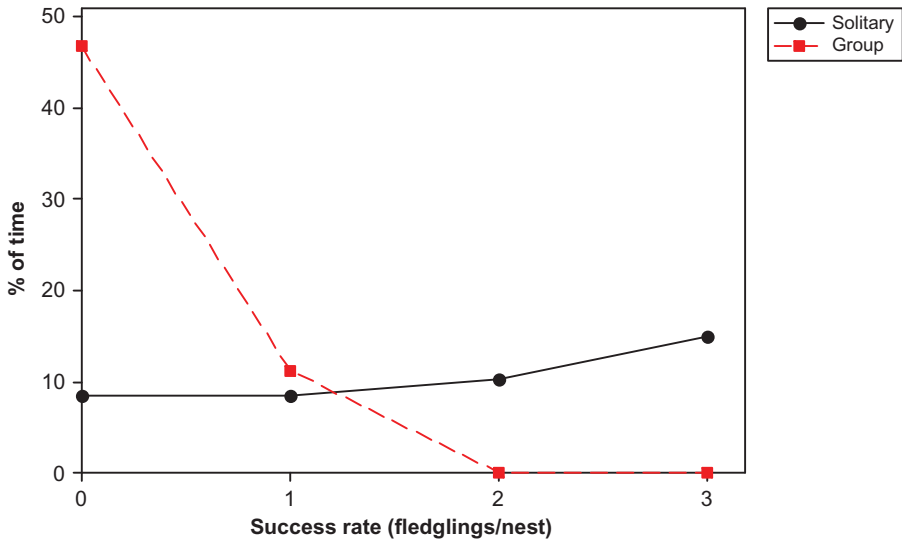


Fig. 6. — (Continued)

c. Wood Stork foraging modes as related to colony success, Scenario 2



d. Blue heron foraging modes as related to colony success, Scenario 2

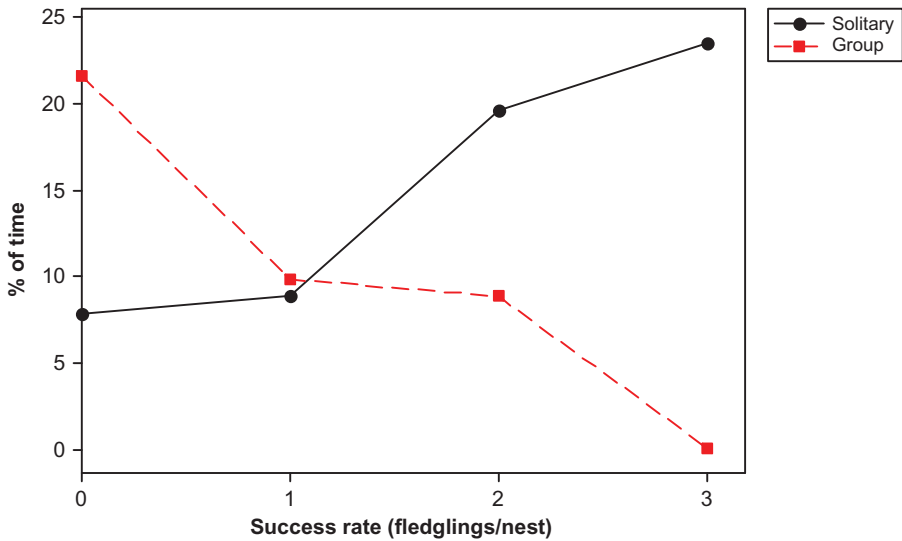


Fig. 6. — Percentage of time of the foraging modes (group vs solitary) of adult Wood Storks and Great Blue Herons as related to colony success under the two examined simulation scenarios. Over the entire foraging period each bird was classified as a “solitary” or “group” forager, depending on the registered frequency of its mode.

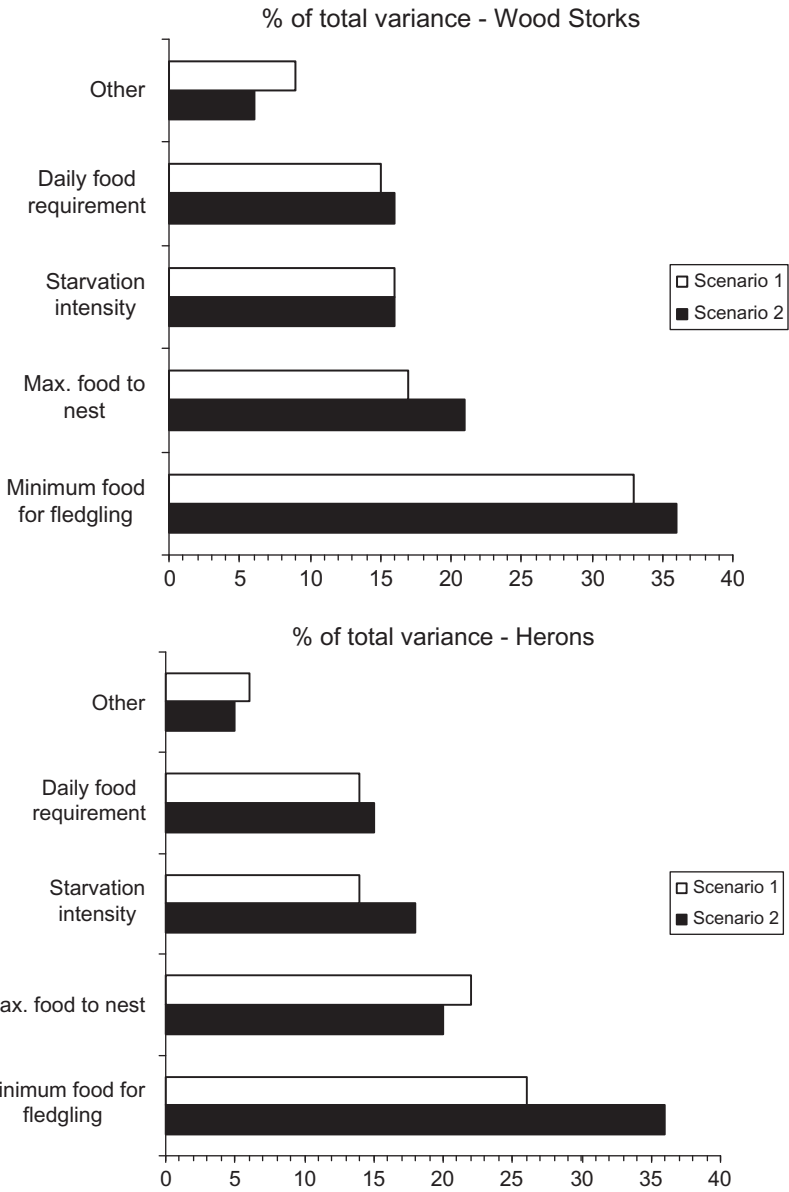


Fig. 7. — Results of model sensitivity analysis and ANOVA. The graphs show the relative contribution (adding to 100%) of each simulation variable to the total variance of the total number of successful fledglings for the two scenarios. Sensitivity analysis was conducted and for each parameter a total of 100 simulations were performed using Latin hypercube sampling. All variables used are listed in Table 1 and Supplement 1. See section “uncertainty-sensitivity to parameter values, statistical analysis” for more details.

DISCUSSION

The model yielded realistic outputs during the “normal” precipitation scenario (Scenario 1). The model predicted three fledglings/nest for normal conditions. This output is close to results reported from field studies. For the year 2006 when normal weather conditions prevailed, there was an average of 2.25 fledglings/nest ($n = 889$ nests in nine colonies) (Florida Fish and Wildlife Conservation Commission), while during the “normal” 1958–1961 period an average of 2.92 fledglings/nest was reported (KAHL 1964). These results are also in agreement with data from field studies provided by FREDERICK & COLLOPY (1988, 1989a, 1989b) and FREDERICK & SPALDING (1994). Based on the fact that under normal weather conditions the model yielded realistic results, all else being equal, it can be used to predict foraging behaviour under altered precipitation regimes.

Effects of precipitation in solitary vs group foraging behaviour

The Wood Stork, as our simulations confirm, is the species most sensitive to variations in water level, because unlike visually hunting species of herons, the stork feeds exclusively by non-visual, tactile methods and its feeding efficiency is directly related to fish density. Initiation and success of wood stork colonies depend on high densities of fish concentrated in ponds and other catchment basins during the dry season. The fish on which the wood storks feed increase in density during the dry season as water levels fall. Great Blue Herons, on the other hand, appear not to be so dependent on concentrated food supplies (they are affected less by prey dilution) because being visual feeders they can meet their energetic requirements by selecting few but large prey items. Although they were also affected by the rainfall it was to a lower degree and the colony maintained a stable population size. Thus, according to our results bird species that use non-visual tactile foraging strategies are more sensitive to climatic changes than birds that use visual foraging strategies. In a study examining the effects of precipitation on the feeding behaviour of a diving bird, it was concluded that increased precipitation resulted in decreased overall energy intake and increased diving time and effort (FINNEY et al. 1999). In addition, examining the factors influencing survival of waterbirds it was concluded that water levels were highly influential (CANEUCCIA et al. 2008; TORRES et al. 2010; ZDUNIAK 2010).

Apart from the effect of precipitation levels per se, timing plays a key role in successful reproduction (CAREY 2009). As both species require approximately 4 months fledging, colonies formed late have insufficient time for development prior to the onset of the rainy season, which raises water levels and causes desertion. Our model examines the effects of altered precipitation regimes in a specific habitat and does not include any evolutionary adaptations to climate, shifts in geographic species ranges and/or phenotypic plasticity to climate. However, all else being equal, our model suggests that delayed precipitation seasons through the year will affect both of the studied species, regardless of their foraging strategy. Such changes in precipitation timing will increase physiological costs of survival and ultimately it depends upon species' adaptation to climate (CAREY 2009; FONTAINE et al. 2009). Our model does not account for the fact that breeding success is dependent on the age and experience of breeders (PYLE et al. 2001). Old pairs may breed early and increased breeding success has been attributed to this (BROWN & ROTH 2002), so in reality timing is not so straightforward a causal effect in successful reproduction as presented here.

Habitat heterogeneity

Wading birds feed primarily on aquatic prey (KUSHLAN 1978). They stand or wade slowly in shallow water areas and stab, grasp or filter their prey (KUSHLAN 1978). Thus they need not only adequate food supplies, but also appropriate water depths for foraging. Home ranges are greatly influenced by food distribution and patch profitability. As suitable foraging conditions are both irregularly distributed and short-lived, these birds have large home ranges and change foraging sites frequently. Successful breeding requires the continuous availability of profitable foraging locations throughout the entire nesting season. Water conditions can change substantially within a week. This has an effect in the local concentrations of fish and macroinvertebrate populations. Two factors related to prey are critical for successful nesting of wading birds: first, sufficient biomass of fish must have grown in the marshes over the previous year to provide food for active colonies. LOFTUS & EKLUND (1994) have shown that the hydroperiod of a marsh and the length of time between complete “drydowns” are closely correlated to the biomass of fish these marshes support. The second critical factor for successful nesting is that fish becomes available to foraging birds in a continuous manner throughout the entire breeding season. Thus, if marshes were flooded deeper, a “normal” drydown would still provide a “drying edge” (an area suitable for foraging, moving as drying progresses) for feeding, but would not completely dry out the deeper sloughs. This would leave a residual fish population to recolonise the marshes when the summer rains begin.

Group vs solitary foraging

In simulations where resources fluctuated rapidly with time, resource predictability decreased, and the foraging birds tended to form groups, in an effort to minimise searching time. If temporal heterogeneity is relatively low as in Scenario 1, then knowledge of the location of profitable feeding sites (assuming an exponential memory decrease) tends to be important, irrespective of the feeding mode of the species. Following the last reversal, birds increased searching time, which resulted in decreased foraging time. Increased precipitation regimes resulted in decreased prey base and decreased profitability of cells in general. That resulted in poor reproductive performance. Poor reproductive performance was attributed to the tendency of both storks and herons to form flocks as in both cases solitary birds were considerably more successful than ones in flocks. Storks in particular were successful almost exclusively when solitarily foraging. In the case of herons, all of the solitary ones were successful. Thus, regardless of the foraging behaviour, in hard weather conditions solitary foraging was more beneficial for wading birds. This result is in agreement with findings reported for wading birds (SMITH 1995) as well as for other bird species such as blackbirds (COURANT & GIRALDEAU 2008). Overall it has been reported that solitary foraging appears unlikely to increase mean food intake rate when exploiting non-renewing patches but may provide a way to reduce the risk of an energy shortfall (BEAUCHAMP 2005). Over 80% of the variance of successful fledglings observed was explained by (i) total food required for fledging, (ii) maximum food brought back to the nest, (iii) daily food requirement, and (iv) starvation threshold for fledging. This result was applicable in all cases regardless of the simulation scenario and species. Interestingly, a high starvation threshold increased the success of the colony.

SYNTHESIS

Bird species using tactile foraging methods are more likely to be affected by variations in water level, as opposed to bird species using visual foraging methods. During harsh environmental conditions solitary foraging becomes the optimal foraging strategy as opposed to group foraging.

ACKNOWLEDGEMENTS

This research was funded in part by the Ecological Research Division, Office of Health and Environmental Research, US Department of Energy, under Contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. and the Science Alliance Center of Excellence, University of Tennessee, Knoxville, TN 37996-1300. A. Moustakas was funded from a NERC, UK, Research Grant (NE-E017436-1). The study was accomplished with assistance from the National Park Service, US Department of the Interior (Cooperative Agreement No. CA-5460-0-9001). The statements, findings, conclusions, recommendations, and other data in this report are solely those of the authors and do not necessarily reflect the views of the US Department of the Interior, National Park Service. Comments of two anonymous reviewers considerably improved an earlier manuscript draft.

REFERENCES

- BEAUCHAMP G. 2005. Does group foraging promote efficient exploitation of resources? *Oikos* 111: 403–407.
- BROWN W.P. & ROTH R.R. 2002. Temporal patterns of fitness and survival in the Wood Thrush. *Ecology* 83: 958–969.
- BUTLER R.W., WHITEHEAD P.E., BREAUULT A.M. & MOUL I.E. 1995. Colony effects on fledging success of great blue herons (*Ardea herodias*) in British Columbia. *Colonial Waterbirds* 18: 159–165.
- CANEPUCCIA A.D., FARIAS A.A., ESCALANTE A.H., IRIBARNE O., NOVARO A. & ISACCH J.P. 2008. Differential responses of marsh predators to rainfall-induced habitat loss and subsequent variations in prey availability. *Canadian Journal of Zoology* 86: 407–418.
- CAREY C. 2009. The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society (B)* 364: 3321–3330.
- COULTER M.C. 1989. Wood Storks of the Birdsville Colony and swamps of the Savannah River Plant. 1988 Annual Report. SREL-37/UC-66e. Aiken, South Carolina: Savannah River Ecology Laboratory.
- COURANT S. & GIRALDEAU L.A. 2008. Conspecific presence makes exploiting cryptic prey more difficult in wild-caught nutmeg mannikins. *Animal Behaviour* 75: 1101–1108.
- CRESSMAN R. & GARAY J. 2011. The effects of opportunistic and intentional predators on the herding behavior of prey. *Ecology* 92: 432–440.
- CUSTER C.M., SUAREZ S.A. & OLSEN D.A. 2004. Feeding habitat characteristics of the Great Blue Heron and Great Egret nesting along the Upper Mississippi River, 1995–1998. *Waterbirds* 27: 454–468.
- CUSTER T.W. & OSBORN R.G. 1978. Feeding site description of three heron species near Beaufort, North Carolina, pp. 355–360. In: Sprunt A. IV et al., Eds. Wading birds. *New York, NY: National Audubon Society Research Report No. 7.*
- DEPKIN E.C., ESTEP L.K., BRYAN A.L., ELDRIDGE C.S. & BRISBIN I.L. 2005. Comparison of Wood Stork foraging success and behavior in selected tidal and non-tidal habitats. *Wilson Bulletin* 117: 386–389.

- FINNEY S.K., WANLESS S. & HARRIS M.P. 1999. The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. *Journal of Avian Biology* 30: 23–30.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION (http://research.myfwc.com/features/view_article.asp?id=33181).
- FONTAINE J.J., DECKER K.L., SKAGEN S.K. & VAN RIPER C. 2009. Spatial and temporal variation in climate change: a bird's eye view. *Climate Change* 97: 305–311.
- FREDERICK P.C. & COLLOPY M.W. 1988. Reproductive ecology of wading birds in relation to water conditions in the Florida Everglades. *Cooperative Fish and Wildlife Research Unit, University of Florida* (ASIN: B0007275ZY).
- FREDERICK P.C. & COLLOPY M.W. 1989a. Nesting success of five Ciconiiforme species in relation to water conditions in the Florida Everglades. *The Auk* 106: 625–634.
- FREDERICK P.C. & COLLOPY M.W. 1989b. The role of predation in determining reproductive success of colonially nesting wading birds in the Florida Everglades. *Condor* 91: 860–867.
- FREDERICK P.C. & MEYER K.D. 2008. Longevity and size of Wood Stork (*Mycteria americana*) colonies in Florida as guides for an effective monitoring strategy in the Southeastern United States. *Waterbirds* 31: 12–18.
- FREDERICK P.C. & SPALDING M.G. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem, pp. 659–691. In: Davis S.M. & Ogden J.C., Eds. Everglades: the ecosystem and its restoration. *Delray Beach, FL: St. Lucie Press*.
- GIBBS J.P. 1991. Spatial relationships between nesting colonies and foraging areas of Great Blue Herons. *The Auk* 108: 764–770.
- HAFNER H. 1997. Ecology of wading birds. *Colonial Waterbirds* 20: 115–120.
- IPCC 2007. Climate Change 2007: Synthesis Report.
- KAHL M.P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecological Monographs* 34: 97–117.
- KATZIR G., LOTEM A. & INTRATOR N. 1989. Stationary underwater prey missed by reef herons, *Egretta gularis*: head position and light refraction at the moment of strike. *Journal of Comparative Physiology (A)* 165: 573–576.
- KIRBY J.S., STATTERSFIELD A.J., BUTCHART S.H.M., EVANS M.I., GRIMMETT R.F.A., JONES V.R., O'Sullivan J., TUCKER G.M. & NEWTON I. 2008. Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conservation International* 18: S49–S73.
- KREBS J.R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). *Behaviour* 51: 99–134.
- KUSHLAN J.A. 1976. Wading bird predation in a seasonally fluctuating pond. *The Auk* 93: 464–476.
- KUSHLAN J.A. 1977. Population energetics of the American White Ibis. *The Auk* 94: 114–122.
- KUSHLAN J.A. 1978. Feeding ecology of wading birds, pp. 249–296. In: Sprunt A., Ed. Wading birds. *New York, NY: National Audubon Society Research Report No. 7*.
- KUSHLAN J.A. 1980. Feeding ecology and prey selection in the White Ibis. *Condor* 81: 376–389.
- LOFTUS W.F. & EKLUND E. 1994. Long term dynamics of an Everglades freshwater fish community. Everglades: Spatial and temporal patterns as guidelines for ecosystem restoration, pp. 461–483. In: Davis S.M. & Ogden J.C., Eds. Everglades: The ecosystem and its restoration. *Delray Beach, FL: St. Lucie Press*.
- MATSINOS Y.G., WOLFF W.F. & DEANGELIS D.L. 2000. Can individual-based models yield a better assessment of population variability?, Chapter 12. In: Ferson S., Ed. Quantitative methods in conservation biology. *New York, NY: Springer Verlag*.
- MITSCHE W.J., GOSSELINK J.G., ANDERSON C.J. & ZHANG L. 2009. Wetland ecosystems. *New York, NY: John Wiley & Sons*.
- MOUSTAKAS A. & SILVERT W. 2011. Spatial and temporal effects on the efficacy of marine protected areas: implications from an individual based model. *Stochastic Environmental Research & Risk Assessment* 25: 403–413.
- OGDEN J.C. 1994. A comparison of wading bird nesting colony dynamics (1931–1946) and (1974–1989) as an indication of ecosystem conditions in the Southern Everglades,

- Chapter 22. In: Davis S.M. & Ogden J.C., Eds. Everglades: the ecosystem and its restoration. *Delray Beach, FL: St. Lucie Press.*
- OWEN D.F. 1960. The nesting success of the Heron *Ardea cinerea* in relation to the availability of food. *Proceedings of the Zoological Society of London* 133: 597–617.
- PADGHAM M. 2011. Relating climatic dynamics in time and space to ecological responses with application to Australian waterbirds. *Ecosystems* 14: 94–111.
- PALMER R.S. 1962. Handbook of North American birds, Vol 1. *New Haven, CT, and London: Yale University Press.*
- POWELL G.V.N. 1987. Habitat use by wading birds in a subtropical estuary. *The Auk* 104: 740–749.
- PYLE P., SYDEMAN W.J. & HESTER M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *Journal of Animal Ecology* 70: 1088–1097.
- SIMPSON K. 1984. Factors affecting reproduction in Great Blue Herons (*Ardea herodias*). *M.Sc. Thesis, University of British Columbia, Vancouver, B.C.* Unpublished.
- SMITH J.P. 1995. Foraging sociability of nesting wading birds (Ciconiiformes) at lake Okeechobee, Florida. *Wilson Bulletin* 107: 437–451.
- STEPHENS P.A., FRECKLETON R.P., WATKINSON A.R. & SUTHERLAND W.J. 2003. Predicting the response of farmland ecology bird populations to changing food supplies. *Journal of Applied Ecology* 40: 970–983.
- TORRES R., MICHELUTTI P., DOMININ J., LEO J., MANGEAUD A., RODRIGUEZ A., POZZI C., PLENCOVICH G., PAGOTS M. & HILLMAN G. 2010. Effects of weather and water level on reproduction of colonial waterbirds in Laguna Mar Chiquita – Banados Del Rio Dulce (Central Argentina). *Ornitologia Neotropical* 21: 383–396.
- WARD P. & ZAHAVI A. 1973. The importance of certain assemblages of birds as “information centres” for food-finding. *Ibis* 115: 517–534.
- WOLFF W.F. 1994. An individual-oriented model of a wading bird nesting colony. *Ecological Modelling* 72: 75–114.
- ZDUNIAK P. 2010. Water conditions influence nestling survival in a Hooded Crow *Corvus cornix* wetland population. *Journal of Ornithology* 151: 45–50.
- ZOU F.S., CHEN G.Z., YANG Q.F. & FELLOWES J.R. 2011. Composition of mixed-species flocks and shifts in foraging location of flocking species on Hainan Island, China. *Ibis* 153: 269–278.