

The Effect of Hydrological Patterns and Untimely, Breeding-Season Flooding on the Numbers and Distribution of Wading Birds in Everglades National Park

Gareth J. Russell^{1,2}, Oron L. Bass, Jr.³, and Stuart L. Pimm²

1. Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996-1610, USA
2. Center for Environmental Research and Conservation, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA
3. National Park Service, Daniel Beard Research Center, Everglades National Park, 40001 State Road 9336, Homestead, FL 33034, USA

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Corresponding author: Gareth J. Russell, Department of Biology, College of Wooster, 931 College Mall, Wooster, OH 44691. Phone: (330) 263 2437. Fax: (330) 263 2378. E-mail: grussell@wooster.edu

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1 Abstract

Field ecologists have long known that the dynamics of water flow in Everglades National Park affect the breeding success of wading birds, and a number of recent studies have identified foraging success as the primary causal link. Data on the number and location of foraging birds are available from the Systematic Reconnaissance Flights, monthly aerial survey of wading birds and surface water condition. We developed a set of regression models that predict the number of foraging birds observed in the Park at the beginning of May, a crucial period in the breeding season of almost all wading birds in this area. As predictors, we converted the observations of surface water condition into three variables that describe a) the amount of surface water in the Park in January (near the beginning of the 'dry' season), b) the rate at which it dries over the subsequent months, and c) the amount of disruption to that drying process. We used an information-theoretic measure, ICOMP(IFIM), to choose on the basis of parsimony between the large set of possible models that incorporate these predictors. We found that most species were best predicted by the same few models, and that the fitted model parameters were also similar. This indicates that the same pattern of surface water dynamics is optimal for most species. The optimal pattern is: 'average' water levels at the beginning of the dry season, a rapid rate of drying, and no disruption in the drying process. A number of disruptions in drying since 1985 have been the result of untimely releases of water from the flow-control structures at the northern boundary of Everglades National Park. Reducing or eliminating these unnatural hydrological events should help wading bird populations to increase.

2 Introduction

Wading birds are conspicuous elements of the landscape of southern Florida, and feelings about their welfare run deep. They are important components of the various wetland ecosystems, as top predators on fish and aquatic invertebrates. They are also one of the main reasons tourists visit areas such as Everglades National Park. Less conspicuous species such as the Cape Sable seaside-sparrow (*Ammodramus maritima mirabilis*) may be under greater immediate threat (Nott et al., 1998), but public concern is typically higher for the larger, more colorful birds. With current controversies over the management of south Florida's water resources sometimes leading to legal action, an understanding of the large-scale ecology of wading birds is crucial.

Ideally, we would like to be able to answer the following question:

How will different water management strategies affect the long-term breeding success of wading birds?

The key phrase here is 'long-term'. There is little doubt that the overall number of wading birds currently breeding in the South Florida region is a fraction of what it was a few decades ago. Exactly how much reduction there has been is open to debate, but the most conservative estimates of historical numbers (see Ogden 1994 and Frederick & Spalding 1994 for largely independent reviews) suggest at least a ten-fold decrease for many species.

An obvious long-term goal would be to raise the number of wading birds as close to near-historical levels as allowed by the overall reduction in habitat area and quality. (Perhaps historical *densities* would be a better goal.) How should we accomplish this in the short term? Wading birds, like most large animals, reproduce relatively slowly, producing 1–3 offspring per year at best. For such species, a significant population increase requires a sustained sequence of successful breeding events. However, the record of wading bird breeding in the region reveals only infrequent, periodic successes (e.g., Ogden, 1994), and little in the way of long-term positive trends for most species. So to answer the long-term, management question above, we need to answer the shorter-term, ecological question below:

How do different water conditions affect the year-to-year breeding success of existing wading bird populations?

Here, we present a partial answer to this question. Our study addresses just one component — foraging — of the wading bird nesting cycle. There is, however, a substantial body of literature indicating that foraging success is one of the most important limiting factors for wading bird reproductive success. In the remainder of the Introduction we will provide a brief overview this argument.

2.1 The importance of foraging and the 'water recession' model

Formal and informal observations over the years have shown that wading bird nesting success in the Everglades is closely related to surface water dynamics (Ogden 1994). Recent studies

have identified foraging efficiency as the main causal link (Hafer & Britten 1983, Frederick & Collopy 1989, Bildstein et al., 1990). The argument may be summarized as follows:

1. Breeding activities are energetically demanding.
2. Wading birds mainly consume aquatic vertebrates and invertebrates.
3. The efficiency with which these can be acquired depends in large part on the water conditions.
4. Poor foraging efficiency leads to late initiation of nesting, high mortality of offspring, abandonment of nests, or any combination of the above.

In sub-tropical South Florida, the effects of timing on reproductive success can be severe. The vast majority of wading birds breed during the dry season (approximately December through the end of May). When the summer rains resume, adult birds of many species will abandon their nests (Kahl, 1964; Kushlan, Ogden & Tilmant, 1975), for reasons we will outline below. If offspring are not sufficiently advanced at this stage to leave the nest and forage independently, they will die. Thus, late initiation of nesting can have disastrous consequences.

So what, precisely, is it about water conditions that leads to high or low foraging efficiency? A number of studies, mostly of wood storks (*Mycteria americana*) and white ibis (*Eudocimus albus*), have suggested that during the dry season, lowering water levels and receding surface coverage tend to concentrate prey in small areas which provide extremely efficient foraging sites (Kushlan 1974, Loftus et al., 1990, Loftus & Eklund 1994). This is sometimes called the 'water recession' model. Reversals in this drying process raise water levels, which is known to slow rates of prey capture (Gawlick, in review) and also allows more mobile prey to disperse over wider areas, increasing search and travel times. In field studies, reversals have been linked to wholesale abandonment of nests (Bancroft & Jewell, 1987; Frederick & Collopy, 1988). (This also explains why birds would abandon nesting at the onset of summer rains, which raise water levels over a large area.)

This paper represents a quantitative test of part the water recession model, in that we will be looking at how surface water dynamics affect the distribution and abundance of foraging individuals of various wading bird species. If the model is basically correct, we should find that bird numbers correlate positively with drying, and negatively with reversals in the drying process.

This paper does *not* represent a test of the link between foraging efficiency and nesting. Our premise is the same as that of the water recession model itself: successful foraging is a *pre-requisite* for successful nesting. It almost has to be so, and the afore-mentioned studies provide a compelling body of evidence. That is not to say that successful foraging will necessarily lead to successful nesting, because other factors, such as disease, predation, or human disturbance, may also reduce success (Frederick & Spalding 1994). But in recent years at least, "availability of food may be the single most important factor limiting the distribution and nesting success of wading birds, especially in the . . . Everglades ecosystem" (Frederick & Spalding, 1994).

Nevertheless, we will present in the Discussion some preliminary data that support the link between foraging efficiency and nesting.

3 The data

3.1 Data collection

Our data come from the Systematic Reconnaissance Survey Flights (SRF), monthly aerial surveys that follow a standard protocol. A fixed-wing aircraft containing two observers flies a prescribed route over Everglades National Park and a small selection of other areas (the southern tip of Big Cypress National Preserve, for example). The route begins in the North-East corner of the Park, and consists of a series of transects following lines of latitude, alternating in direction East-to-West and West-to-East. Each transect is 2 km further south than the previous one. During each transect, observations begin and end when the aircraft crosses pre-determined points that correspond roughly to the boundaries of the Park.

One observer records surface water condition. From 1985 to 1989, this was done using a three-point scale: 'dry', 'transitional' and 'wet'. 'Dry' means little or no surface water, 'transitional' means alternating patches of dry ground and water, and 'wet' means mostly continuous surface water. From 1990 onwards a five-point scale was used: 'dry-dry', 'dry-wet', 'dry-transitional', 'wet-transitional' and 'wet'. For backwards compatibility, the categories of the five-point scale are subcategories of the three-point scale, in that 'dry-dry' and 'dry-wet' are subsets of 'dry', and 'dry-transitional' and 'wet-transitional' are subsets of 'transitional'. Thus the five-point scale can be collapsed into the three point scale if required. The observer records the surface water condition when observations begin in each transect, and then whenever the condition changes, the new condition and the location (longitude) of the change are recorded.

Both observers also record the presence of wading birds. Each observer looks out of a different side of the aircraft, and observes a strip approximately 150m wide. When either individual birds or clumps of birds are sighted, the observer notes the location (longitude), the number of birds, and the species or other category. Seven wading-bird species are identified to species: great egret (*Casmerodius albus*), great blue heron (*Ardea herodias*), great white heron (*Ardea herodias occidentalis*), white ibis, glossy ibis (*Plegadis falcinellus*), wood stork and roseate spoonbill (*Ajaia ajaja*). Other species, not distinguishable from the air, are put into the categories 'small dark herons' (little blue herons [*Egretta caerulea*] and tricolored herons [*E. tricolor*]) and 'small white herons' (Snowy egrets [*E. thula*], cattle egrets [*Bubulcus ibis*] and occasionally immature little blue herons). We note that of the birds identified to species, great white heron and great egret are easily confused from the air. Great egrets are far more abundant than great white herons, so potential errors of this kind will have a small proportional effect on the records of great egrets, but a large proportional effect on the records of great white herons. As a consequence, we regard the records of great white herons with suspicion, and exclude them from our analyses of individual species numbers.

We also exclude glossy ibis. Glossy ibis almost never nest in Everglades National Park, and their appearances and disappearances there seem more linked to their population dynamics in regions further north (where they forage in, for example, rice fields), than to conditions in the Park itself (O. L. B., personal observation). Indeed, the records of glossy ibis show a large spike in numbers in 1988, a year in which conditions within ENP were ‘average’ in many ways.

Finally, we note that the SRF data are often pooled into the following feeding guilds: ‘long-legged, visual feeders’ (great blue herons, great white herons, great egrets), ‘long-legged, tactile feeders’ (wood storks, roseate spoonbills), ‘short-legged, tactile feeders’ (white ibis, glossy ibis), and ‘short-legged, visual feeders’ (small dark herons, small white herons). We will not show any results for these composite groups, because each is numerically dominated by just one of its component species or groups, and the results for that guild hardly differ from those for the species or group in question. More details about the SRF wading bird surveys can be found in Russell, Portier & Bass (2001).

3.2 Strengths and limitations of SRF data

The SRF data have many strengths, including a consistent survey protocol with exactly equal effort applied to every location in the Park, and repetition at approximately the same dates every year, for many years. They are also subject to sources of error and unknown quantities. These include:

1. *Incomplete coverage.* The survey records observations from a 300m strip along each transect. This is 15% of the total area (transects are 2km apart).
2. *Varying visibility biases.* The observers in the aircraft cannot see every bird below them, and so record a proportion of those that are actually present.

The problem of incomplete coverage is minor. An estimated count for the whole park can be obtained multiplying total observed bird numbers by 6.667. Confidence intervals are more tricky, as they depend on autocorrelation in the survey design and/or the true distribution of birds, but may nevertheless be obtained (Russell, Portier & Bass 2001).

The problem of varying visibility biases is much less tractable, because the visibility proportion will vary by species, type of ground cover, lighting conditions (and therefore time of day, time of year, weather, etc.). Determining the correction factor under all these circumstances would require intensive ground surveys in remote areas of the Park under all possible conditions, combined with simultaneous aerial flights. Logistically, this is almost impossible to arrange (and would be prohibitively expensive).

The problems described above, particularly the second, mean that the SRF data do not provide a meaningful estimate of the actual number of wading birds in Everglades National Park. At best — with incomplete coverage corrected for — they may provide minimum estimates, but we cannot know the degree of underestimation. And so we cannot, for example, use the SRF data compare the numbers of different species.

In fact, the goal of the SRF surveys was never to estimate the true number of birds in any one year. The SRF data were designed to be, and are, a good record of *changes in the numbers of each species from year to year, both in the Park as a whole and in different areas of the Park*. Each year's surveys cover the same area, over approximately the same set of dates. So if the number of, say, great egrets is twice as much in one year as in the previous year, it is reasonable to assume that the same is approximately true of the actual number of great egrets. If the observed number of roseate spoonbills in the southern coastal mangroves drops by a factor of three, the actual number almost certainly dropped by a similar factor. So even without the appropriate correction factors, the SRF data provide a powerful tool for investigating the causes of changes in wading bird numbers and distribution over time. They also provide a tool for management, in that strategies which increase the number of birds observed during the SRF survey will certainly increase the actual numbers. In this paper, all our calculations will be based on the uncorrected, observed number of birds.

3.3 Initial data processing

The raw data consist of {transect, longitude, species, count} for the birds and {transect, longitude, new condition} for the surface water. These are converted into maps, where each map consists of an array of 2km by 2km cells and one row of cells corresponds to a transect. For the bird observations, a map is made for each species. All the observations of that species that fall in a particular cell (i.e., those whose longitude falls between the longitudes that define the east and west edges of the cell) are combined to give a single value for the cell. For the observations of surface water, the observed condition is interpolated between the records of changes and the cells in between are given appropriate values. The cells in which the change occurs are given the new condition. Fig. 1 shows an example of the map data (survey date: January 7th., 1985; species data shown: great egret)

3.4 Dates used in this analysis

The SRF wading bird survey began in January 1985, and has run until the time of writing (December 2000). Typically, flights occur once a month during December through May, which corresponds to the 'dry season' in South Florida, and once in August, the middle of the rainy season. Exceptions are 1985 (the first year) and September 1992 to December 1993 (following Hurricane Andrew), when there was a survey in every month; 1987, when there was no survey in December; and 1998, when there was no survey in January.

In this paper, we consider the data from 1985 to 1998 (fourteen years). The data for 1999 and 2000, while collected, have not been fully error-checked at the time of writing. Furthermore, we consider only the dry-season data, i.e., data collected in December through May, because this is the period during which foraging determines nesting success (e.g., Frederick & Spalding, 1994). For convenience, we will refer to a 'season' (dry season, breeding season, etc.) by the year in which the January–May months fall, but the reader should note that the December data from

the previous calendar year are part of a given season. So, for example, ‘the 1995 dry season’ means December 1994 through May 1995.)

For all but three of the fourteen years under consideration, there are data for each of the six dry-season months. For 1985 (the first year) and 1988, there are no data for the first dry-season month (December 1984 and December 1987 respectively). For 1998 (the most recent year), there are no data for January. Thus the total number of dry season dates is $(6 \times 14) - 3 = 81$.

4 Methods (data processing)

The raw SRF data on the hydrological state of the Park refer only to the surface continuity of water. Clearly, for wading birds, the actual depth of water is important. There are a number of ways we could get at this depth information. One would be to ignore the SRF observations entirely. Everglades National Park contains a network of water depth gauges that give accurate point depths. In principle, these could be combined with topological information to interpolate water depths over the entire area. In practice, there are problems. One is that the distribution of depth gauges is extremely clumped: there are many gauges in the eastern portion of the park, but only a few, scattered gauges in the western area. Another problem is caused by the fact that Everglades National Park is very flat, with a total elevation range of under 3 meters. As a result, the topology is difficult to measure directly. Instead, in a somewhat circular procedure, it is estimated from a model that includes hydrological information. Unfortunately, when this procedure is used there are discrepancies between the estimated depths and the SRF observations of surface water. (In particular, an observation of a ‘transitional’ cell should coincide with a prediction of an average water depth around zero, but often doesn’t.)

One could argue reasonably that the SRF observations are just as likely to be wrong as the model. We prefer to use the SRF data for two reasons. First, they are direct observations, and the uncertainty surrounding them is straightforward and based on understood physical constraints. Second, they are collected at the same time and at the same spatial scale as the data on the wading birds.

Until an improved topological model of the Park is available, we use an alternative technique to obtain water depth information based on the SRF data alone. For each cell, we assign values of 1, 0.5 and 0 to dry season dates in which that cell is classified as ‘dry’, ‘transitional’, and ‘wet’ respectively (using the SRF three-point classification). The average of these scores over time gives an index for each cell whose value must fall in the range 0 (always wet) to 1 (always dry). Actual values range from 0.074 (wettest on average) to 0.993 (driest on average). (Using all dates incorporates the considerable year-to-year variation in total water in the Park and allows the index to resolve even the wettest and driest cells.) We transform the actual values to have a $\{0, 1\}$ range, and call the result a ‘hydrotopology’. These are not absolute heights in any sense, but are relative to a) other cells, and b) the surface water. For example, they don’t take into account the gradual downward slope of the Park from its north-eastern corner (about

2m above sea level) to its southern and western boundaries with the Gulf of Mexico. They are, however, ideal for our purposes, because it is water depth, rather than topology *per se*, that we are interested in. Fig. 2A shows the hydrotopology of the Park. One can clearly see the three major channels, or sloughs, that run North-East to South-West, and through which water currently flows (from West to East these are East Slough, Shark Slough and Taylor Slough).

The next step is to generate an index of water depth for each cell on each date. For this, we use the fact that there is one SRF observation category that does include depth information. 'Transitional' cells, being a mixture of small pools and dry ground, are assumed have an average water depth of zero. For each cell on each date, we find the ten nearest cells that are transitional. We calculate the mean 'height' of those cells, based on the hydrotopology. This is an estimate of the level of the water surface in the vicinity of the focal cell on the same $\{0, 1\}$ scale as the hydrotopology. The focal cell is then assigned a depth that is the difference between the water surface level and its own 'height' from the hydrotopology. For example, suppose a cell has a hydrotopological height of 0.22, and the heights of the ten nearest transitional cells are $\{0.41, 0.52, 0.37, 0.40, 0.43, 0.43, 0.47, 0.38, 0.45, 0.41\}$. The average of these is 0.43, so the cell is assigned a depth of $0.43 - 0.22 = 0.21$. The range of possible depths is $\{-1, 1\}$, where negative values indicate height above the mean surface water, and positive values indicate depth below the mean surface water. Figs. 2B and 2C show raw SRF hydrological data and the corresponding depth map for January 1985.

5 Methods (modelling)

5.1 Determining predictor variables

We are interested in measuring the 'success' of a breeding year for wading birds, using data on foraging. Although species begin nesting at different times, most must continue nesting into and/or through the month of May to successfully rear a brood (Kale & Meahr, 1990; Ogden 1994). Large numbers of birds foraging in May are a sign of ongoing nesting. Conversely, few birds present late in the dry season (for example, in 1987 and 1988) usually indicates abandonment of nesting, often accompanied by a move out of the ENP area. Thus, the number of birds seen in May provides a measure of 'success'. This is the variable that we will try to predict.

To make our predictions, we attempted to quantify the three factors of the water recession model (see Introduction) that are believed to affect the foraging success of most species of wading bird in the Everglades. These are:

1. The overall amount of surface water.
2. The rate at which that water dries over the breeding season.
3. Disruptions in the drying process.

We used the following three-stage procedure:

1. For each species, extract from the data only those cells in which that species has ever been recorded by the SRF (during the dry season). We do this because, while some species (e.g., great egret, white ibis) are found in many locations within ENP, others (e.g., roseate spoonbill) are more restricted. Clearly, it is the water dynamics in these local areas that will primarily determine foraging success. Dynamics in other regions may correlate with foraging behavior, but this correlation will be weak and indirect. Fig. 3 shows the local areas for each species.
2. Using the previously-derived hydrotopology, calculate the average water depth in the species' local area at each survey date, to produce a timeseries of mean depths over the dry season of each year. As an example, Fig. 5 shows the timeseries for just one species (great egret), in three years (1985, 1987, 1991).
3. Fit a linear regression model to each of the within-year timeseries of mean park water depth, using the January to May data. We ignore December, because it represents the very beginning of the dry season and its hydrological state is a poor predictor of subsequent water patterns. We use the intercept of the fitted model as a measure of 'starting' surface water, the slope (multiplied by -1) as a measure of the rate of drying, and the standard deviation of the residuals as a measure of disruption of the drying process. Hereafter, when referring to the variables explicitly, we will use the italicized terms *water depth*, *drying rate*, and *disruption*. Fig. 4 shows the fitted regression lines (in blue), and the residuals as vertical black lines.

As illustration, Fig. 5B shows the monthly depths and regressions for the full set of years for great egret, and Figs. 5C–5E show the derived variables. They will be used to predict the number of birds seen in May (Fig. 5A). One advantage of using the results of a linear fit is that the variables as described are structurally independent of one another.

We now have three independent variables for each species that capture different aspects of the water dynamics of the Park that we believe might be important. However, we have no *a priori* reason to suppose a particular form for the relationship between any of them and the number of birds. The relationship might be positive, negative, or with an inflexion point (for example, an intermediate level of water depth might be optimal). Even if there is no inflexion point, the relationship might be linear or curvilinear. And of course, we might be completely wrong — the variable might not be important at all. All these possibilities are covered by allowing each variable to assume one of four forms: 'not present', 'linear', 'squared', and 'quadratic' (i.e., linear and squared). There are therefore $4^3 = 64$ possible combinations of variables. Assuming that we always include a constant term, this means that for each species, we have the task of evaluating 64 possible models as predictors of the number of observed birds.

5.2 Choosing the best model

To choose between the models, we use statistics based on information theory. All statistical procedures involve a trade off between model fit and model complexity. More complex models always fit better, but some of the variables may contribute little, and the models become increasingly hard to interpret. In standard hypothesis testing, the trade-offs are made on an ad hoc basis, but information-theory statistics incorporate the trade-off directly. They consist of a single number, which is the sum of two parts. The first part, which is common to all such statistics, is the 'lack of fit'. Lack of fit is measured by $-2\ln(L)$, where L is the likelihood of the data given the model (with parameters fitted by the method of maximum likelihood). The second part is the 'penalty term', and this is where various statistics differ. The most well known information-based statistic is Aikaike's Information Criterion (AIC), in which the penalty term is simply $2k$, where k is the number of free parameters in the model (Aikaike, 1973). Recent developments include ICOMP and ICOMP(IFIM) (Bozdogan, 2000). In ICOMP, the penalty term is a measure of the complexity of the covariance matrix of the model parameters. It penalizes not just the number of parameters, but also any interrelationship between them. (It is an axiom of statistics that a model whose parameters are independent is to be preferred over one whose parameters are correlated, and ICOMP incorporates this explicitly.) In ICOMP(IFIM), the penalty term is a measure of the complexity not just of the parameter covariance matrix but also the structure of the residuals. It is always the case that $AIC < ICOMP < ICOMP(IFIM)$ for a given model. All three statistics can be considered indices of lack of parsimony, and ICOMP and ICOMP(IFIM) are considered advances over AIC. The statistics described above are simple to apply: one simply fits all the models that are considered possibilities, and orders them according to the statistic of choice. Smaller values are better (more parsimonious). In this paper, we use ICOMP(IFIM) (and assume normally-distributed errors). Use of the other statistics produces minor differences in the ranking of the models that do not affect our overall conclusions.

6 Results

Table 1 shows the best five models (out of the 64 possible) for each species and group, using ICOMP(IFIM) as our index of parsimony. The second column describes each model using a three-letter grouping. All models have an intercept term. The first, second and third letters describe the form of the *water depth*, *drying rate* and *disruption* variables respectively. '___', 'L', 'S', 'Q' mean 'not included', 'linear', 'squared' and 'quadratic' respectively, as described above. So, for example, 'SLL' indicates the following model: $birds\ in\ May = intercept + water\ depth^2 + rate\ of\ drying + disruption$.

The most striking feature of the results is the similarity of the 'best' models for most species (as shown in Table 1). The model 'SLL' is either the first or second choice in six of the seven independent groups. For great egret, 'SLL' does not appear in the top five models, but the top two models are 'QLL' and 'LLL'. *Drying rate* and *disruption* are always linear except in

two of the top five models for white ibis. Finally, the signs of the parameters are also generally consistent.

The results can best be summarized visually. Fig. 6 shows the forms of the fitted functions for each variable, for each species and group, from the top five (most parsimonious) models in each case. Each plot shows the functions over the range of data for that variable and in that species' local area. The plots show the consistency among the models well. The most common model can be expressed in words thus:

The Park should begin with an intermediate amount of water, and should subsequently dry quickly and smoothly.

This fits exactly with the intuition of ENP biologists.

There are, of course, some exceptions to this picture. Great egrets are unusual in that they seem to prefer a wetter beginning to the breeding season. We note that the best model (and another in the top five) includes a quadratic form for *water depth* that suggests there is an optimum initial value, but one that is towards the top end of the range of the data. For great blue herons, the best model and two others in the top five include no relationship with *disruption*, and the remaining two models include, uniquely, a positive relationship. This is an interesting result that should prompt further study of the relationship between great blue heron foraging and disruption in the drying process. We note, however, that even when included in the model, the positive value of the linear *disruption* parameter is low (compared to the large negative values typical of other species). This suggests that the disruption is simply not that important for great blue herons. Roseate spoonbills have the most unusual set of models, in that they show a strong preference for a wet beginning to the dry season, and, again uniquely, they seem to prefer a low rate of drying. That spoonbills should stand out is not unexpected, because they have the most restricted range. While individual birds may be found occasionally in the 'golden crescent' (the boundary region between the inner edge of the coastal mangrove forests and the interior grasslands), they are only found consistently in the very southernmost tip of the park, including southern Cape Sable (Fig. 3).

Fig. 8 shows the data for each species and group, and the predicted values of the most parsimonious model as chosen by ICOMP(IFIM). The models explain 47–93% of the observed variation in the number of birds in May, averaging 64%. The best fits are for roseate spoonbill and great egret. The worst fit is for small dark herons.

Clearly, the numbers of most species are predicted most efficiently by very similar combinations of variables, and therefore by very similar water conditions in Everglades National Park.

7 Discussion

As discussed in the introduction, it is already established that hydrological conditions affect wood storks and white ibis nesting in South Florida, and that similar conditions affect them

in similar ways. We have here confirmed that in terms of foraging at least, the similarity in hydrological needs can be extended to include great blue herons, roseate spoonbills, small dark herons (as a group) and small white herons (as a group). This supports the water recession model as an appropriate model for wading birds in general. We here restate it, in a slightly expanded form:

1. Wading birds of all kinds forage in areas of surface water, and there is an optimal depth (or range of depths) of water for each species, based on type of prey, bird morphology (leg length, bill length, etc.) and hunting strategy.
2. It is best for that depth to have been reached though a fairly rapid drying process, because this tends to concentrate prey in a few areas ('pools'), where they are more easily caught. Rapid drying also provides a constant supply of new pools, which is important because many species of wading bird forage in high-density aggregations, and can deplete a foraging area quickly.
3. Increasing water depth leads to prey dispersal. Even optimal depths are almost useless if they occur after increases, especially if the ground surface was previously above water entirely (because most prey will not have survived).
4. Therefore, a pattern whereby Everglades National Park begins with intermediate water levels, and dries quickly and continuously, is optimal for almost all wading species. Too much or too little initial water, too slow drying, and disruptions and reversals in the drying process, are all harmful.

That the optimal conditions turn out to be similar is perhaps surprising. Prey items differ widely among species, from larger fish, amphibians and other vertebrates (taken by great egrets, great blue herons, great white herons and wood storks), through smaller fish and free-swimming invertebrates (smaller herons) to bottom-dwelling and interstitial invertebrates (ibises, roseate spoonbills) and even terrestrial arthropods (ibises, cattle egrets). Naturally, methods of acquiring prey also differ, including 'wait and strike' (herons of all sizes), 'stalk and strike' (egrets of all sizes), 'stalk and grab' (ibises), 'grope and grab' (wood storks) and 'sieve' (roseate spoonbills). (See Kale & Maehr (1990) for species summaries.) But while different species undoubtedly find different water depths optimal, they presumably *all* benefit from high prey concentrations. The water recession model should therefore apply to all species whose main food source is aquatic, and that is all of them except, perhaps, cattle egrets. More generally, the dependence of wading birds on dry-downs to concentrate their prey is typical of seasonally inundated landscapes in the tropics and subtropics worldwide. The main differences between species will occur in where they are foraging at any given point in time. We will examine this in a future study.

7.1 The link to nesting

Data on nesting are abundant, but patchy in time and space, inconsistent in survey method, and often reported without crucial information (such as whether counts are of individuals, pairs, nests, etc.). Reliable timeseries for given areas are extremely hard to construct. We are currently in the middle of a project to compile historical wading bird nesting records for South Florida, going back to Victorian times. However, for this paper we attempted to put together a preliminary set of nesting data for the 1985–1998 period for three of the more abundant species. We then compared the nesting records with the SRF May survey data, to see if our contention that foraging is related to nesting is justified.

1. *Wood stork*. The wood stork data were easy to compile. In Everglades National Park in recent years, wood storks have nested almost exclusively at a traditional rookery known as Cuthbert Lake. This site is in the south of the Park, and is relatively easy to reach. Perhaps because of this, nest count data from two separate sources agree closely, and so we are confident in the estimates. Also, the vast majority of these birds will be foraging in the body of the Park (see typical wading bird travel distances given by Bancroft et al., 1994), so the Park's SRF survey should accurately represent foraging birds. A simple, linear regression of nesting numbers against SRF counts shows a significant positive relationship ($R^2 = 0.65$, $p = 0.0015$).
2. *Great egret*. The great egret nesting counts are less consistent, but we are reasonably confident in the estimates for a good number of years. Unlike wood storks, great egrets nest in many locations in the Park. Some of these sites are relatively central, that is, on the mainland and a fair distance from the park boundary. These include Cuthbert Lake, East River and Rodger's River Bay. Great egrets also nested in significant quantities on Frank Key, which is an island off the southern coast of the Park, and in a number of sites just south of Tamiami Trail, which marks the boundary between Everglades National Park and the Water Conservation Areas (WCAs) to the North. Birds from Frank Key are believed to forage in the Park, so nesting numbers there should certainly be reflected in SRF numbers. The same is *not* true of the Tamiami colonies, as birds may just as easily forage in the WCAs, and thus avoid the Park's SRF survey. Conversely, birds nesting in the WCAs may forage in the Park. A regression of the estimated number of birds in just the Park, against the SRF survey, is not significant. But a regression using combined nesting numbers in the Park and in the southern portion of the WCAs is both positive and significant ($R^2 = 0.51$, $p = 0.031$).
3. *White ibis*. White ibis are the most problematic. The SRF data show a rapid decline from large numbers in 1985 to almost none in 1990 and 1991, followed by leap to almost 1985 levels in 1992, followed by another rapid decline to almost none in 1995 (Fig. 7). The nesting data are even more variable, in that the 1992 estimate of around 5000 nests is almost 10 times as high as the next best count. The good news is that the 1992 nesting boom is re-

flected in the SRF's jump in numbers. Other than this, however, the data for the remaining years show little relationship. The problem with linking White Ibis to SRF numbers in the Park is inherent in their nest sites. In the Park, almost all white ibis nest either on Frank Key or in the Tamiami and adjacent colonies, with very few in more central mainland sites. Only the Frank Key populations are *expected* to forage in the Park, and unfortunately, as stated above, there are the data about which we are least certain. The Tamiami birds could be foraging in the WCAs. However, a regression using combined nesting numbers in the Park and in the southern portion of the WCAs (as per great egrets) is not significant either. We reserve judgement on the White Ibis at this time, pending clarification of the nesting numbers in Frank Key. We *do* note that the failure of the regression is due to years in which high SRF counts are associated with low nesting numbers. As outlined in the Introduction, this is not incompatible with the water recession model, as nesting may fail for other reasons. What *would* be incompatible are years in which low SRF counts are associated with high nest counts. We do not observe such years.

Clearly, the link to nesting needs to be examined more closely. Overall, we believe that the SRF surveys provide a valuable tool for monitoring the foraging behavior, and therefore the *potential* breeding success, of wading birds. From a management perspective, if we wish to restore wading bird numbers to anything like former levels, our primary goal should be to get the foraging component right.

7.2 Disruption of drying: the main anthropogenic influence

Although the model-choosing procedure indicates that all three hydrological variables (water depth, drying rate and disruption) are important, we here focus on disruption because it is the most anthropogenic in origin. In particular, dry-season releases from the 'S-12' water control gates at the northern boundary of Everglades National Park have an immediate impact on wading bird foraging, re-wetting areas that had previously dried and increasing depths generally.

To illustrate the effects of disruption more clearly, for each species and group we plotted the residuals from the best model minus its disruption component, against disruption itself (Fig. 8). (We exclude great blue heron because its best model does not include disruption.) These plots clearly show the negative impact that disruption in the drying process has on wading bird numbers. The lines are a simple fitted linear regression. Although there is still plenty of scatter around these lines, the importance of disruption can be seen by examining the range in numbers (on the *y*-axis) spanned by the regression. For example, for great egrets, the range is about 750 birds. The number of great egrets seen in May ranges from about 100 to nearly 2000. This means that disruptions seen to date have contributed about 40% of the total variation in great egret numbers. Other approximate values are 33% (roseate spoonbill) and 25% (white ibis, wood stork, small dark herons and small white herons). Disruption of drying processes is disruptive indeed.

7.3 The future of wading birds in Everglades National Park

Wading birds are not doing well at the moment. The last fifteen years include breeding seasons that were almost complete failures, with wholesale abandonment of nests. On the other hand, it is clear that when given the right conditions, the birds can stage a successful nesting cycle (Gawlick, 2000). What is required for long-term recovery is that these conditions prevail on a year-after-year basis. Luckily, we now know what those conditions are: a moderate amount of surface water that dries rapidly and smoothly. This is, in fact, the 'normal' dynamic of the southern Everglades.

Variation from the dynamic may be caused by unusual rainfall patterns, or occasional extreme events such as hurricanes. In recent times, however, these natural sources of variation have been swamped by the results of water management decisions. **[I'd really like to have a citation for this...]** In particular, the demands of flood protection and water supply have meant that in naturally dry years, water is withheld from Everglades National Park in areas to the north, and in naturally wet years, water is flushed into the Park periodically from these same areas. These anthropogenic events increase the natural amplitude of rainfall-driven variation, and disrupt the natural progress of drying.

This paper shows clearly the results of disruption and extreme conditions on wading birds. These factors also affect other species. For example, breeding of the Cape Sable seaside-sparrow is extensively disrupted when water levels are too high late in its nesting cycle (Curnutt et al., 1998; Nott et al., 1998), and American alligators (*Alligator mississippiensis*) experience high egg mortality as a result of management-induced flooding (Kushlan & Jacobsen, 1990).

Disruption, being largely anthropogenic in origin, is the variable that is most under human control. There is therefore hope that we can improve the situation for wading birds and many other species by allowing a more natural, gradual dry-down. New legislation has recently been passed that mandates the adoption of a new water management plan (U.S.A.C.E., 1999) for South Florida. The models developed in this paper are particularly useful in this context because they can potentially be used to predict the outcome of alternative water management plans on wading bird foraging (and therefore breeding) success, and to track the results of actions that are taken. For this to be the case, of course, the SRF surveys must continue in their present form, which is something we strongly recommend.

Encouragingly, the new plans call for a 'more natural' flow of water through the system. It remains to be seen if the flow will be natural enough to allow the wading birds to recover to something like their historic numbers.

8 Acknowledgments

We would like to thank D. Martin Fleming for helping to initiate the SRF wading bird surveys in Everglades National Park, and all the subsequent observers for their efforts. Mario Alvarado was tireless in cross-checking the SRF data and Dale Gawlick and Frank Sawicki contributed

both nesting data and their considerable insight. During the period of analysis, GJR was supported in whole and SLP in part by NPS cooperative agreement 5280-7-9016.

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10 Tables

Table 1. The best five models for each species, out of the 64 possible combinations of linear and squared versions of three predictor variables derived from that species' area of occurrence. See text for description of the model codes. ICOMP(IFIM) is obtained by adding the appropriate penalty term to the lack-of-fit measure, here given by $2\ln(L)$.

Species	Model	k	Best-fit parameters								Statistics	
			Intercept	Water depth		Drying rate		Disruption		r -sq	-2ln(L)	ICOMP(IFIM)
				Linear	Squared	Linear	Squared	Linear	Squared			
Great	QLL	5	1148	4203	-7985	9912	.	-26352	.	0.74	197.4	215.0
Egret	LLL	4	1154	3464	.	9250	.	-28257	.	0.72	198.3	215.7
	Q_L	4	1417	5027	-6907	.	.	-29731	.	0.70	199.2	216.6
	L_L	3	1406	4334	.	.	.	-31196	.	0.69	199.8	216.8
	_LL	3	812	.	.	24065	.	-19632	.	0.52	205.9	220.3
Great	SL_	3	15	.	-758	2133	.	.	.	0.55	127.8	136.3
Blue	SLL	4	0	.	-924	2282	.	614	.	0.57	127.2	137.3
Heron	_L_	2	13	.	.	1752	.	.	.	0.47	130.0	137.4
	QL_	4	20	188	-1542	1765	.	.	.	0.62	125.4	137.5
	QLL	5	7	182	-1652	1903	.	514	.	0.63	125.0	138.3
White	SLL	4	878	.	-21742	45524	.	-34436	.	0.63	214.5	232.1
Ibis	_SS	3	741	.	.	.	775006	.	-803454	0.52	218.2	233.3
	_LL	3	1150	.	.	32656	.	-46732	.	0.55	217.2	233.6
	SS_	3	390	.	-34975	.	1275808	.	.	0.61	215.1	233.8
	_SL	3	1348	.	.	.	720041	-45022	.	0.56	217.0	233.8
Roseate	SLL	4	117	.	5202	-1679	.	-5014	.	0.92	129.8	140.7
Spoonbill	S_L	3	89	.	4135	.	.	-4508	.	0.90	133.3	142.2
	QLL	5	113	-241	5841	-1340	.	-4503	.	0.93	128.9	143.1
	Q_L	4	91	-397	5541	.	.	-3835	.	0.92	131.0	144.1
	Q_	3	25	-883	7124	0.82	142.3	153.6
Wood	SLL	4	187	.	-3502	8292	.	-7592	.	0.62	169.4	178.9
Stork	QLL	5	204	873	-7074	6876	.	-7790	.	0.67	167.6	180.0
	_LL	3	236	.	.	6038	.	-9973	.	0.56	171.7	180.7
	SL_	3	-2	.	-5428	10062	.	.	.	0.51	173.2	182.7
	LLL	4	222	-186	.	6830	.	-9413	.	0.56	171.5	184.0
Small	SL_	3	6	.	-5272	9502	.	.	.	0.47	172.1	181.4
Dark	SLL	4	49	.	-4830	8989	.	-1767	.	0.48	172.0	182.0
Hérons	QL_	4	12	900	-8940	8131	.	.	.	0.52	170.7	182.9
	QLL	5	75	953	-8515	7308	.	-2557	.	0.53	170.4	183.3
	_LL	3	144	.	.	5357	.	-6016	.	0.35	175.1	184.5
Small	SLL	4	330	.	-5704	16481	.	-13573	.	0.54	191.6	203.9
White	_LL	3	412	.	.	12925	.	-17451	.	0.50	192.7	204.4
Hérons	QLL	5	379	1584	-12216	13551	.	-14397	.	0.58	190.3	205.7
	SL_	3	-6	.	-9165	19797	.	.	.	0.46	193.9	206.4
	LLL	4	410	-26	.	13042	.	-17364	.	0.50	192.7	208.5

11 Figures

Figure 1. An example of SRF data for one species (great egret) on one survey date (January 7th., 1985). The underlying colors represent surface water condition (see key for details). The white circles represent the total number of birds observed in that particular cell. The size of the circle is proportion to the logarithm of the number of birds (again, see key for details).

Figure 2. A: Hydrotopology of Everglades National Park, derived from observations of surface water over the period 1985 to 1996. blue areas are low, brown areas are high. B: Surface water map of Everglades National Park for January 1985, from raw SRF observations. Brown indicates dry, green indicates transitional, blue indicates wet. C: Pseudodepth map of Everglades National Park for January 1985, derived from the observations of surface water in part B and the hydrotopology of part A. Colors are continuous but based on the same scheme as the raw data map. Green represents zero depth. Increasing amounts of blue represent surface water of increasing depth. Increasing amounts of brown represent dry ground of increasing height above the mean surrounding water level. See text for details.

Figure 3. Local area of occupancy for each species, defined as the set of cells (black squares) in which that species has ever been seen during SRF surveys in the dry season (December through May).

Figure 4. Month-by-month dry season mean water depth in the great egret local area (see Figure 3) for three example years. The thick black lines show a linear regression fitted to the data for January through May, and black vertical lines show the residuals from this regression. The regression parameters are used to derive three independent variables that summarize aspects of the drying process for that year.

Figure 5. A: The number of great egrets seen in May of each year. This is the dependent variable that we would like to predict. B: Timeseries of the mean water depth in each dry season month, over whole park. The thick black lines are a linear fit to the data for January to May in each year. The regression parameters are used to generate the following three predictor timeseries (see Figure 4 and accompanying text for details): C: Water depththe amount of water in the Park in each year, given by the intercepts of the fits. D: Drying ratethe rate of drying of water in the Park in each year, given by the slopes of the fits multiplied by 1. E: Disruptionlack of continuity of the drying process in each year, given by the standard deviation of the residuals around the fits.

Figure 6. Functional forms of the variables included in the five most parsimonious models for each species and group (see Table 1). Black indicates the most parsimonious model, and successively paler grays indicate the second, third, fourth and fifth most parsimonious

respectively. Horizontal lines indicate that the variable was not included in a particular model

Figure 7. Fits of the most parsimonious model (thick lines) to the data (thin lines) for each species and group.

Figure 8. For those species in which the most parsimonious abundance model includes disruption, this figure shows the residuals of that model with the disruption term not included, plotted against disruption itself (squares). The lines show a simple fitted regression. These plots show quite clearly the negative influence of disruption on wading bird foraging abundance, and the degree to which it can influence the numbers of birds seen.

Great Egret, 1/7/1985

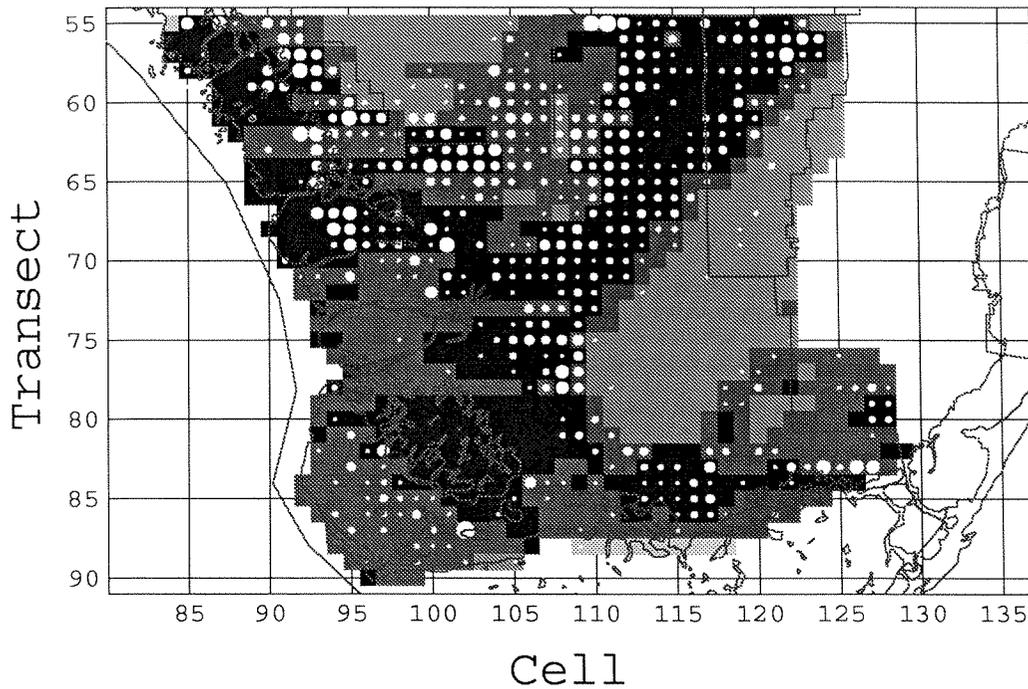


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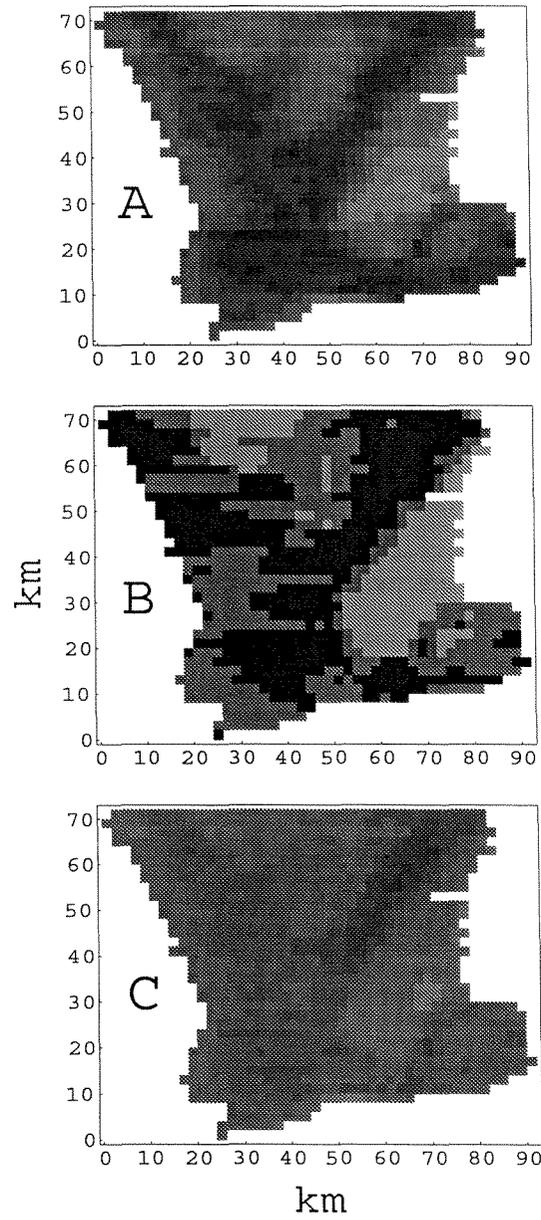


Figure 2:

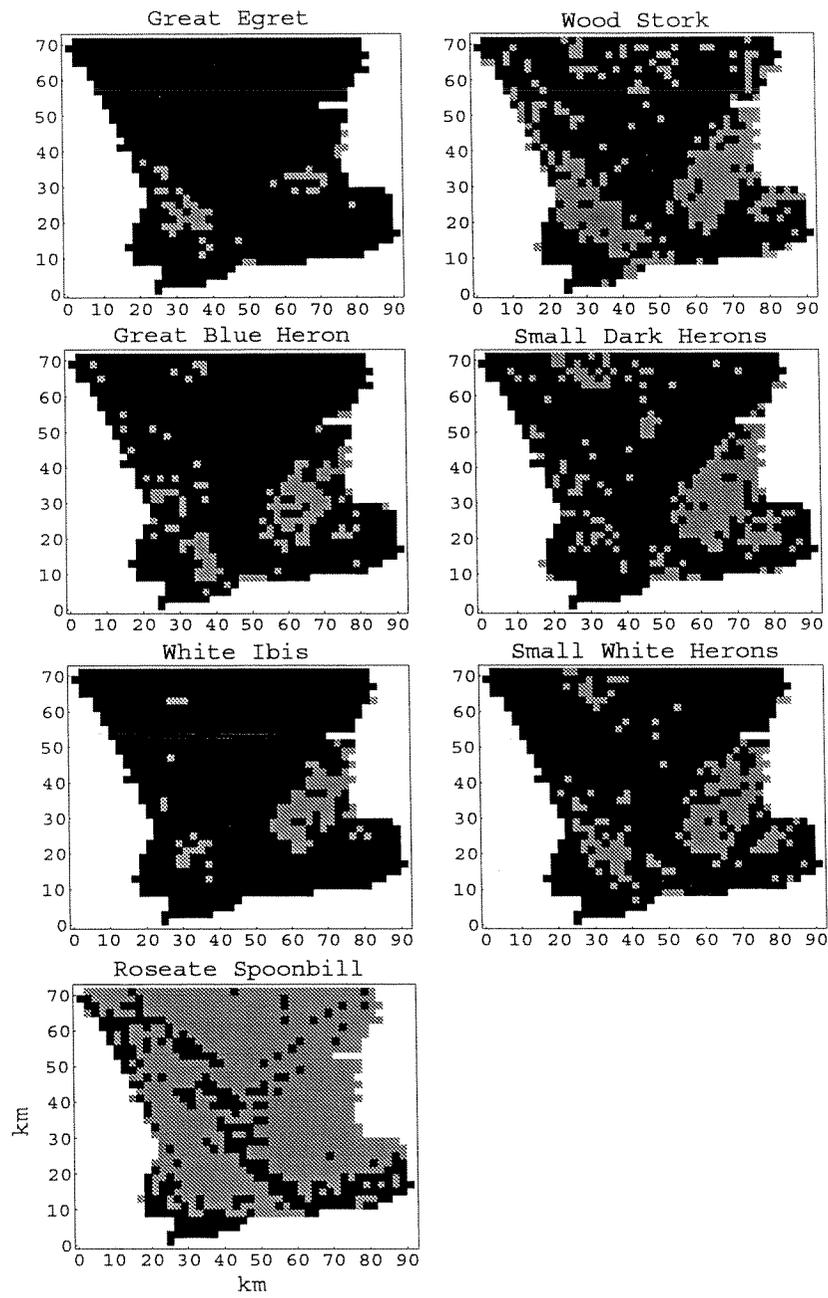
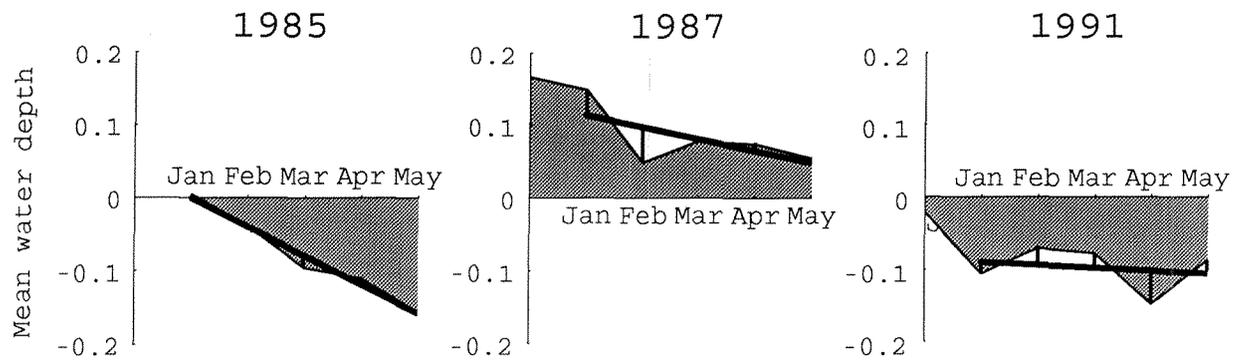


Figure 3:

Figure 4:



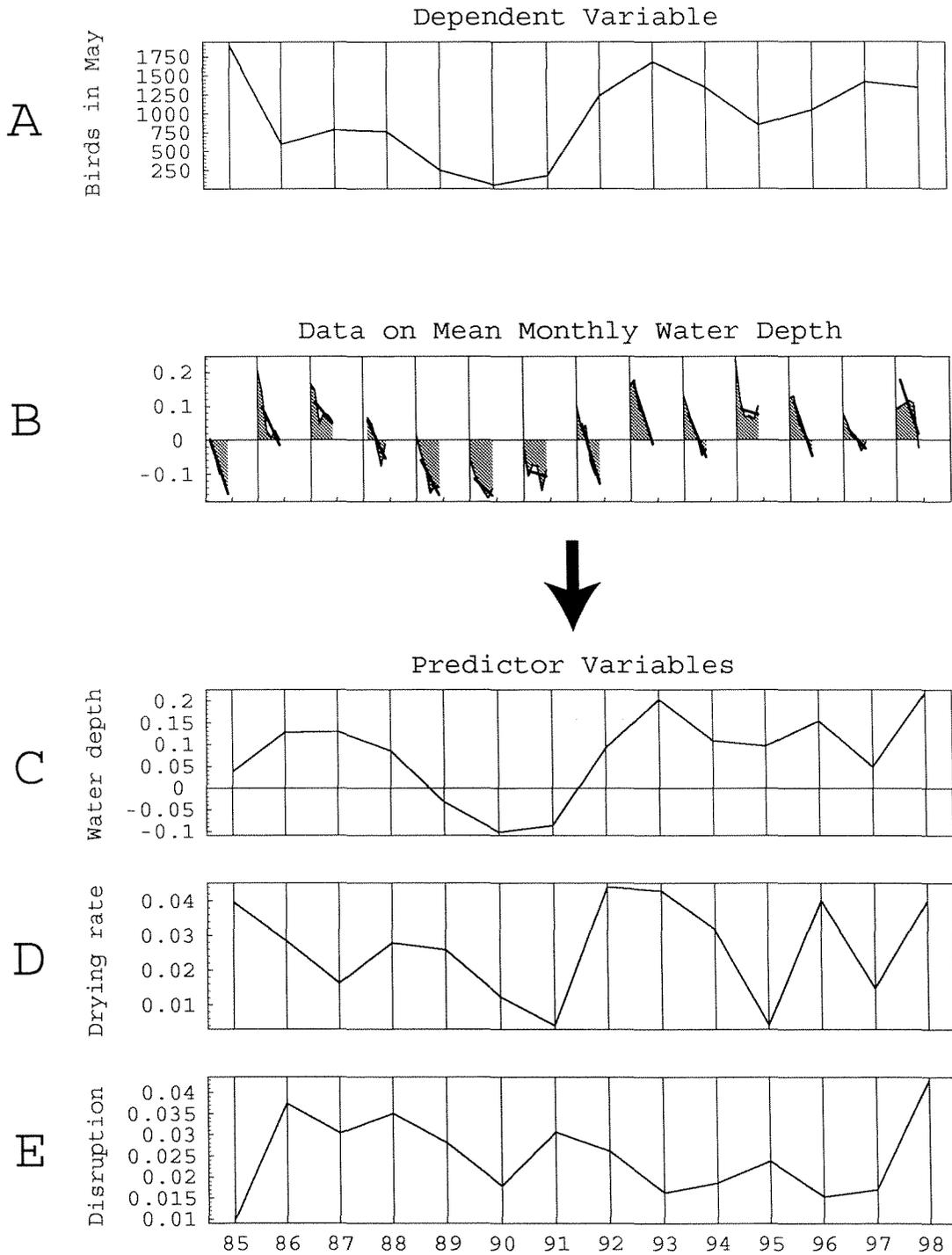


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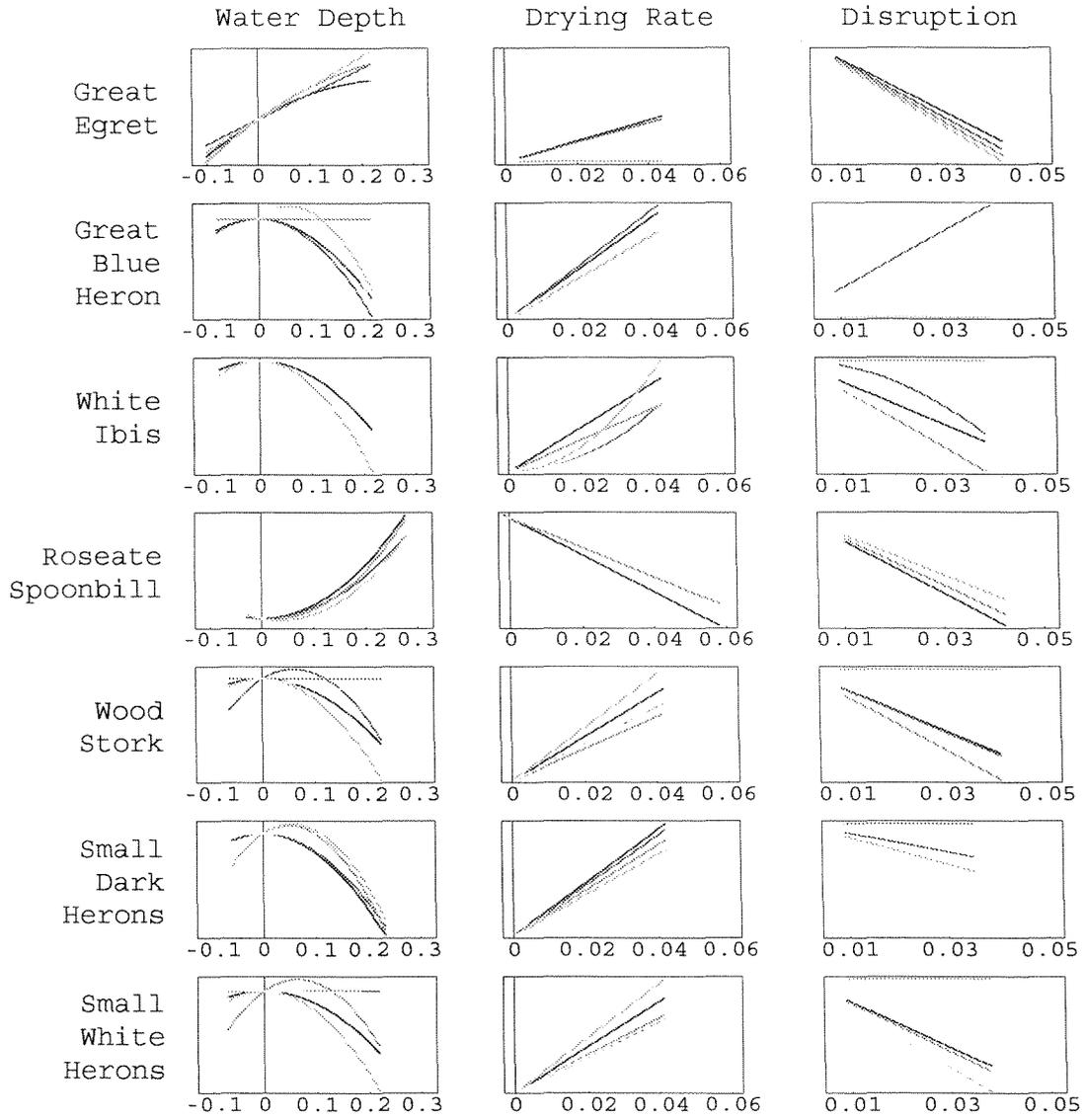


Figure 6:

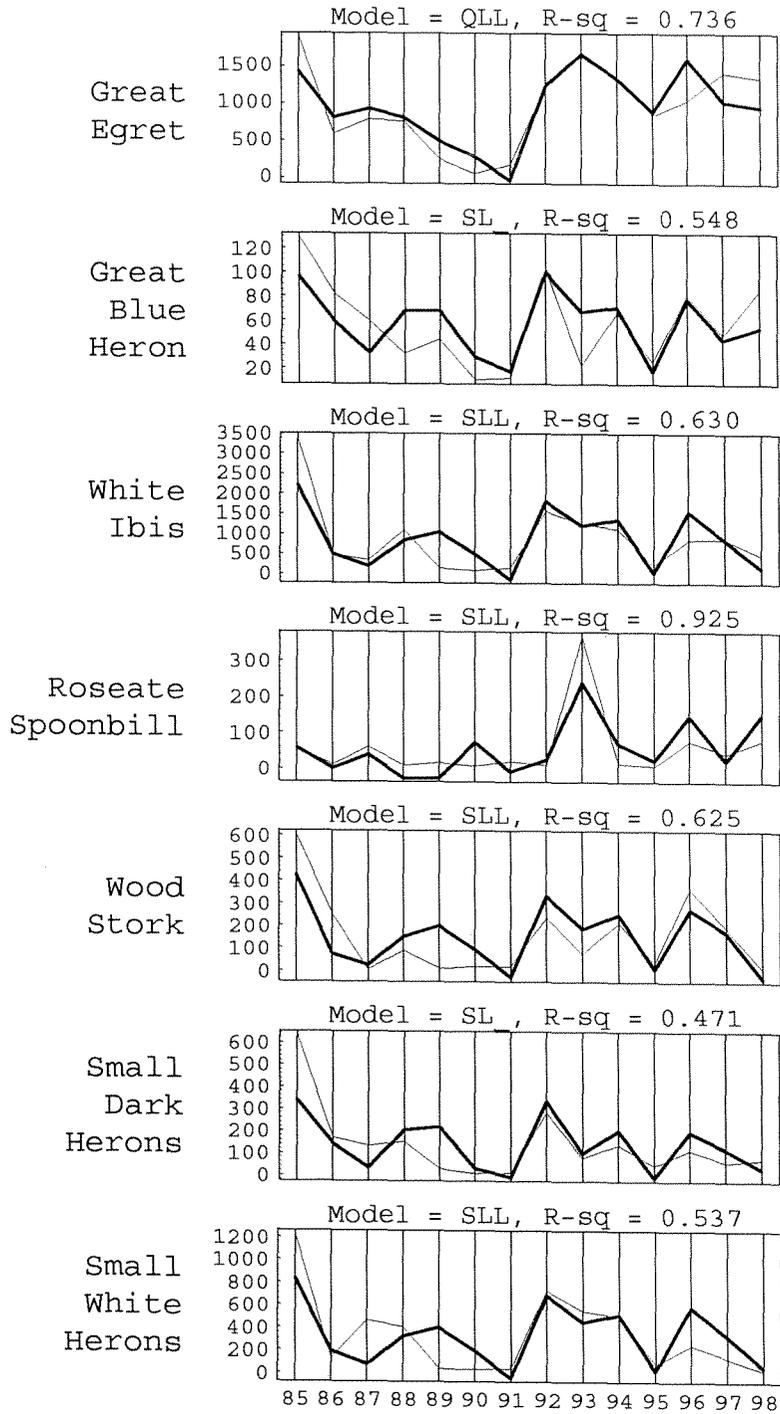


Figure 7:

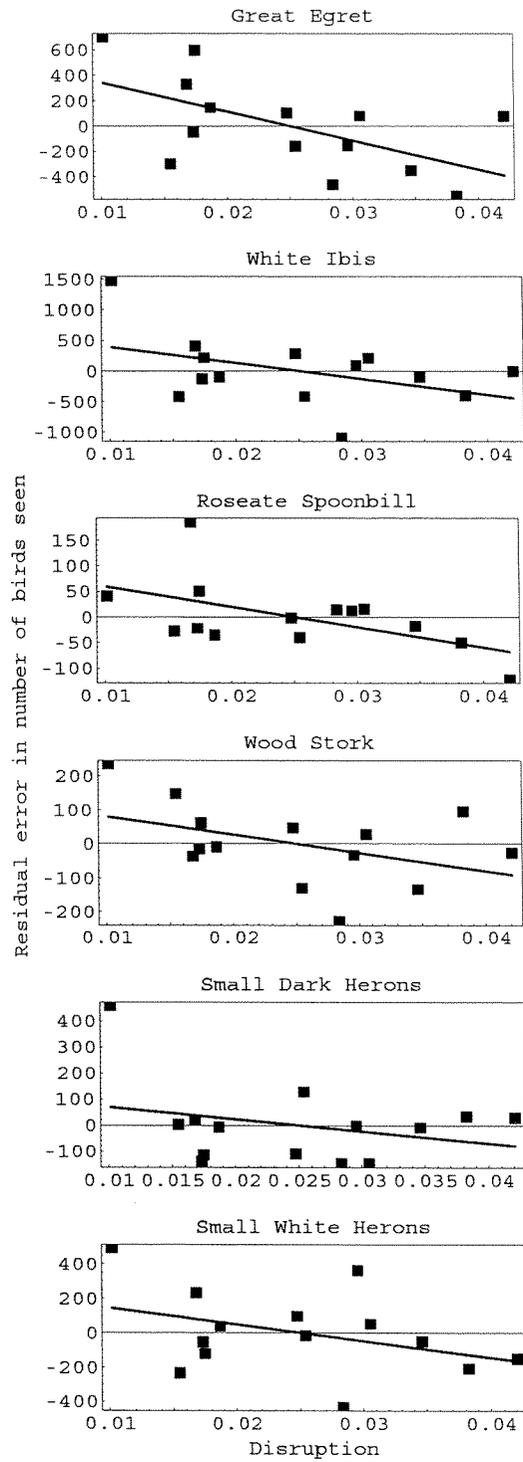


Figure 8: