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ORIGINAL RESEARCH

Fallen Nestlings and Regurgitant as Mechanisms of Nutrient Transfer from Nesting Wading Birds to Crocodilians

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Abstract Positive interspecific interactions can shape fundamental wetland ecosystem dynamics, including energy transfer and spatial distribution of nutrients. Birds, by foraging in one location and nesting in another, commonly act as between-ecosystem nutrient vectors. However, the distribution of nutrients within nesting areas and mechanisms of transfer to other trophic levels are poorly understood. We report on measurements of available food transferred from nesting long-legged wading birds to American alligators (*Alligator mississippiensis*) in the Everglades of Florida, USA. Using throughfall traps, a historic dataset on nesting success and a literature-parameterized alligator energy budget, we estimated the potential food available to alligators via regurgitant and nestling carcasses, and compared that to alligator food requirements. Although dropped regurgitant is of little importance to scavenging alligators, we estimate that nestling carcasses throughout the ecosystem could support the energetic requirements of hundreds of alligators for periods of several months. This resource occurs during the dry season, when alligator thermoregulatory opportunities are relatively scarce and female alligators are mobilizing resources for egg-laying. Our results indicate that through fallen nestlings, wading bird nesting colonies have strong potential to benefit alligators. This facilitative exchange may be globally widespread, forming a keystone process in many tropical and subtropical wetlands.

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Introduction

Positive ecological interactions have received much attention as structuring mechanisms shaping populations and communities (Bertness and Callaway 1994; Stachowicz 2001; Bruno et al. 2003; Kiers et al. 2010). One common currency of positive exchange is the transfer of nutrients (Stachowicz 2001). When species' demographic or life history strategies employ movement across habitat boundaries, these organisms can create strong nutrient links between ecosystems and enrich nutrient regimes for entire communities. Pacific salmon (*Oncorhynchus* spp.), for instance, fertilize the freshwater rivers in which they spawn with marine-derived nutrients they accumulate while feeding at sea. These subsidies can pass through additional nutrient transport vectors to affect aquatic, riparian and terrestrial communities, from primary producers to apex predators (Hilderbrand et al. 1999; Helfield and Naiman 2001; Chaloner et al. 2007; Janetski et al. 2009; Hocking and Reynolds 2011).

Nutrient transfer underlies many fundamental wetland ecosystem processes as well (Bertness 1984; Frederick and Powell 1994; Ellison et al. 1996; Høberg et al. 2002), and large populations of birds that breed colonially in wetlands frequently act as significant nutrient vectors (Bildstein et al. 1992; Frederick and Powell 1994). Nesting waterbirds can consume large amounts of prey over a nesting season: a colony of 500 wood stork (*Mycteria americana*) pairs, for example, is estimated to consume over 100,000 kg of fish during a breeding season (Kahl 1964). A portion of those nutrients are inevitably concentrated near nesting colonies. In the Everglades, typical nesting colonies of long-legged wading

birds (herons, egrets, ibises, storks, and spoonbills; simply "wading birds" hereafter) are estimated to deposit phosphorus at about 20 times the areal atmospheric deposition rates (Frederick and Powell 1994), and a white ibis (*Eudocimus albus*) colony in Okefenokee Swamp, Georgia showed vegetative effects of nutrient enrichment years after it was abandoned by birds (Oliver and Schoenberg 1989).

The fate and mechanisms of transfer of such large quantities of deposited nutrients in breeding colonies are not well understood. Although one obvious mechanism is bottom-up food web effects through nutrient enrichment of waters and soil, there may also be more direct transfer to predators and scavengers. Crocodilians are top predators and scavengers in many subtropical and tropical wetlands, and have diverse diets (McIlhenny 1935; Taylor 1979; Delany and Abercrombie 1986; Wolfe et al. 1987; Magnusson et al. 1987; Barr 1997; Gabrey 2010; Rosenblatt et al. 2015). Crocodilians have been observed routinely eating chicks that fall out of nests into the water in breeding colonies (Dusi and Dusi 1968; Coulter and Bryan 1995), and large regurgitant meals may also be accidentally dropped or purposefully vomited by adult birds and chicks (Byers 1951; Furness and Hislop 1981; Coulter et al. 1999; Clarke and Prince 2008; Nell 2014). Many colonial nesting birds lay more eggs than they can raise and adjust brood size to fit available food resources through several processes of brood reduction (Ricklefs 1965; O'Connor 1978; Clark and Wilson 1981; Mock 1984, 1985; Stenning 1996). This often amounts to 1–2 chicks being ejected alive or dead from each nest, and this may be an important form of nutrient deposition that comes in an appropriate package for large-bodied carnivores like crocodilians.

Some birds may seek out breeding locations near crocodilians. Several papers describe birds consistently nesting over water with crocodilians present (Dusi and Dusi 1968; Jenni 1969; Robinson 1985; Post and Seals 1991, 1993; Coulter and Bryan 1995). Hudgens (1997) even demonstrated that blue-billed malimbes (*Mulimbus nitens*) positioned their nests in clusters around African dwarf crocodile (*Osteolaemus tetraspis*) dens along flooded river banks in Ghana. This apparent attraction may be to utilize crocodilian presence for protection from nest predators: crocodilians are largely unable to access nests by climbing (but see Dinets et al. 2014), but themselves consume many ground-based nest predators (Taylor 1979; Magnusson et al. 1987; Shoop and Ruckdeschel 1990; Barr 1997; Luiselli et al. 1999).

For the large, mixed-species, wading bird nesting colonies in the southeastern United States, medium-sized, semiaquatic mammals such as raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) present the greatest nest predation threat. Even small numbers of these nocturnal predators can cause entire wading bird colonies to abandon their nests (Rodgers 1987; Frederick and Collopy 1989a). Recent research suggests that wading birds actively choose nesting sites above American alligators (*Alligator mississippiensis*), and that there is a mutually exclusive distribution of alligators and mammalian predators (Burtner 2011). Together with evidence that alligators readily target and consume mammals (Shoop and Ruckdeschel 1990; Barr 1997; Rice 2004), there is reasonably strong evidence that alligators deter mammalian nest predators. It remains unclear whether alligators also benefit from associating with wading bird colonies.

We hypothesize that alligators benefit from associating with wading bird nesting colonies via one or a combination of the following mechanisms: (1) fallen material from nests (e.g., nestlings, regurgitant), (2) predation on adult and juvenile birds, (3) greater nearby aquatic prey abundance fueled by nutrients in bird guano, and (4) consumption of nest predators drawn to colonies. We report here on measurement of the potential energy available to alligators from nestling carcasses and dropped regurgitant in wading bird colonies, and use a modeled alligator energy budget to assess the significance of energy derived from colonies. We predict that the food potentially available from wading bird colonies is non-trivial to alligators and that most of these benefits are in the form of nestling carcasses.

Methods

Study Area

The study area encompassed Water Conservation Areas 1–3 (WCAs) of the Everglades, a ~3500 km^2 wetland region in Miami-Dade, Palm Beach, and Broward Counties, Florida (Fig. 1). The field research took place in Water Conservation Areas 3A (WCA 3A) and 3B (WCA 3B). Most of WCA 3A consists of ridge-and-slough landscape: slightly elevated ridges dominated by sawgrass (*Cladium jamaicense*) with embedded tree islands of coastalplain willows (*Salix caroliniana*), swamp bay (*Persea palustris*), dahoon holly (*Ilex cassine*), and other trees/shrubs, and deeper-water sloughs dominated by floating aquatic plants (e.g., *Nymphaea odorata*, *Utricularia* spp.). WCA 3B comprises sparse sawgrass (*C. jamaicense*) marsh dotted by small willow-dominated tree islands, and pond apple trees (*Annona glabra*) that line partially filled-in canals (for more detail, see Lodge 2010). Wading bird nesting colonies are predominantly located in inundated, lower-elevation islands with the longest hydroperiods; in our study area these islands are typically dominated by willow (Frederick and Collopy 1989a).

Dropped Regurgitant

To quantify fallen regurgitant from nests, we placed throughfall traps in two nesting colonies in 2013–

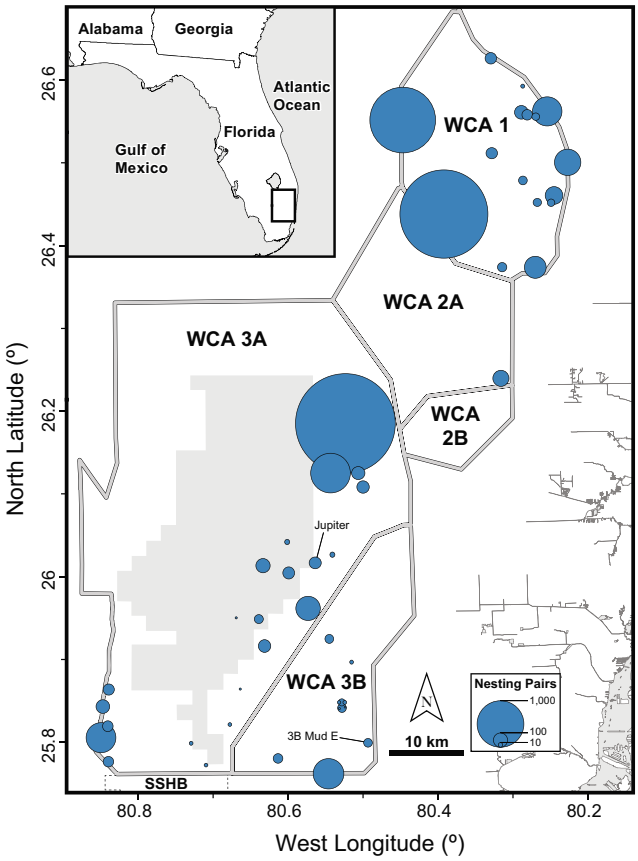

Fig. 1 Map of the study area (Water Conservation Areas 1–3 of the Everglades, Florida) with locations and total nest starts (size of marker) for all wading bird nesting colonies observed through aerial surveys in 2014; the two colonies where throughfall traps were placed (Jupiter and 3B Mud E) are indicated. The gray area inside WCA 3A denotes the size of the region in the Shark Slough hydrological basin (SSHB) used for an alligator population estimate; SSHB's location south of WCA 3A is labeled, and its northernmost boundaries outlined

2014. The trap openings were 1 m^2 each and traps were constructed from tarp, flexible and rigid tubing, and fiberglass screen. The trap sides were steep, smooth, and deep (~1 m), to allow samples to fall to rigid tubing attached at the bottom and prevent scavengers from removing material. The nesting colonies ("Jupiter" and "3B Mud E"; Fig. 1) consisted almost exclusively of great egret (*Ardea alba*) nests. Vegetation in Jupiter (26.015°, −80.563°) was dominated by coastalplain willows, and in 3B Mud E (25.797°, −80.492°) by pond apple.

In 2013, throughfall traps were placed in colonies near active nests along east–west transects, with each transect beginning when the first nest was observed as we proceeded into the colony from the outside, and ending when nests were no longer seen. Sequential transects were then placed 10 m north or south and parallel to the previous. Each nest found along a transect that was at least 10 m from the previous one was marked for nest success observations and throughfall trap placement. We placed traps at random distances (0–5 m) and directions from each marked nest.

We caught nothing in traps over 3 m away from nests or in traps placed under unsuccessful nests (0 chicks reaching branchling stage) in 2013, so in 2014 we changed the sampling design to allow for more efficient trap placement. We placed ten traps near isolated nests (≥5 m from closest neighbors): one under the nest, two at a distance of 1 m, three at 2 m, and four at 3 m. All traps were placed at random azimuths from the nest, excluding those combinations that would make the traps overlap. In both years, traps were only placed in locations under the canopy, but never in a position where vegetation would interfere with them catching items falling from the canopy.

We checked the throughfall traps once per week until we no longer observed chicks near the marked-nest areas. During these visits we observed marked nests for presence of eggs or chicks, and removed non-food waste (e.g., sticks, leaves) and edible material from the traps. The edible material was immediately analyzed when we had a drying oven available and frozen when we did not. After drying to constant weight, we characterized edible material by prey animal type (e.g., fish, crayfish) and measured the length (to the nearest 0.1 cm) and mass (to 0.1 g) of each piece; some very small items (≤0.1 g) of similar lengths had to be weighed together. We used a caloric conversion of 21.5 kJ g^{-1} dry matter (Kushlan et al. 1986).

We used trail cameras in 2013 to ascertain whether the throughfall traps attracted chicks because chick attraction to traps would bias our estimates on a per-unit-area basis. Each colony had four cameras placed on a randomly-selected throughfall trap, which were changed weekly. The cameras were programmed to take pictures when movement was detected, and 1 min was set as the minimum length of time between pictures. We did not observe any great egret chicks on or near the throughfall traps in either colony. Camera trap images also confirmed that scavengers did not remove significant amounts of food from traps, as we did not view any scavengers in traps.

Nestling Carcasses

We calculated potential nestling-carcass energy per nest-week (cE_n, in kJ nest-week^{-1}) and per year (cE_y, in GJ year^{-1}) for great egrets, white ibises, and wood storks as follows:

$$cE_n = W_n^{-1} p_h \mathrm{E}(cE|h)$$
$$cE_y = N_s p_h \mathrm{E}(cE|h)$$

where W_n is the number of weeks from hatch to branchling stage (3, 2, and 8 for great egrets, white ibises, and wood storks, respectively), p_h is the probability of a nest hatching

≥1 nestling, E($cE \mid h$) is the expected nestling-carcass energy from nests that hatched ≥1 nestling, and N_s is the yearly total nest starts. For each species we estimated average cE_n. We calculated cE_y only for species-years in which we observed ≥10 nestlings dying, to afford us sufficient resolution for E($cE \mid h$) estimates.

Parameter estimates were derived from multiyear nest success surveys. During these surveys, each marked nest was assessed for the number of eggs and/or chicks every week until chicks were old enough to walk away from the nest upon approach. We will refer to chicks before this age as nestlings and after as branchlings. We defined this age for the white ibis, great egret, and wood stork as 14 days, 21 days, and 55 days, respectively (Kahl 1964; Frederick and Collopy 1989b). After chicks became branchlings, they could no longer be associated with individual nests, and were not counted by us even though they would not be independent of parental feedings for several more weeks (Hylton et al. 2006; Heath et al. 2009; McCrimmon et al. 2011). In 2013–2014, surveys included searching at marked nests for whether dead nestlings fell to the ground or stayed in the nest, to estimate how often nestling carcasses would remain out of an alligator's feeding range.

Nests that fail are less likely to be observed, as some would presumably start and fail either before surveys began or between surveys. Thus, observed nests have higher success than the true population nesting success, and not correcting for this biases the final estimate. We corrected our calculations of p_h using Mayfield's (1975) method of pro-rating survival during incubation, over 13 years of nest success surveys (1993–1995, 2003–2006, and 2009–2014). Average estimates for each species were calculated using methods outlined by Hensler and Nichols (1981).

We did not use Mayfield-corrected estimates for E($cE \mid h$) because we could not assume that chick-loss events were always independent within nests. This is based on the fact that abandonment is the primary cause of nest failure in wading birds (Frederick and Collopy 1989b), and abandonment is often synchronized in part or all of a colony. This distinction is important for E($cE \mid h$) because using constant daily survival rates based on Mayfield estimates might change the distribution of ages of dead nestlings compared to the clustered distribution that would be associated with abandonment events. Because mass and energy per carcass do not scale linearly with nestling age, this would affect our final summations. We acknowledge that we are missing some very young chicks because some nests will fail before being observed, but we believe any bias will be small, because small chicks provide relatively small amounts of bioenergy and would be less conspicuous to an alligator.

To estimate numbers and sizes of young birds that might have been available as food for alligators, we analyzed data from 14 years of nest success surveys between 1993 and 2014: 1993–1995, 2002, 2003, and 2006–2014. For each nest we estimated hatch dates for all chicks observed, using a randomly generated date between the chick's initial observation date and the day before the previous survey into that colony. Death dates were estimated similarly, substituting the last day the chick was observed alive for initial observation date. We matched each death date with the most recent hatch date to estimate the age at death, as we assumed that the youngest chick would always be the most likely to die. Chicks with death ages greater than the branchling age were considered "successful," because we are only considering those that survived through the nestling stage.

We estimated mass at death using reported values for chick age–mass relationships in each species (Kahl 1962; Kushlan 1977; Custer and Peterson 1991; Coulter et al. 1999) to create Gompertz growth curves, using the following equation:

$$m_i = M_\infty \exp\{-B\exp[-kt_i]\}$$

where m_i is mass at time i, M_∞ the asymptotic mass, B the position parameter, k the rate parameter, and t_i the time since hatching in days at time i. We estimated the energy from each chick by assuming a linear increase from 2.9 kJ g^{-1} wet mass at hatching to 8.4 kJ g^{-1} at fledging (Dunn 1975). Here we define fledging as the age at which a species begins to fly away from the colony: 50, 40, and 60 days for great egrets, white ibises, and wood storks, respectively (Coulter et al. 1999; Heath et al. 2009; McCrimmon et al. 2011). For the calculation of the expected value of food energy from nests that hatched chicks, E($E \mid h$), we only used nests that hatched a chick and were "fully-observed" (i.e., all chicks were observed until branchling age).

Alligator Energy Budget

We created an alligator energy budget using a formula for individual metabolic rate (I, in kJ day^{-1}) as a function of temperature (T, in Kelvin) and mass (M, in kg; Gillooly et al. 2001; Brown et al. 2004; McCoy and Gillooly 2008):

$$I = i_0 M^b \exp\left\{-\frac{E_i}{k}\left[\frac{1}{T} - \frac{1}{T_{20^\circ C}}\right]\right\}$$

where i_0 is the temperature- and mass-independent normalization constant, b the mass-scaling exponent, E_i the average activation energy of metabolic reactions (in electron volts, eV), k the Boltzmann's constant (8.62×10^{-5} eV K^{-1}), and $T_{20^\circ C}$ the standardization temperature (293 K). We used the mass-scaling exponent from estuarine crocodile (*Crocodylus porosus*) standard metabolic rate (SMR; Seymour et al. 2013). To parameterize temperature dependence, we obtained raw data from a study on SMR in juvenile alligators (Lewis and

Gatten 1985) from Robert E. Gatten (University of North Carolina at Greensboro). For comparisons to nestling-carcass energy we assumed the following: average spring body temperatures of 299 K (Howarter 1999), 85.7 % digestion efficiency (Staton et al. 1990), and a similar distribution of masses to that from 39 adult females caught near tree islands in 2013–2014 (Nell 2014). For comparisons to a population's requirements, we used the population size of mature females (range [760; 1572]) estimated for a 756 km^2 portion of the Shark Slough hydrological basin (Dalrymple 2001); this area of marsh (hereafter "SSHB") is located just south of our study area (Fig. 1) and contains the same focal habitat-types (ridge-and-slough, tree islands). We used estimates for adult females because they have the greatest influence upon alligator population dynamics (Taylor et al. 1991).

Statistical Analyses

All analyses were conducted in R v3.1.1 (R Core Team 2014), and means are given±SD unless noted otherwise.

Throughfall traps were categorized by distance from the nest. We computed the summary statistics separately based on these categories to assess an average square meter at that distance. We calculated each distance-category's representative ring area (A_d, in m^2) as such:

$$A_d = \begin{cases} 2\pi(r_t + d - 0.5) & \text{if } d > 0 \\ 1 & \text{if } d = 0 \end{cases}$$

where r_t is the throughfall trap radius (0.564 m) and d is the horizontal distance from the nest in meters.

The following equation was then used to calculate regurgitated prey energy per nest-week (rE):

$$rE = p_s E_p \sum_{d=0}^{d_{max}} A_d p_{p,d}$$

where p_S is the probability that a great egret nest will be successful, E_p is the mean prey-energy (kJ) on weeks where prey were caught, d_{max} is the maximum trap distance at which regurgitant was collected, A_d is the area of the representative ring at distance d, and $p_{p,d}$ is the mean probability of a 1 m^2 area catching prey on a given week at distance d (weighted for the number of observation-weeks for each nest). We calculated p_S using Mayfield estimates for incubation and nestling success, as described for hatch proportion above.

To assess variability in the final estimates, we used a combination of nonparametric (E_p and $p_{p,d}$) and parametric bootstrapping (p_S). We used parametric bootstrapping for p_S because the Mayfield estimates were based on large sample sizes, the raw data cannot be resampled, and confidence intervals for Mayfield estimates are assumed to follow a normal distribution (Hensler and Nichols 1981). We conducted 10^6 simulations for each parameter, then inserted the resulting vectors into the equation above as such:

$$\begin{bmatrix} rE_1 \\ \vdots \\ rE_{10^6} \end{bmatrix} = \begin{bmatrix} p_{s,1} \\ \vdots \\ p_{s,10^6} \end{bmatrix} \begin{bmatrix} E_{p,1} \\ \vdots \\ E_{p,10^6} \end{bmatrix} \sum_{d=0}^{d_{max}} A_d \begin{bmatrix} p_{p,d,1} \\ \vdots \\ p_{p,d,10^6} \end{bmatrix}$$

where $p_{p,d,1} \cdots p_{p,d,10^6}$ represents a vector of each simulation's mean for $p_{p,d}$. Averages were based on median rE, and confidence interval bounds were the 2.5th and 97.5th percentile rE.

We estimated variability in nestling carcass energy similarly to regurgitant energy. For average nestling-carcass energy per nest-week (cE_n) and total yearly nestling-carcass energy in our study area (cE_y), we conducted parametric and nonparametric bootstrap simulations that resulted in a series of vectors for simulation B from 1 to 10^6:

$$cE_{n,B} = W_n^{-1}\left[p_{h,B}\mathrm{E}(cE|h)_B\right]$$
$$cE_{y,B} = N_s\left[p_{h,B}\mathrm{E}(cE|h)_B\right]$$

where $\mathrm{E}(cE \mid h)_B$ is the mean $(cE \mid h)$ for simulation B and $p_{h,B}$ is a single random deviate from the distribution of Mayfield nest survival rates during incubation. We used the 50th, 2.5th, and 97.5th percentiles of simulation estimates for averages and lower and upper confidence bounds, respectively.

Using the data for standard metabolic rate (SMR) in juvenile alligators, we conducted a linear regression of the logarithm of mass-corrected metabolic rate ($\ln[I M^{-0.829}]$) on standardized temperature (k^{-1} $[T^{-1} - (T_{20°C})^{-1}]$). The slope estimated the activation energy, E_i, and the intercept (C) the logarithm of the temperature- and mass-independent normalization constant (i_0) for SMR, $C=\ln(i_0)$ (Gillooly et al. 2001; Brown et al. 2004). Since metabolic rates are higher in the field, we estimated the field metabolic rate (FMR) i_0 value using an equation from 55 species of non-crocodilian, ectothermic reptiles (Nagy et al. 1999). We assumed the equations for alligators and the non-crocodilian reptiles were equal at the latter's log-mean mass and at the average summer body temperature for Everglades alligators, 302 K (Howarter 1999).

Results

Dropped Regurgitant

A total of 60 traps were installed under successful nests in great egret colonies in 2013–2014 (20 in 2013, 40 in 2014). Only one of 26 throughfall traps that were over 2 m horizontal distance from a nest caught any regurgitated fish, and, upon examination of aerial photographs, that throughfall trap was closer to another nest than to the marked one. Thus we only used data from traps 2 m or less from nests (d_{max}=2), resulting in 34 traps available for analysis. The probability of a trap catching regurgitant during any week ($p_{p,d}$) was 0.447±

0.345, 0.0619±0.105, and 0.0111±0.0427 for traps 0, 1, and 2 m from nests, respectively. The variability was quite high, particularly at the 2 m distance, where a single fish was caught by a single trap.

Regurgitant was present in traps in only 29 of 202 total trap-weeks. In three of these weeks, samples were lost before dry mass could be obtained, so they were used for $p_{p,d}$ but not E_p. Fish were the only prey-type confirmed as regurgitant in throughfall traps, consistent with the primary diet of great egrets (McCrimmon et al. 2011). Although most fish caught were small (47.8 % were <5.0 cm long), the majority of fish mass (66.0 %) was contained in a relatively small number (n= 11, or 15.9 % of counts) of large (≥10 cm long) fish; a trap had a 2.3±6.5 % chance of catching a large fish on a given week. Combined mass of fish from fish-present trap-weeks ranged from 0.1 to 24.7 g (mean 9.41±7.52 g), resulting in energy (E_p) from 2.15 to 530 kJ (mean 202±161 kJ). We observed no signs of scavenging and only small amounts of decomposition (typically <10 % loss via visual assessment, and no more than 25 %) in fish samples.

We calculated great egret nest success (p_S) to be 0.405± 0.000784, using Mayfield estimates of incubation and nestling success from 2132 to 1236 nests (29,164.4 and 22,202.0 nest-days), respectively. Combining these estimates resulted in 33.7 ($CI_{95\%}$ [15.3, 57.6]), 35.3 ($CI_{95\%}$ [7.1, 79.1]), and 11.4 ($CI_{95\%}$ [0.0, 40.8]) kJ nest-week^{-1} for ring areas 0, 1, and 2 m from nests, respectively. The final estimate of mean regurgitant bioenergy was 80.5 ($CI_{95\%}$ [22.4, 177.5]) kJ nest-week^{-1} (Fig. 2).

Nestling Carcasses

Of 362 dead chicks from all surveyed nests of all species in 2013–2014, 44 (12.2 %) remained in the nest. We observed 17 of 91 (18.7 %), 14 of 187 (7.5 %), and 13 of 84 (15.5 %) carcasses in nests for great egrets, white ibises, and wood storks, respectively.

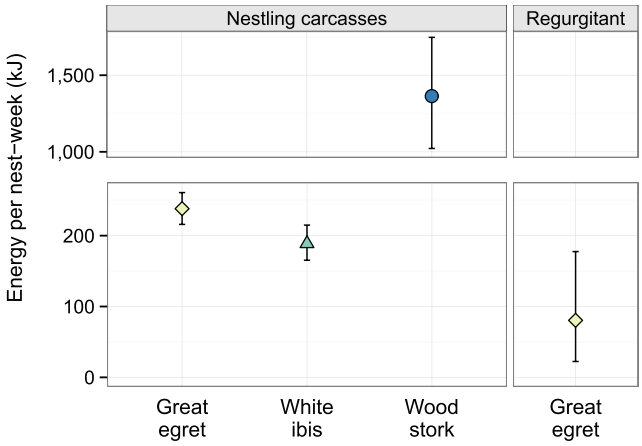

Fig. 2 Estimated potential food energy per nest-week from great egret (*Ardea alba*), white ibis (*Eudocimus albus*), and wood stork (*Mycteria americana*) nestling carcasses, and great egret regurgitant. Error bars indicate the $CI_{95\%}$; note the break in the y-axis

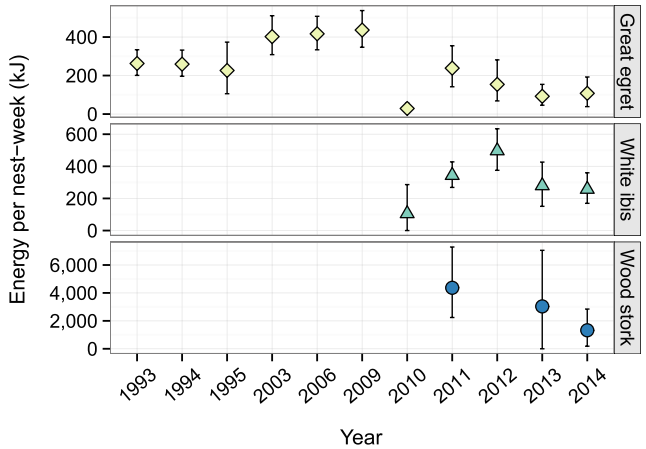

Fig. 3 Nestling carcass bioenergy per nest-week for great egrets (*Ardea alba*), white ibises (*Eudocimus albus*), and wood storks (*Mycteria americana*). Points represent average estimates, and error bars represent the $CI_{95\%}$; note the date breaks before 2009

Mayfield estimates of p_h were based on 3348 nests and 42, 878.9 nest-days. Great egrets and wood storks had very similar average p_h (0.502 and 0.507, respectively), while white ibises had the lowest (0.373).

We analyzed 828, 394, and 53 great egret, white ibis, and wood stork nests, respectively (1275 total) for E($cE \mid h$). Average estimates of nestling-carcass energy per nest-week (cE_n) were highest for wood storks, and lowest for white ibises (Fig. 2). Differences in annual nest success resulted in high variability in per-nest-week carcass energy (Fig. 3). Nestling-carcass energy per year (cE_y) over the study area varied considerably by species and year (Fig. 4). The slope of energy produced per nest start was highest for wood storks, and

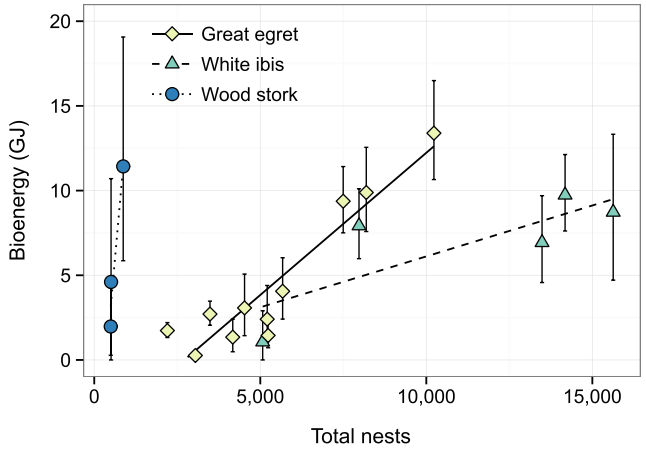

Fig. 4 Relationship between a year's total great egret (*Ardea alba*), white ibis (*Eudocimus albus*), and wood stork (*Mycteria americana*) nest starts and nestling-carcass bioenergy in the study area. Points represent average estimates, and error bars represent the $CI_{95\%}$. Lines represent expected values for the regressions of average estimates on total nest starts

lowest for white ibises; the confidence intervals for wood stork estimates were the widest of all three species.

Alligator Energy Budget

The regression of log-mass-corrected metabolic rate on standardized temperature (R^2=0.903, $F_{1,60}$=560, $p<2.2\times10^{-16}$) informed our final model of alligator field metabolic rate (I, in kJ day^{-1}) as a function of mass (M, in kg) and temperature (T, in K):

$$I = 30.6M^{0.829}\exp\left\{-\frac{0.775}{k}\left[\frac{1}{T}-\frac{1}{293}\right]\right\}$$

where k is the Boltzmann's constant. We estimated a daily food requirement of 821.4 kJ day^{-1} for an adult female alligator and 0.6242–1.291 GJ day^{-1} for the mature female population of SSHB.

Discussion

Importance of Dropped Regurgitant

Bioenergy per nest-week from dropped regurgitant was considerably lower than from dead nestling carcasses for all bird species examined (Fig. 2). Large dropped fish, which comprised most of the regurgitant mass, were extremely rare. Small fish were more common but were less valuable food packages and would presumably be much less conspicuous and consumable for an alligator. Thus, regurgitant appears to provide the least food energy through time and space, and is usually not in a form that an alligator could eat. These results supported our prediction that regurgitant would be of minor importance as food for alligators.

Nestling Carcasses

We observed 7.5–18.7 % of nestling carcasses remaining in nests. Two sources of error may affect these estimates. First, we have not estimated the number of nestling carcasses that were scavenged or preyed upon in the nest prior to our visits. Secondly, it is unclear how many of the carcasses that were observed dead in the nest eventually fell out and became available to alligators. Despite these limitations, it appears that most carcasses reach the ground. What proportion reach alligators is a topic of future study, but evidence suggests that alligators often associate closely with nests: We often observed, heard, or found other evidence (e.g., tracks, crushed field equipment) of alligators near nests in colonies during surveys, and field cameras took several images of alligators under nests. During surveys of tree islands in our study area, Burtner (2011) observed evidence of alligators in 96 % of colony sites, but in only 53 % of islands without wading bird nesting colonies. Thus alligators may be recognizing nests as food sources and seeking them out, which would increase the proportion of carcasses reaching alligators.

Wood storks appeared to offer the most potential food for alligators via nestling-carcass bioenergy per nest-week, which is not surprising given the large size of stork chicks. Annual differences in nest success and numbers of nest starts had strong effects upon annual bioenergy available from nestling carcasses over the study area. We cannot ascertain which species typically has the highest cE_y, as our confidence intervals for wood stork estimates were very wide, and we had no nest success data on white ibises or wood storks in years with very high total nest starts. Thus the nestling carcass bioenergy from white ibises and wood storks that we present here is probably a conservative estimate. That wood storks appear to offer similar amounts of food energy per year in our study area to white ibises contradicts the much higher yearly total nest starts for white ibises in most years. This discrepancy is primarily due to the longer time we could survey wood stork nests (8 weeks for storks, 2 for ibises) and the much larger sizes stork chicks reached over this longer nestling period. If we only include wood stork nestlings up to 2 weeks of age, average per-nest-week food energy is much closer to white ibises (285 kJ nest-week^{-1}), so area-wide food energy would typically be significantly less than that offered by white ibises.

The quantity of nestling-carcass bioenergy potentially available to alligators in the WCAs is substantive compared with alligator energy budgets. Based on our estimate of alligator energy requirements and on average bioenergy for years with nest success data for all three species, nestling carcasses could have entirely supported the food requirements of 512, 300, and 208 adult female alligators for 60 days during the bird nesting seasons of 2011, 2013, and 2014, respectively. This translates to 32.5–67.3 %, 19.1–39.5 %, and 13.2–27.4 % of the 760–1572 mature females estimated to live in SSHB. These years were not particularly productive in terms of total wading bird nest starts, and in more productive years nestling carcass bioenergy may be significantly higher. If our regression predictions are representative for white ibis and wood stork nestling-carcass bioenergy in 2009, this very productive year could have supported 1185 adult female alligators (or 75–156 % of the mature female population in SSHB) for 2 months. While this example is probably the upper end of the effect, we use it here to illustrate that the food energy from nestling carcasses can in some years strongly affect food opportunities for a large portion of the alligator population.

Yet nesting colonies are not ubiquitous across the landscape, and demographic groups other than mature females undoubtedly also consume nestling carcasses. Thus food benefits from colonies are likely concentrated into fewer individuals than suggested by the example above, and these would

not be entirely breeding females. In our study area, the number of nesting colonies (sites having ≥3 focal-species nests) ranged from 41 to 121 annually between 2001 and 2014. How many alligators derive benefits from each colony is probably a function of alligators' ability to detect and travel to it and the abundance of alligators nearby. Because wading bird nesting colonies are noisy, malodorous sites, detectability is likely high. Alligators can travel tens of kilometers in pursuit of food opportunities (Rosenblatt and Heithaus 2011; Lance et al. 2011), and it seems likely alligators would readily discover breeding colonies. Though alligators are often territorial, they can occur at very high densities either in response to dense food sources or when hemmed in by limited surface water. Spacing behavior in wading bird colonies is probably an important unknown factor in estimating how food from wading birds becomes distributed to the alligator population.

Our results allow comment on the importance of only one of four hypothesized pathways of nutritional benefit to alligators. Juvenile and branchling birds are larger, more-valuable food packages than nestlings and might fall within the alligator's feeding range much more often due to their increased mobility outside the nest. In a study using posture-sensing radio transmitters on tricolored heron (*Egretta tricolor*) chicks, Frederick et al. (1993) found nearly 200 % higher mortality in branchlings than nestlings. Wading bird nesting colonies also greatly increase nutrient deposition through guano (Frederick and Powell 1994; Oliver and Schoenberg 1989), but how these subsidies affect aquatic prey abundance and availability through varying hydrological regimes remains uncertain. Also unclear is whether mammalian nest predators attempt to cross water barriers and are intercepted by alligators or if they avoid water altogether; these predators could constitute extremely valuable food opportunities for colony alligators.

Food inputs from colonies probably have a pronounced effect on alligators in our study area. Everglades alligators are in poorer condition compared to other alligator populations, presumably due to food limitations (Jacobsen and Kushlan 1989; Kushlan and Jacobsen 1990; Mazzotti and Brandt 1994; Dalrymple 1996). The period of wading bird nesting (the dry season) is also a metabolically demanding time for female alligators. Reproductively active female alligators mobilize body resources for egg-laying in June–July (Mazzotti and Brandt 1994). Everglades alligators have less of the aquatic refuge they require for effective thermoregulation (Terpin et al. 1979; Seebacher et al. 2003), and, in particularly dry regions/years, they have a higher cost of locomotion. The occurrence of wading bird nesting aggregations during the dry season is therefore supplementing nutrition to thermally stressed, food-limited female alligators at a critical stage of reproduction. Given the magnitude of the potential food source described herein, it seems likely that presence or size of wading bird nesting colonies could strongly influence alligator population dynamics.

The ecological relationships we report here are likely to have broad applicability in tropical and subtropical wetlands. Many wetland systems have food-limited crocodilian populations (Hutton 1987; Campbell et al. 2008; Wallace and Leslie 2009; Mazzotti et al. 2012), and numerous studies demonstrate colonially nesting birds associating with crocodilians (e.g., Post and Seals 1991; Hudgens 1997; Burtner 2011). Analogous species-groups of birds and crocodilians co-occur in wetland regions throughout the world (e.g., floodplains in Western Australia, the Amazon, India, and Africa). In these systems, crocodilians serve vital ecological roles by structuring communities via consumptive and non-consumptive effects (Cott 1961; Bondavalli and Ulanowicz 1999; Nifong and Silliman 2013; Hanson et al. 2015), providing between-habitat nutrient linkages (Fittkau 1970; Subalusky et al. 2009; Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013; Nifong et al. 2015), and creating local disturbances and landscape heterogeneity through burrowing and nesting activities (Kushlan 1974; Deitz and Jackson 1979; Kushlan and Kushlan 1980; Hall and Meier 1993; Palmer and Mazzotti 2004). Thus, nutrient subsidies from colonially nesting birds may help maintain and reinforce a keystone series of processes performed by crocodilians in many tropical and subtropical wetlands.

Conclusions

We demonstrate here the potential for significant nutritional benefits to alligators that associate with wading bird nesting colonies. Food benefits to alligators from colonies via nestling carcasses are more significant than via regurgitant. Nestling carcasses available in most years in the Everglades ecosystem constitute an important supplementation to Everglades alligators' otherwise limited food base. This effect is large enough that a substantial portion of the alligator population may be supported for several months of the year. Since this is also the time of year when alligators have least access to aquatic refuge and are mobilizing resources for breeding, it seems likely that this food supplementation may affect alligator demographics. Further studies should focus on the availability of nestling carcasses to alligators, attraction of alligators to colonies, and the realized fitness impacts of nesting colonies on alligators.

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