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Wading Bird Nestling Diet as a Measure of Food Availability in the Everglades

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Abstract. Lack's Brood Reduction Hypothesis asserts that hatching asynchrony in most altricial birds is a reproductive strategy in which sibling competition for resources, such as food, works to reduce brood size in times of limited resources. Wading birds in the Florida Everglades are considered to be indicators of the overall ecosystem health and function, since their populations are limited by the amount of food available in the landscape. As such, knowledge of food availability has great implications toward Everglades landscape management and wading bird population monitoring. To determine if wading birds were food limited during the 2013 nesting season, we collected and analyzed the mass of regurgitated boluses collected from little blue heron, snowy egret, tricolored heron, and wood stork nestlings. Our results suggest that food was not limited during the 2013 nesting season. We also discuss the importance of long-term studies in order to obtain data from both "good" and "bad" years in terms of prey availability, thus providing valuable information on Everglades ecosystem health and functioning for management and restoration efforts.

Introduction

The variety of reproductive strategies that exist today have evolved from a series of tradeoffs between energetic costs and timing of reproduction. These strategies are environmentally or energetically constrained, and sometimes both (Cogalniceanu et al. 2013). Reproductive strategies also have a profound impact on other aspects of survival such as sibling competition (Smiseth et al. 2007). Avian reproductive strategies are of particular interest due to the nature of successive egg-laying and hatching. In most altricial birds (young born in an undeveloped state and require feeding by the parents), incubation begins before the last egg is laid, causing variation in the time of hatching (hatching asynchrony), and variation in the age and size of nestlings. This variation provides the older and larger nestlings with a competitive advantage for obtaining resources, such as food provided by the parent (Wiklund 1985, Stoleson and Beissinger 1997). These earlier-hatched, larger nestlings often out-compete the later-hatched, smaller nestlings and may even engage in siblicide if resources are limited (Mock et al. 1991, Legge 2002, Margalida et al. 2004).

Lack's Brood Reduction Hypothesis (1947) asserts that hatching asynchrony is a reproductive strategy that relies on sibling competition to reduce brood size. By introducing age and size variation within the nest, resources can be allocated to the nestlings most likely to survive, fledge, and reproduce in the future. Brood reduction can be beneficial in times of food scarcity by insuring that some of the nestlings survive (Lack 1968, Amundsen and Slagsvold 1996). Studies on various altricial bird species such as the zebra finch (*Taeniopygia guttata*) (Skagen 1988, Mainwaring 2012) and bluethroat (*Luscinia svecica*) (Smiseth 2003) have supported the brood reduction hypothesis, with higher survival rates among asynchronously hatched broods during food shortages. A recent study on white ibises (*Eudocimus albus*) in the Florida Everglades (Herring et al. 2011) showed that when food was limited, the stress level of nestlings was negatively related to hatch order, but when food was abundant, stress was not significantly different between first- and second-hatched siblings.

Asynchronously-hatched avian species in food-limited habitats, such as wading birds in the Florida Everglades (Kushlan 1993, Gawlik 2002, Crozier and Gawlik 2003), may be indicators of food availability during a given nesting season. The effects of asynchronous hatching on sibling competition are particularly significant in these species because nestlings compete over parental forage delivered to the nest, rather than each individual being fed directly by the parent (Smith 1997). In these instances direct competition among the siblings determines who eats more rather than begging intensity as in many other altricial bird species (Smith 2005). Food boluses (stomach regurgitations) collected from little blue herons (*Egretta caerulea*) in the Tampa Bay Region (Rodgers 1982), tricolored herons (*Egretta tricolor*) and snowy egrets (*Egretta thula*) in the Florida Everglades (Strong et al. 1997), and little blue herons, tricolored herons, and snowy egrets in Lake Okeechobee (Smith 1997) have been used to determine the prey composition of these species' respective diets. However, assuming Lack's Brood Reduction Hypothesis applies to all wading birds in the Everglades, nestling boluses and how bolus mass potentially differs among siblings can provide a metric for the amount of food available to wading bird species throughout their foraging landscape. Wading birds of the Everglades are considered "bioindicators", or indicators of the overall health of the ecosystem (Kushlan 1993) and some species such as the wood stork (*Mycteria americana*) have suffered great population declines since drastic changes were made to the hydrologic patterns of the wetlands (Kahl 1964). Changes in hydrologic patterns are influential for wading bird survival since wading birds require certain hydrologic conditions for optimal foraging (Gawlik 2002, Lantz et al. 2011, Dorn et al. 2011). For these reasons, knowledge of food availability has great implications toward Everglades landscape management and wading bird population monitoring. This project analyzed the mass of regurgitated boluses collected from little blue heron, snowy egret, tricolored heron, and wood stork nestlings in order to investigate food limitations during the 2013 nesting season in the Florida Everglades.

Study Species

We chose several study species to best account for the variety of size and foraging strategies of wading birds in the Florida Everglades. Little blue herons, snowy egrets, and tricolored herons belong to the taxonomic family Ardeidae, and are significantly smaller in size than wood storks. These three species are considered visual feeders due to their reliance on visual cues for foraging, and wood storks are considered tactile feeders because their beaks snap in response to touch sensations (Ogden 1976, Gawlik 2002). Tricolored herons and snowy egrets are known to consume similar fish species such as *Poecilia latipinna* and *Fundulus* spp. (Boyle et al. 2012, Strong et al. 1997). Current information on wood stork diets is limited and outdated (Kahl 1964, Ogden 1976) because it predates the drastic hydrological changes imposed upon the Everglades through development of the region and flood control efforts (Willard and Bernhardt 2011), which can alter the prey community on which wading birds depend.

Objectives

Our first objective was to determine the differences in the amount of food consumed by wood stork, little blue heron, snowy egret, and tricolored heron nestlings as a function of age and hatch order. We hypothesized that due to the nature of asynchronous hatching (Lack 1947) and food being the limiting factor in these species' habitat (Gawlik 2002), earlier-hatched nestlings would consume larger prey amounts than later-hatched nestlings. Our second objective was to test for a change in food bolus mass throughout the season. Since nestlings require more calories and nutrition as they grow (Smith 1997), we hypothesized that bolus mass would increase throughout the nesting season. Our third objective was to determine whether the rate of food increase throughout the nesting season varied with hatch order. We hypothesized that if food became limiting during the nesting season, the food consumption of the later-hatched nestlings would begin to decline first, and the earlier-hatched nestlings would follow as food became more limited. If food availability did not become limited throughout the season, the food consumption of the later-hatched and earlier-hatched nestlings would continue to increase as they grew and none would decline because there would be sufficient food for all. These three objectives served to test for the effects of asynchronous hatching on nestling food consumption (bolus mass) in order to determine whether food was limited during this particular nesting season.

Research Methods

Study Sites

Our study took place within three nesting colonies in south Florida during the 2013 nesting season (Fig. 1). We sampled for little blue herons, snowy egrets, and tricolored herons at Hidden Colony in Water Conservation Area 3A, and for these three species plus wood storks at Tamiami West and Paurotis Pond colonies in Everglades National Park. We chose these colonies due to their repeated use by wading birds, relative accessibility, and abundance of the species of interest. Hidden Colony and Tamiami West are both in freshwater tree islands. Hidden Colony is mainly comprised of bald cypress (*Taxodium distichum*), whereas Tamiami West is dominated by poisonwood (*Metopium toxiferum*), pond apple (*Annona glabra*), and willow (*Salix* spp.). Paurotis Pond is located in brackish water close to Florida Bay, and is dominated by red mangrove (*Rhizophora mangle*).

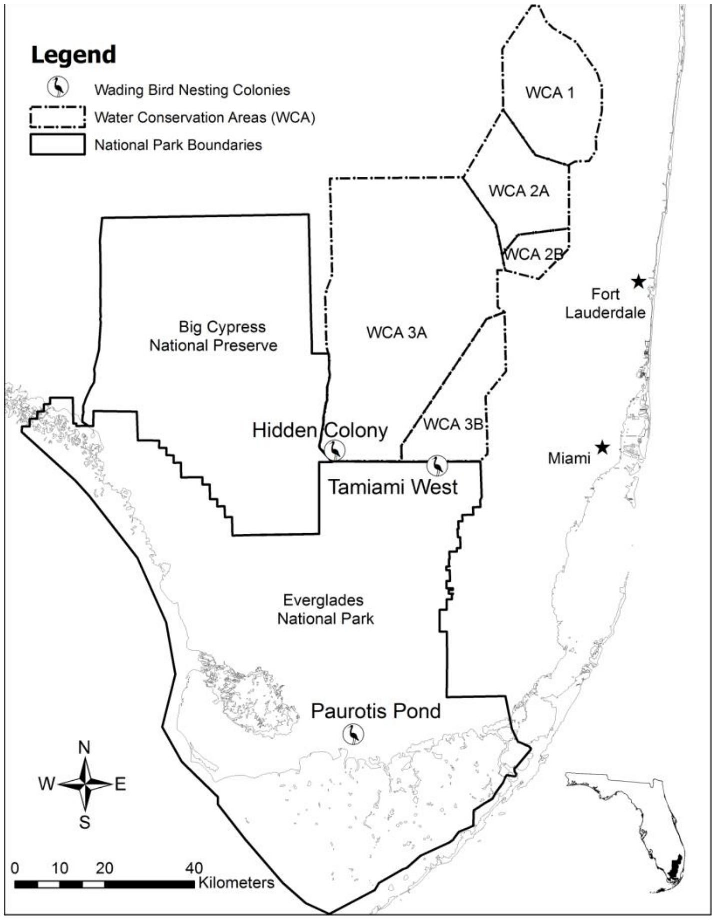

Figure 1 Wading bird colonies in South Florida, USA, from which food boluses were collected in 2013. (Source: South Florida Water Management District GIS Data Catalog)

Field Procedures

We visited each colony once to twice a week during the wading bird nesting season (approximately March through May). We did not sample on days with adverse weather conditions. Tamiami West was accessed by foot, Hidden Colony by airboat, and Paurotis Pond by kayak due to motorized boat restrictions. Once in the colony, we moved locations frequently so that no nest was disturbed for more than 30 minutes. Nestlings readily regurgitate in the presence of humans, allowing easy bolus collection. In the event that a nestling did not voluntarily regurgitate, we gently massaged its trachea in order to induce regurgitation. We collected each bolus in a marked Ziploc bag, noting the date of collection, species of bird, age (in weeks) of the nestling, and hatch order of the nestling (“A” for the first-hatched chick, “B” for the second and so on). Collections began when nestlings of the colonies were about 1 week old and continued until they were about 4 weeks old. Nestling hatch order was easy to determine due to obvious size differences among siblings (Wiklund 1985). We kept a record of which nests we sampled by using a Garmin GPS unit to mark waypoints for the locations of individual nests to avoid repeat sampling. After we collected a bolus, we fed the nestling approximately the same amount of food in small baitfish in order to offset any effect we may have had on nestling food intake for that day.

Lab Procedures

Boluses were transferred from the Ziploc bags into labeled jars filled with Prefer, a color fixative for preserving the original color of the samples. After 3 days, we transferred the boluses to a solution of 70% Ethanol for preservation. We poured each bolus through a 0.6 micrometer mesh net, rinsed with water, and then sorted each prey item under a magnifying lens using tweezers. We measured the mass of each prey item to the nearest 0.01 g and then calculated total bolus mass by summing the mass of all individual prey items within each bolus. Boluses were analyzed in this way in order to remove debris and obtain an accurate total mass of actual prey consumed. Data was entered into Excel spreadsheets for storage and analysis.

Statistical Analysis

A mixed model is a statistical tool that uses both fixed and random effects to test for the statistical likelihood of a relationship between 2 or more conditions (SAS Institute 2008). To determine the effects of hatch order and age on bolus mass, we ran two sets of mixed models using SAS statistical software (SAS Institute 2008): one for wood stork and one for family Ardeidae (includes little blue herons, snowy egrets, and tricolored herons). Since bolus mass was not statistically different ($p > 0.05$) among little blue herons, snowy egrets, and tricolored herons, we pooled the species together to increase sample size and statistical power. In our first set of mixed models, nest was treated as a random term and hatch order and age as fixed effects in order to determine the effect of both hatch order and age. For our second set, we removed age and ran the models with only hatch order as a fixed effect in order to determine the effect of hatch order alone. For our third set of mixed models, we removed hatch order and ran the models with only age as a fixed effect in order to determine the effect of age alone. We did not include colonies as fixed effects in our models because all 3 colonies are within the foraging radius of all bird species, meaning that they all had access to the same foraging grounds, regardless of nesting colony (Strong et al. 1997, Herring and Gawlik 2011).

To test for a seasonal increase in bolus size and determine whether the rate of food increase throughout the nesting season varied with hatch order, we performed a regression analysis of the pooled bolus mass throughout the nesting season for little blue herons, snowy egrets, and tricolored herons using SigmaPlot (SigmaPlot Version 12.x 2013). Wood stork bolus data contributed to the mixed model analyses, but we did not run a regression analysis on wood stork boluses due to small sample size (n=14). We used 95% confidence intervals to determine if the rate of change was statistically different between chicks with different hatch orders.

Results and Analysis

We collected a total of 81 boluses during the 2013 nesting season. Twenty boluses were from nestlings of unknown hatch order, leaving 61 samples for data analysis with hatch order (Table 1). Our largest sample size was 25 for tricolored herons and our smallest was 9 for snowy egrets. Wood storks had the highest mean and range of bolus masses, 44.27 ± 38.36 g and 12.58-166.75 g respectively. Little blue herons had the lowest mean bolus mass (2.94 ± 3.91 g). Tricolored herons had the smallest range of bolus masses (0.06-13.95 g). Although we expected a larger mean bolus mass from wood storks due to their larger body sizes, a mean of 44.27 g is particularly large due to an outlier bolus (166.75 g) containing an exceptionally large prey item. Without the outlier, the mean mass was 34.85 ± 15.75 g.

All mixed models, which were used to determine the differences in the amount of food consumed by the nestlings as a function of age and hatch order (objective one), showed an insignificant effect ($p > 0.05$) of age or hatch order, separately or together, on food bolus mass for wood storks and the pooled family Ardeidae (Table 2). However, age had a slightly stronger effect than did hatch order, particularly for the wood stork.

Our test for a change in bolus mass over the nesting season (objectives two and three) excluded wood storks due to small sample size (only 3-6 boluses per hatch order category; Fig. 2). We omitted hatch order D (the latest-hatched nestlings) from the Ardeidae regression analysis also due to small sample size (n= 2). R^2 values for all hatch orders were less than 0.1 with overlapping confidence intervals, indicating a low likelihood that the rate of food increase throughout the nesting season varied with hatch order (Table 3). The regression line for hatch order A had a positive slope ($b = 0.075$), suggesting a positive relationship between bolus size and time, whereas the slopes for hatch orders B and C all had varying degrees of negative slopes, suggesting negative relationships. The increasing slope magnitudes with decreasing hatch orders B and C (-0.110 and -0.436 respectively) suggest that hatch order C consumed less than B, and B less than A as the nesting season progressed. However, the 95% confidence intervals for all parameter estimates overlapped zero, so the positive and negative signs for the parameter estimates cannot be determined with certainty.

Table 1 Descriptive statistics of collected bolus masses in South Florida, 2013. LBHE= little blue heron, SNEG= snowy egret, TRHE= tricolored heron, WOST= wood stork.

Species	**Sample Size (n)**	**Mean Bolus Mass (g)**	**Standard Deviation**	**Bolus Mass Range (g)**
LBHE	13	2.94	3.91	0.01-14.85
SNEG	9	6.07	4.32	0.98-15.37
TRHE	25	5.26	3.77	0.06-13.95
WOST	14	44.27	38.36	12.58-166.75

Table 2 Mixed model effects of age and hatch order on bolus mass in South Florida, 2013. Ardeidae= family including little blue herons, snowy egrets, and tricolored herons. $CL_{95\%}$= Confidence Limit of 95%.

Model		Estimate	SE	$CL_{95\%}$	p-value
Ardeidae					
Age and Hatch Order	Intercept	3.57	3.64	-3.86-11.01	0.3344
	Age (weeks)				
	1	-2.75	2.56	-8.45-2.96	0.3084
	2	-1.22	2.42	-6.62-4.18	0.6257
	3	2.44	2.52	-3.18-8.06	0.3556
	4	0.42	3.09	-6.46-7.29	0.8948
	Hatch Order				
	A	2.86	2.94	-3.70-9.41	0.3542
	B	0.95	2.96	-5.65-7.55	0.7539
	C	2.06	3.04	-4.71-8.83	0.5129
Hatch Order	Intercept	2.9316	2.83	-2.82-8.68	0.3072
	Hatch Order				
	A	3.14	2.95	-3.43-9.70	0.3124
	B	1.26	2.97	-5.35-7.87	0.6804
	C	1.82	3.09	-5.06-8.69	0.5688
Age	Intercept	5.80	2.21	1.27-10.34	0.0137
	Age (weeks)				
	1	-2.93	2.55	-8.43-2.57	0.2703
	2	-1.38	2.40	-6.56-3.80	0.5747
	3	2.33	2.52	-3.11-7.78	0.3708
	4	-0.33	2.98	-6.77-6.10	0.9127
Wood Stork					
Age and Hatch Order	Intercept	65.38	35.37	-22.98-153.73	0.1156
	Age (weeks)				
	1	-52.80	51.32	-195.29-89.70	0.3617
	2	-39.19	26.41	-112.50-34.13	0.2120
	Hatch Order				
	A	16.65	28.35	-62.07-95.36	0.5886
	B	12.31	29.85	-70.56-95.18	0.7012
Hatch Order	Intercept	12.58	40.40	-86.26-111.43	0.7660
	Hatch Order				
	A	42.96	43.63	-78.16-164.09	0.3805
	B	32.99	45.12	-92.27-158.25	0.5052
	C	15.00	46.55	-114.26-144.25	0.7635
Age	Intercept	80.58	20.28	28.44-132.72	0.0106
	Age(weeks)				
	1	-68.00	40.57	-167.27-31.27	0.1447
	2	-44.04	23.13	-100.63-12.56	0.1056

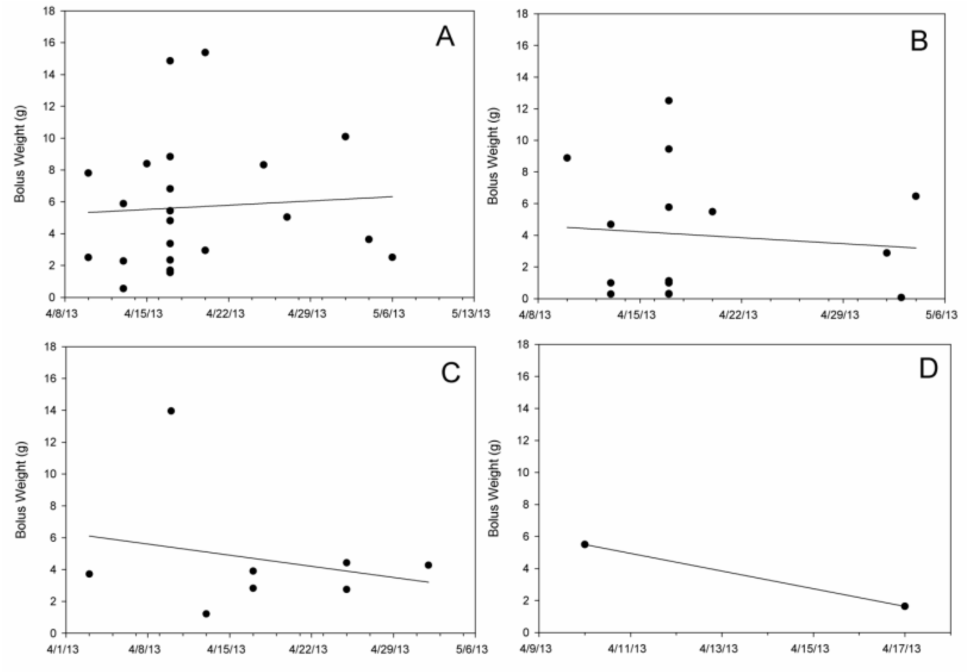

Figure 2 Regression plots of little blue heron, snowy egret, and tricolored heron nestlings changes in bolus mass throughout the nesting season according to hatch order (A, B, C, and D) in South Florida, 2013.

Table 3 Regression parameters of Ardeidae bolus mass change over time in South Florida, 2013. D hatch order chicks were omitted due to small sample size (n=2).

		Parameter Estimates			
Hatch Order	**N**	**Intercept**	**Slope**	**Slope CL$_{95\%}$**	**R^2**
A	22	5.342	0.075	-0.656–0.806	0.0023
B	15	4.495	-0.110	-1.020–0.800	0.0052
C	8	6.319	-0.436	-1.788–0.916	0.0941

Discussion

Our results suggest that food was not limited during the nesting season of 2013 as the mixed models found no significant effect between nestling hatch order and bolus mass, or between nestling age and bolus mass, with p values greater than 0.05 for both bird categories (wood storks and family Ardeidae). Our best performing models included only age (in weeks), suggesting that age differences in weeks, or more specifically, large size differences between nestlings are more significant than hatch order in determining bolus mass. This is expected since nestlings should consume more food as they grow and require more energy and nutrition throughout the nesting season. The regression analysis showed no significant correlation between rates of food intake throughout the nesting season and hatch order due to overlapping confidence intervals. While no definitive results were obtained, the positive slope for hatch order A suggests that the earliest hatched nestlings continued to consume larger amounts as they grew throughout the season, and the increasing magnitudes of negative slopes for hatch orders B, C, and D suggest that D nestlings suffered greater losses in food intake than C, and C suffered greater losses than B. These slopes reflect our hypothesis that as food availability decreased throughout the season, the later-hatched nestlings would consume less food and potentially starve, and the earlier-hatched nestlings would follow after. However, our statistical certainty in the sign of the slope is limited. Larger sample sizes would likely yield more definitive results and improve our statistical certainty.

The most plausible reason for our results is that the 2013 nesting season was not a year in which food was limited. Lack (1968) claimed that in times of food scarcity, some offspring would survive and in times of abundance, all would survive. With an abundance of food for this nesting season, all of the nestlings had enough to eat, regardless of hatch order. These results may indicate that this year's environmental conditions such as hydrologic patterns were more conducive to efficient foraging. Forbes (1994) postulated a threshold at which the effects of asynchronous hatching can be observed can be determined using historical data that includes "good" and "bad" years in terms of food availability. Food availability in the 2013 nesting season likely never reached this threshold, causing all nestlings to consume plenty of food regardless of hatch order.

Other factors may have played a significant role in determining food bolus sizes as well. Parental experience would have had a significant impact on the amount of food available to nestlings, causing bolus size to be dependent upon the foraging success of the parents. More experienced or healthier parents are likely to be better foragers and may provide more food for their young (Amundsen and Slagsvold 1998).

Future studies would likely benefit from collecting data on the parents in addition to the nestlings. Assessing the age and overall health of the parents may indicate their level of experience and foraging success. This can confirm or refute the possibility of parental experience and condition having a larger impact on bolus masses than food limitations. Assessing the overall health and condition of each nestling at the time of fledging may also prove to be beneficial. A high fledging rate does not guarantee high quality fledglings (Amundsen and Slagsvold 1996). Heavier, healthier nestlings will likely survive longer past fledging and this may be where the effects of asynchronous hatching are made evident. Weighing nestlings and determining their overall health at fledging may produce more definitive results on the effects of hatching asynchrony during a food-limited year. Studies aiming to utilize wading bird nestling food bolus masses as a measure of food availability in the Everglades should span over several years in order to obtain data from both "good" and "bad" years in terms of prey availability (Forbes 1994). This would likely uncover the effects of asynchronous hatching, and support our assumption that Lack's hypothesis applies to these wading birds, by taking into account years with varying conditions and thereby overcoming the obstacle of a particular year not reaching the threshold at which the effects are observable. It would also allow the investigator to more closely identify when this food availability threshold exists, providing valuable information on Everglades ecosystem health and functioning for management and restoration efforts.

Acknowledgements

We thank the FAU Office of Undergraduate Research and Inquiry for their generous grants that made this research possible.

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