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PULSED BREEDING OF LONG-LEGGED WADING BIRDS AND THE IMPORTANCE OF INFREQUENT SEVERE DROUGHT CONDITIONS IN THE FLORIDA EVERGLADES

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Abstract: At the scale of ecosystems and regions, numbers of nesting long-legged wading birds are often highly variable from year to year, and much of this variation is thought to reflect variation in production or availability of prey animals in wetlands. Based on observations during and following a severe drought in the Florida Everglades (1989–1992), we predicted that large nesting events would be more likely immediately following droughts than at other times. Using a 38-year history of wading bird nesting events in the Florida Everglades, we tested the hypothesis that ''supranormal'' annual nesting events (numbers of nests >1 standard deviation above the long-term mean) would occur more frequently during the period of up to two years after severe droughts (stages <1 standard deviation below the mean) than after non-drought years. Within this database, we identified 8 supranormal events and 8 severe droughts; 7 of the nesting events occurred immediately after a drought, and 7 of the droughts were followed by a supranormal nesting event. There was a highly significant association between the two types of events. Because many studies suggest that wading bird reproduction is food-limited, this result implies that post-drought conditions somehow result in exceptional productivity and/or availability of small fishes and macroinvertebrates. We propose two biological mechanisms for this pattern and suggest that rare, severe droughts in the Everglades are a forcing function for wading bird population cycles and large-scale movements through the action of pulsed productivity in the aquatic food web.

Key Words: Everglades, Ciconiiformes, pulsed productivity, drought, avian reproduction

INTRODUCTION

Long-legged wading birds (order Ciconiiformes) may nest in a variety of degrees of coloniality, ranging from only a few nesting pairs to breeding aggregations that may contain hundreds of thousands of individuals (Hancock and Kushlan 1984, Hancock et al. 1992). Variation in size of annual breeding events (numbers of nesting birds within any defined area) is to some extent dependent on species, but there is also considerable among-year variance in the magnitude of breeding events and the residence time of individual colonies (Bancroft 1989, Spaans 1990, Frederick et al. 1996, Hafner et al. 2001). Although there are many examples of annual variation in breeding numbers, the generality of this observation has never been documented in a systematic way, and the specific causes of annual fluctuations in breeding are poorly understood.

This variation in size of breeding events is often thought to be a response to the suitability of local breeding conditions (Erwin et al. 1996, Frederick and Ogden 2001). The size of wading bird breeding aggregations has been correlated with a variety of environmental factors that are related to foraging conditions, including rainfall (Carrick 1962, Ogden et al.1980, Den Held 1981, Hafner et al. 2001), the availability of freshwater prey (Bildstein et al. 1990), and continuous periods of falling surface water levels, which concentrate prey animals (Kushlan et al. 1975, Frederick and Collopy 1989).

Thus, the high annual variability in wading bird nesting appears to reflect the suitability of local foraging conditions. Suitability of foraging conditions is strongly associated with the availability of preferred prey animals (Gawlik in press), determined by both density of animals and vulnerability to capture. Numbers of nesting birds may therefore reflect the productivity of local wetlands, and for this reason, it is im-

portant to understand the mechanisms by which water and weather conditions translate into avian reproduction.

The Florida Everglades is a wetland ecosystem that has previously sustained large populations of breeding wading birds (>100,000 pairs/yr), which have formed some of the largest ciconiiform aggregations recorded (Ogden 1994). The numbers of nesting birds in this ecosystem have been documented since the 1930s through a variety of methods (Frederick and Ogden 2001), and both historical and present populations are known to be highly variable from year to year. For example, the estimated number of birds nesting between 1931 and 1946 varied from highs of 195,000–245,000 birds in 1934 to lows of <10,000 in 1938, and none nesting in 1939. The population has also undergone a decrease of more than 90% during the period 1931–1994 (Ogden 1994). The common species in these Everglades colonies were, in rough order of abundance, White Ibis (*Eudocimus albus* Linnaeus), Snowy Egret (*Egretta thula* Molina), Tricolored Heron (*Egretta tricolor* Muller), Little Blue Heron (*Egretta caerulea* Linneaus), Great Egret (*Ardea albus* Linnaeus), and Wood Stork (*Mycteria Americana* Linneaus).

One of the ecological paradoxes of the Everglades has been that such large populations of aquatic birds could be supported in an ecosystem that has been characterized as extremely nutrient-poor (Gunderson and Loftus 1993, Turner et al. 1999, Frederick and Ogden 2001). One of the mechanisms by which this wading bird biomass could be supported is the action of seasonal drying events, which may greatly concentrate and make available the otherwise low biomass density of aquatic prey animals (Kushlan 1977, Walters et al. 1992). However, the record of nesting also shows very high interannual variability, suggesting that the number of nesting birds in any year is strongly affected by other biotic or physical processes that operate at longer than seasonal time scales. After witnessing a particularly large breeding event in 1992 immediately after a severe drought during 1989–1991, we hypothesized that antecedent droughts somehow organized a pulse of secondary productivity for future years, in such a way as to support exceptionally large breeding aggregations of birds temporarily.

In this paper, we (1) demonstrate that supranormal events occur in the Everglades, (2) use a 38-year record of nesting events in the Everglades to test for an association between exceptionally large nesting aggregations and antecedent droughts, and (3) review the evidence that wading bird breeding events in a variety of ecosystems are often quite variable in size from year to year at the level of ecosystems and regions. We discuss these results in light of current knowledge about prey community dynamics and wetland management.

METHODS

Using data from several sources, we constructed a 42-year history of nesting records and water-level recordings in the Everglades ecosystem. We defined the Everglades as the region of freshwater marshes extending southward from the south shore of Lake Okeechobee to and including the downstream mainland estuaries located between the north shore of Florida Bay and the complex of rivers south of Lostman's River. We divided our data into the periods 1931–1946 and 1974–1998, periods during which the results of consecutive annual surveys of nesting were available (see Ogden 1994 and Frederick and Ogden 2001). These data came either from a published database (Ogden 1994) or from more recent unpublished records (Table 1). We categorized nesting in any year as being either low to normal, or supranormal (numbers of nests in any year >1 standard deviation in excess of the long-term mean). Because the nesting population has decreased by more than 90% between the two periods of record, we allowed the criteria for supranormal to be different during the two periods (mean plus one standard deviation = 75,635 breeding birds and 18,310 breeding birds during 1931–1946 and 1974–1998, respectively). For any year in which a range of estimates of nesting attempts were reported by different sources, we used the midpoint of that range.

We hypothesized that supranormal breeding events should be significantly more likely during the period of up to two years after droughts than at other times. We picked two years because the actual end of any drought (onset of normal rains) and its potential ecological effects was often difficult to assign to a particular month. For each annual nesting in the Everglades, we categorized the surface-water conditions during the previous two years as being very wet, wet to normal, normal to dry, or very dry. These categorizations were taken directly from stages at hydrologic recording stations in Everglades National Park (gauge NP203) and (after the creation of the Water Conservation Areas in 1962) the southern part of Water Conservation Area 3 of the Everglades (gauge 3A–4). Very dry or very wet conditions were defined as those in which the January maximum or minimum stage was in either deficit or excess, respectively, of one standard deviation of the period-of-record mean maximum or minimum monthly stage. January was used as the benchmark for breeding season hydrology because it is regarded as the beginning of the dry season and the beginning of spring nesting (Kushlan et al. 1975). For years prior to the installation of gauging stations (all years during 1931–

Table 1. Data used to test for a relationship between antecedent droughts and supranormal nesting events (supercolonies) in the Everglades of Florida. See Methods for data sources.

Nesting Year	Median Number of Nesting Birds	Categorization of Actual Nesting[1]	Water Conditions During Year Preceding Nesting	Water Conditions During Current Year	Supercolony Predicted?
1931	100,000	S	No data		
1932	45,000	NL	Wet	Too dry for nesting	0
1933	207,500	S	Very dry		1
1934	220,000	S	Normal		1
1935	36,000	NL	Wet to normal	Too dry for nesting	0
1936	60,000	NL	Dry	Too wet for nesting	0
1937	35,000	NL	Wet to normal		0
1938	10,000	NL	Wet to normal		0
1939	0	NL	Wet to normal		0
1940	150,000	S	Very dry		1
1941	70,000	NL	Wet to normal		1
1942	"low"	NL	Very wet		0
1943	"low"	NL	Normal		0
1944	"Higher than 1943"	NL	Dry	not enough information	0
1945	"low"	NL	Normal		0
1946	25,000	NL	Normal to dry	Too dry for nesting	0
1974	27,000	NL	No data		
1975	56,472	S	Dry		1
1976	50,000	S	Dry		1
1977	41,000	S	Dry		1
1978	9,000	NL	Normal		0
1979	18,000	NL	Wet to normal		0
1980	6,500	NL	Wet to normal		0
1981	10,000	NL	Wet to normal		0
1982	17,000	NL	Wet to normal		0
1983	5,500	NL	Wet to normal		0
1984	7,000	NL	Wet to normal		0
1985	5,000	NL	Wet to normal		0
1986	17,444	NL	Dry	Too wet for nesting	0
1987	19,132	NL	Normal		0
1988	37,828	S	Normal		0
1989	10,364	NL	Normal to wet		0
1990	13,878	NL	Very dry	Too dry for nesting	0
1991	9,616	NL	Very dry	Too dry for nesting	0
1992	56,500	S	Very dry		1
1993	14,168	NL	Normal	Too wet for nesting	0
1994	20,868	NL	Wet to normal		0
1995	23,850	NL	Wet to normal		0
1996	21,916	NL	Wet to normal		0
1997	20,178	NL	Wet to normal		0
1998	17,626	NL	Wet to normal		0

1. S = supercolony, NL = normal to low.

1946), we relied on hydrologic characterizations noted by National Audubon Society wardens who regularly patrolled the nesting areas of what later became Everglades National Park. These annual unpublished reports are housed in the library of the research center at Everglades National Park. The Audubon wardens were very conscious of rainfall and surface water conditions because they strongly affected travel conditions, and the wardens often commented on these variables. For these reasons, the distinction between drought and non-drought years was unambiguous.

We predicted *a priori* that supranormal breeding events should follow droughts by up to two years, provided that the water conditions in the year being examined for nesting were not those with extremely high water or droughts. We used Chi-squared tests to compare the association between predicted and actual nesting responses.

To examine the generality of the pattern of highly variable nesting numbers in other wading bird populations, we searched for databases and records that included four or more years of breeding wading bird survey counts in an area or region; data from single colonies were not accepted. We calculated coefficients of variation in these annual counts and identified the percentage of years in each database in which nesting numbers were supranormal.

RESULTS

Table 1 shows the data and categorizations of nesting and water conditions in 42 years of record in the Everglades. In four of those years (1931, 1943, 1944, 1974), we were unable to categorize either nesting numbers or water conditions accurately enough to satisfy our criteria. Those years were excluded from the analysis, leaving 38 years in the dataset.

We predicted that supranormal nesting would occur in 8 of the years based solely on the criterion of having both a drought in either or both of the 2 years preceding nesting and an absence of extreme hydrologic conditions during the year of nesting. Based on actual numbers of reported nesting birds, we categorized 7 of the years as supranormal nesting events. With two exceptions, our observations matched predictions. During 1941, we predicted a supernormal nesting based on preceding drought, and the nesting event was categorized as just below the threshold for supranormal events during that period (70,000 birds reported nesting—the threshold for supranormal during the period was 75,635 birds, a difference of 7%). In addition, there was one year in which supranormal conditions occurred in the absence of preceding drought. During 1988, supranormal nesting was not predicted because the previous two years were normal to wet, but the numbers of pairs actually nesting exceeded supranormal status for the period.

The association between supranormal nestings and droughts was significantly different than predicted by chance alone (Chi-squared corrected for continuity = 25.99, $p \ll 0.001$).

Table 2 shows the variation in annual nesting numbers of wading birds from 11 different studies. The coefficient of variation in annual breeding numbers (CV) ranged from 16 to 89%, with the majority of studies (57%) in excess of 70%. We found that supranormal breeding events were represented in 13–25% of years, and all studies showed at least one supranormal year. In the Everglades, we found an annual CV of 70–89% (depending on period used), and a total of 21% of the years were supranormal. The frequency distribution of breeding event sizes indicates that su-

Table 2. Variation in numbers of nesting pairs of wading birds during multi-year studies.

Location	Years	Mean	s.d.	CV	Percent of Years "Supernormal"[A]	Waterbird Species (see below)	Source
Everglades, Florida	1931–1946	79,875	71,395	89.4	21	B	Ogden 1994
	1974–1991	21,434	15,025	70.1	24	B	Ogden 1994
Coastal Texas	1973–1980	58,094	18,186	31.2	13	C	Texas Colonial Waterbird Society 1982
South Carolina	1988–1989, 1994–1996	15,518	2,462	15.8	25	C	Dodd and Murphy 1996
Guyanas	1971–1986	24,765	16,613	67.1	20	D	Spaans 1990
Florida Bay	1960–1987	468	313	66.8	15	E	Powell et al. 1989
Camargue, France	1967–1998	84	30	40.0	16	F	Hafner et al. 2001
Coastal Yucatan Peninsula	1982–1986	2,301	970	40.0	17	G	Lopez Ornat and Ramo 1992
Intermountain West-US	1985–1997	3,363	2,266	67.4	15	H	Earnst et al. 1994
Coastal Yucatan Peninsula	1992–1996	2,072	1,748	84.3	20	I	Baldassare and Arengo 2000
Great Britain	1924–1992	4,458	971	21.8	19	J	Greenwood et al. 1994
Big Cypress, Florida	1982–1985	8,257	3,427	42.0	25	B	Bancroft et al. 1998

A. Breeding numbers greater than mean plus one standard deviation.
B. Wood Storks *Mycteria americana*, White Ibises *Eudocimus albus*, Great Egrets *Ardea albus*, Tricolored Herons *Egretta Tricolor*, Snowy Egrets *Egretta thula*, Little Blue Herons *Egretta caerulea*.
C. All species listed under footnote 2 (above), with Reddish Egrets *Egretta rufescens* Gmelin.
D. Scarlet Ibis *Eudocimus ruber* Linnaeus.

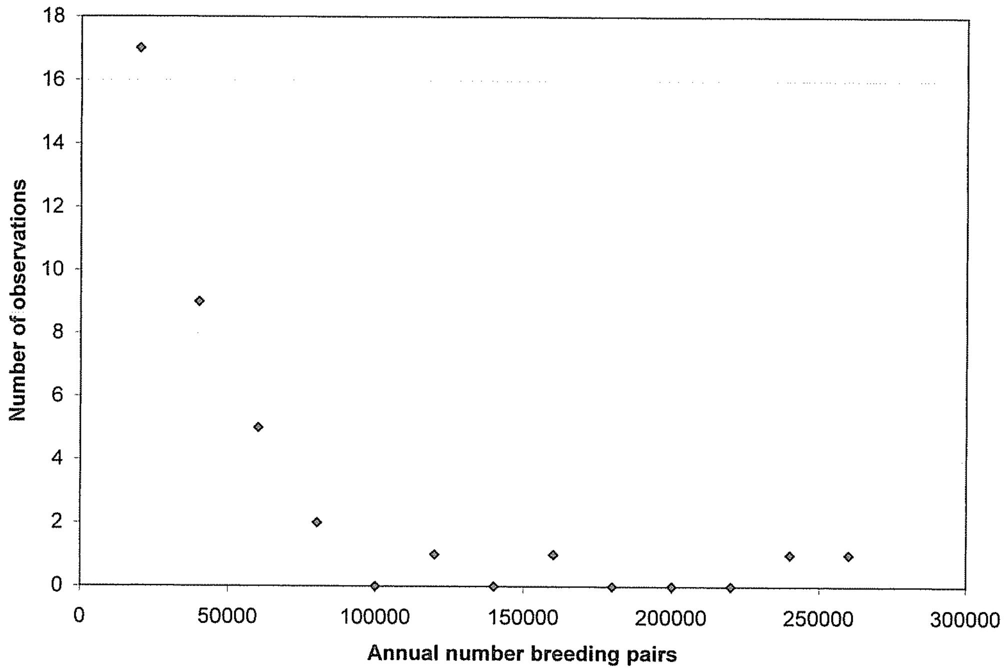

Figure 1. Frequency distribution of annual numbers of wading bird nests in the Florida Everglades in categories of 20,000 pairs, n = 38 years total.

pranormal events are relatively infrequent in the Everglades (Figure 1).

DISCUSSION

Association of Supranormal Breeding and Droughts

We have shown that breeding by Everglades wading birds is characterized by high interannual variability in nesting effort, with interannual variation being nearly as large (89%) as the long-term mean. We also have presented evidence of an association between supranormal nesting events and antecedent droughts. We feel that this analysis is robust because the categorizations of extremely high nesting numbers and of drought conditions were unambigiously determined using the available records.

The association of nesting and droughts was statistically significant, yet it rests on a sample of relatively few supranormal nesting events (n = 8). It is worth noting, however, that the association between antecedent droughts and nesting was extremely close. We found that 6 of the 8 supranormal nesting years were predicted correctly. The seventh year (1941) was within 7% of the value for our definition of supranormal nesting, a difference that could easily be attributed to estimation error. If 1941 is accepted as a supranormal nesting year, then all but one of the supranormal nestings would have been correctly predicted.

Post-Drought Pulses of Secondary Productivity

We have not demonstrated a causal relationship between antecedent droughts and supranormal nestings in the Everglades, but the association seems strong enough to warrant an explanation. Numerous lines of evidence have suggested that size and success of wading bird reproductive events is driven largely by the availability of prey animals (summarized in Frederick and Ogden 2001). We therefore propose that supranormal nesting events in long-legged wading birds occur as a result of environmental disturbances that facilitate exceptional productivity and/or availability of prey animals in wetlands (see also Gawlik in press). We propose two main mechanisms to explain specifically how the Everglades wetland may function in this regard.

The first mechanism involves the release of nutrients that usually accompanies desiccation and fires typical during Everglades droughts (Gunderson and Loftus 1993). The release of nutrients would lead to exceptional primary production at the time of reflooding, with a concomitant increase in primary and secondary consumers. This process would account for a pulse of fishes and macroinvertebrates available to wading birds following a drought, with a rapid decrease in productivity as nutrients are taken up by perennial vegetation. Although this mechanism is plausible given the dynamics known for other ecosystems, there is to date no information concerning such a pulse in primary productivity after droughts for the Everglades.

A second mechanism relies on a drought-induced release of small fish populations from larger piscine predators. During severe droughts in the Everglades, a significant portion of the marsh fish and macroinvertebrate populations are evidently killed through desiccation. Upon reflooding of the marsh surface, the smaller omnivorous fishes would be able to reproduce much more rapidly (generation times of 3 months in mosquitofish *Gambusia holbrooki* Girard) than the large predatory ones (2 years for largemouth bass *Micropterus salmoides* Lacepede). This lag in post-drought response by large predatory fishes would allow a period of (at minimum) several months during which the small fishes would be largely released from the predation pressure of the larger fishes. This ''top-down'' control has been suggested as a mechanism controlling Everglades fish community composition (Kushlan 1976, 1980) and secondary productivity (Walters et al. 1992). Note that both predator-release and nutrient-release hypotheses could be operating in concert and do not necessarily offer competing predictions.

Pulsed flooding and pulsed productivity have been reported previously in studies of major river/wetland ecosystems (Llowe-McConnell 1975, Welcomme 1979, Junk et al. 1989), with strong effects on production and community composition of invertebrates (Golladay et al. 1997) and fish community structure and yield (Merron and Bruton 1995, Piozat and Crivelli 1997, Gutreuter et al. 1999). The main mechanism seems to be that during flooding, wetted area available for primary and secondary productivity is extended into new, oxic resource zones.

Pulsed Flooding and Waterbird Productivity in Other Systems

We have shown that in a variety of studies, locations, and species, supranormal nesting is characteristic of many wading bird populations. The idea that flood/drought cycles may be intimately involved in pulsed productivity of waterbirds has been known for some time to students of wetland ecosystems in more arid zones (Weller 1999). For example, Kingsford et al. (1999) linked boom and bust periods of waterbirds in arid zones of Australia with rainfall and water flows, and two studies have related breeding effort of European herons to drought conditions in African wintering areas (Hafner et al.1994, Fasola et al. 2001). Similarly, duck reproductive effort in the prairie pothole region of the U.S. is closely predicted from rainfall and number of ponds available (Sorenson et al. 1998). In these cases, the presence of water alone seems to be sufficient to stimulate pulses of productivity, and it is unclear whether the intervening dry periods play a role in avian productivity. Presence of water alone has not explained variation in numbers of nesting wading birds in the Everglades (Kushlan et al. 1975, Frederick and Collopy 1989).

Effects Of Wetland Pulsing on Animal Movements

Pulsed productivity in wetlands may also have strong effects on the movements of birds well outside the wetland of interest (Kingsford et al. 1999, Weller 1999). In the Everglades, we believe that most of the birds that recruited to breed during supranormal events came from outside the area. If the majority of ''extra'' birds breeding in supranormal events were entirely local, then they must have bred very infrequently because supranormal events in the Everglades occurred in less than 25% of years. Breeding in 25% of the years is quite unlikely to maintain populations of these wading birds, with annual productivity at less than two chicks and lifespans considerably less than 20 years (Frederick 2001). This example serves to illustrate the idea that pulsed productivity can have effects at large geographic scales, and that even large wetlands like the Everglades may be functionally linked to other wetlands by hydrological cycles (Bennetts and Kitchens 1997), and infrequent pulses of productivity.

Droughts almost certainly have an important function in the natural cycling of marsh systems like the Everglades. The avoidance of long-hydroperiod, stable water conditions through pulsed flooding and occasional droughts in the Everglades has been associated with the maintenance of vegetation patterns (Busch et al. 1998), maintenance of nesting vegetation for Snail Kites (*Rostrhamus sociabilis* Viellot; Bennetts and Kitchens 1997), maintenance of densities and standing stocks of small fishes in both estuarine and freshwater habitats (Loftus and Ecklund 1994, Lorenz 1999), density of crayfishes (Jordan et al. 1998), and community composition of fishes (Kushlan 1976). Extended periods of drying therefore may be integral to the natural functioning of wetlands, and the inclusion of natural drought dynamics in the management of wetlands may generally be beneficial (Bouffard and Hanson 1997).

We do not wish to imply that droughts are the only type of disturbance controlling secondary productivity in wetlands like the Everglades, nor that the variation in breeding wading birds is generally due to a single type of ecological events. Instead, our findings should be used as an example of the importance of relatively rare, large-scale ecological events in structuring the population cycles and large-scale movements of birds in wetlands. Biological processes in most wetland ecosystems are likely to be strongly entrained to natural cycles of drought and flood, and we suggest that this entrainment is the basis for pulses of secondary productivity and the consequent support of large populations of vertebrates. We hope that this work encourages others to examine the ecological role of other kinds of infrequent, large-scale disturbances in wetland ecosystems.

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