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A Telemetry-based Study of Snowy Egret (*Egretta thula*) Nest-activity Patterns, Food-provisioning Rates and Foraging Energetics

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Abstract.—To better understand how birds balance the demands of reproduction and food-provisioning, Snowy Egrets (*Egretta thula)* were studied from May-July 2009 and 2010 in a mixed-species colony in Wichita, Kansas. Observations included 68 h of scan samples at 34 nests which yielded >11,000 instantaneous records; the durations of 57 food-provisioning trips made by eight radio-tagged birds; 73 records of foraging locations, and 27 h of foraging activity and aggressive intraspecific interactions. Adult activities at the nest included sitting (41% of the time), standing (18%), preening (10%), nest maintenance (7%) and feeding chicks (<1%). Incubating adults spent significantly more time sitting but less time standing than did adults with chicks. The amount of time that both parents were away from the nest increased significantly with chick age. Multiple regression analysis with AIC modeling showed that Julian date, chick stage, and year were important predictor variables in nest activity patterns. Mean food-provisioning intervals (242 ± 22 min; range = 52-539 min) differed among radio-tagged birds, but did not differ by time of day or date. Round-trip flight distances averaged 16.1 ± 3.2 km (range = 6-49 km), and also differed among birds. Distances to foraging sites were combined with published energetic values to estimate flight costs. Compared with birds that used distant foraging sites (>18 km from the colony), birds that used sites near the colony (<3 km) had higher capture efficiencies but caught smaller prey, had much higher rates of aggression, and lower rates of energy intake. *Received 8 February 2011, accepted 19 March 2012.*

Key words.—*Egretta thula*, energetics, food-provisioning, foraging behavior, nest-activity budget, reproduction, Snowy Egret, wading birds.

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Animals face the challenge of matching energy gains with energy expenses so that they maintain a positive balance (Paynter 1974). Activities such as migration and reproduction comprise a relatively small percentage of the annual time budget but on a per-unit basis are very expensive (Mock 1991). Most factors that affect activity budgets are related to the location, abundance and availability of food (Drent and Daan 1980). Insofar as such decisions affect fitness, birds should be under selection pressure to optimize their use of time and energy. This principle has been supported by laboratory and field studies (Paynter 1974; Wakeling and Hodgson 1992; Frey-Roos *et al.* 1995; Thomas and Hedenström 1998; Maccarone *et al.* 2010).

Wading birds perform daily activities such as foraging and flying, and seasonal activities such as migration and incubation. Snowy Egrets (*Egretta thula*) have at times appeared unable to modify their behavior in ways that optimize energy inputs and costs. For example, they have used microhabitats with low prey abundance, which resulted in low rates of energy intake (Brzorad *et al.* 2004; Maccarone and Brzorad 2005, 2007). Snowy Egret foraging behavior can be explained by their strategy called "searching," where the amount of time spent at a site is related to giving-up prey densities (Gawlik 2002). In another study of food-provisioning flights, Snowy Egrets adjusted their wing-beat frequencies to maintain a constant air speed under a range of wind conditions, but this resulted in rates of energy consumption 20% higher than predicted (Paynter 1974; Maccarone *et al.* 2008). Here, Snowy Egret nesting patterns were used to determine activity budgets during the breeding season. In addition, radio-telemetry was used to document food-provisioning patterns, foraging habitat selection, prey-capture efficiency, and rates of intraspecific aggression at foraging sites.

Adults might respond to increased food demand by capturing larger prey (Hampl *et al.* 2005) or by bringing more prey back to the nest on each trip. Both strategies would require their crop to increase in volume. Digestive plasticity has been found in some birds and is often expressed as an enlarged gut in order to increase capacity (Martinez del Rio and Karasov 1990; Prop and Vulink 1992; Karasov 1996). Whether the crop of a Snowy Egret can be enlarged or whether a bird controls when and how much food passes from its crop is not known. However, if an egret's crop holds a finite volume, then a bird cannot greatly increase its payload for each trip. A "delivery window" thus exists when food is available for feeding chicks, before it moves to the gizzard. Therefore, we predict that parents will respond to increased food demand by making briefer feeding trips so that more trips can be made each day. To be useful, an energetic model must be based on detailed, empirical observations (Cairns *et al.* 1987). An accurate model for Snowy Egrets will contribute to a better understanding of their reproductive biology and ecology.

METHODS

Study Site

Snowy Egrets were studied at a mixed-species colony in Wichita, Kansas, from May-July 2009 and 2010. The colony sits in a residential area surrounded by houses (see Maccarone *et al.* 2008 for a complete site description). The population at this colony typically exceeds 1,000 pairs, of which about 60% are Cattle Egrets (*Bubulcus ibis*). Other species included Great Egrets (*Ardea alba*), Black-crowned Night-herons (*Nycticorax nycticorax*) and Little Blue Herons (*Egretta caerulea*). Snowy Egrets comprised about 10% of the breeding population both years.

Nest-Activity Patterns

Activity was recorded for a random sample of 34 nests (twelve in 2009, 22 in 2010) that provided an unobstructed view to an observer. To minimize disturbance, observers sat 25 m from the colony edge and trained a spotting scope on each study nest to record adult activity. Scans were repeated every 5 min so that each nest provided 12 records/h. The use of scan sampling to quantify nest activity is well-represented in the literature, and has been applied to Great Blue Herons (*Ardea herodius;* Dowd and Flake 1984), Yellow-crowned Night-herons (*Nyctanassa violaceus*; Laubhan *et al.* 1991), and Great Egrets at a nearby colony (Maccarone *et al.* 2010). Scan intervals reported in such studies ranged from 1-15 min. The 5-min interval used here was judged to be sufficient to ensure independence of samples. The procedures for data collection and analysis outlined in Martin and Bateson (1993) and Bart *et al.* (1998) were followed.

Activities included sitting, standing, preening, feeding chicks, nest maintenance (nest repair, turning eggs) and time away from the nest. At the start of each period, the time of day and breeding stage for each nest were recorded. Breeding stage was based on nest content. If chicks were present, the number and size of chicks were recorded. Chick size was determined relative to adult size. Breeding stages were coded by using a 0 for eggs and 1, 2, and 3 for small (c. 1-10 day), medium (c. 11-20 day) and large (>20 day) chicks, respectively. Size categories were adjusted as eggs hatched and chicks grew. In cases when a nest contained both eggs and chicks for a few days, we considered the nest to contain small chicks.

Food-Provisioning Intervals

Radio-telemetry was used to document foraging habitat selection, foraging efficiency and behavioral interactions, and to estimate energetic benefits and costs. In mid-May, adult birds were captured at feeding sites (USFWS Permit MB175760-0). Egret decoys were used to attract birds to small basins (Crozier and Gawlik 2003) which had been recessed in wet sediment, filled with water and stocked with live fish. Before sunrise, modified leg-hold traps were set in and around the basins. Basins were monitored until a bird was captured or all fish were consumed. Each captured bird was weighed, marked, outfitted with a transmitter (Model RI-2C, Holihil Ltd., Ontario, Canada) and released. Birds were observed until they flew out of view, and allowed one day to adjust to the transmitter. A transmitter added < 3% to a bird's body weight. Birds were tracked with the use of a Model R4000 receiver (Advanced Telemetry Systems, Isanti, MN). Tracking was done approximately every other day from late May to early August. Time of day and the bird being monitored were randomized so that all time periods and birds were well represented.

A food-provisioning interval was defined as the period between when a bird departed the colony and when it returned. The colony was monitored at random times between 05h15-21h30 to document provisioning trips. For each trip, the departure time and disappearing bearing were recorded from a position outside the colony. When an egret left the colony it was usually tracked by automobile to its first foraging site. If the bird left that site, it was followed to subsequent sites and then eventually back to the colony. When a departing bird was followed, the locations of all foraging sites were marked onto maps. Straight-line distances between all legs of a trip were later combined, from which the total flight distance was determined. Some flight velocities for radio-tagged birds were determined by dividing the total distance flown by the elapsed time; others were determined when a bird was observed in the air and its speed was recorded directly from the automobile speedometer. Previous experience with Snowy Egret flight patterns showed that birds maintain a constant air speed regardless of wind direction or velocity (Maccarone *et al.* 2008). Published values for flight costs for a

Snowy Egret (Maccarone *et al.* 2008) were then used to estimate energy expenditure for each trip. On some occasions, observers remained at the colony to record departure and arrival times for radio-tagged birds, which were not followed.

Foraging Activities

On 16 occasions totaling 27 h, radio-tagged birds were observed feeding. Strike rates (number of strikes/min) and foraging efficiency (number of successful strikes/number of total strikes) were recorded, and prey items were identified by type (e.g. fish, frog or tadpole). Prey size was estimated by comparing prey length to the length of a Snowy Egret bill (7.9 cm) (Bayer 1985; Brzorad *et al.* 2004). A length × weight regression ($R^2 > 0.90$) previously established by measuring a random sample of 113 fish collected at this site (Maccarone and Brzorad 2007) was used to convert body lengths into weights. Petersen and Ward (1999) determined the energy value of Sand Shiners (*Notropis stramineus*) to be 6703 J/g wet weight, which was used to estimate the energy content of fish. This species often comprises the majority of fish captured by egrets in this area (Maccarone and Brzorad 2007). Although body lengths of Leopard Frogs (*Rana pipiens*) were estimated as with fish, frog body weights were determined with a different regression model (Hatai 2005). Estimated weights were then compared with Leopard Frog specimens for accuracy. Using a value of 24.69 kJ/g ash-free for Leopard Frogs (Cummins and Wuycheck 1971), the energy/g wet weight was estimated from the energy value per ash-free weight of bony fish (22.16 kJ/g ash free = 6.25 kJ/g wet weight). The energetic value of prey was compared with the costs for foraging flights (Brzorad *et al.* 2004; Maccarone *et al.* 2008). From these values, an estimate was made for the energetic cost for each food-provisioning trip.

Aggressive interactions that involved radio-tagged birds were recorded in three different microhabitats: a weir (small waterfall) and its adjacent shallow river, both located 3 km from the colony, and two ponds located 18 and 24 km from the colony. Aggressive interactions included fights, displacements, chases and displays such as feather erections. The duration and outcome for each interaction were recorded, along with the bird involved and type of microhabitat.

Statistical Analysis

For each hour of nest observation, the proportion of time that the attending parent spent in each activity was determined. Multiple stepwise regression analysis with forward selection was used to examine the variation in each category of nest activity. Independent variables included nest content (eggs vs. chicks), number of chicks in the nest, chick size (1-3), Julian date, time of day and nest. Nest observations in 2009 began and were completed a week earlier than in 2010, and so year was included in some analyses. Akaike Information Criterion (AIC) was used to select the best model for each nest activity category (Anderson 2008). ANOVA was used to compare nest activity categories by nest content (eggs vs. chicks), and to examine variation among birds in the durations of provisioning intervals by time of day. For this analysis, food-provisioning intervals were assigned to one of three time blocks beginning at 05h30. Virtually all feeding sites visited by radio-tagged egrets fell into two categories: near the colony (<3 km) and far from the colony (>18 km). ANOVA was used to compare foraging parameters as well as the size of prey captured at near and distant locations. Pearson's correlation was used to measure the relationship between the duration of provisioning intervals and (a) Julian date, and (b) distance from the colony. χ^2 analysis was used to compare prey-capture efficiency by microhabitat. We report means and standard errors throughout.

RESULTS

Nest-Activity Patterns

Based on 11,228 instantaneous samples in both years, overall activity patterns differed by nest content (Fig. 1). Compared with adults with chicks, incubating adults spent only half as much time standing (9 + 1% vs. 20 + 3%) ($F_{1,\ 360} = 25.1$, $P = 0.0001$),

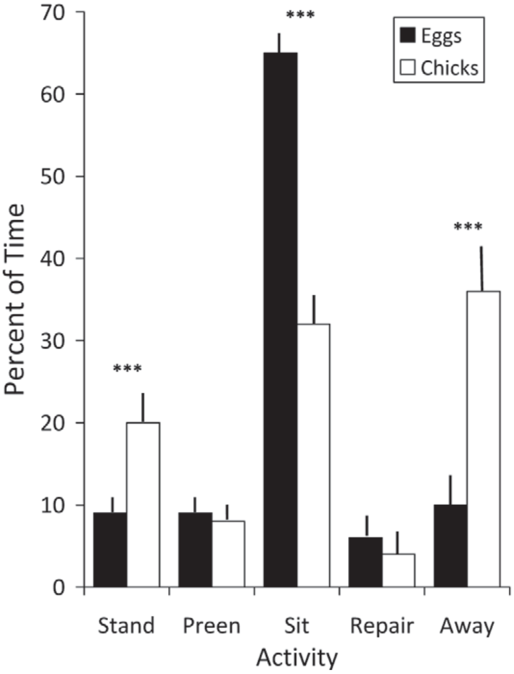

Figure 1. Mean (±1 SE) percentage of time that adult Snowy Egrets engaged in different nest activities. Percentages are based on 68 h of scan samples at 34 random study nests, which yielded 11,228 instantaneous records. Significant differences between nests with eggs and those with chicks were determined by one-way ANOVA: *** P < 0.001.

but twice as much time sitting (65 + 2% vs. 32 + 3%) ($F_{1, 360}$ = 79.3, P = 0.0001). Adults with chicks spent significantly more time away from the nest than did incubating adults (36 ± 4% vs. 10 ± 2%) ($F_{1, 360}$ = 42.6, P = 0.0001). The proportion of time that both parents were away from the nest increased with chick stage ($F_{3, 356}$ = 39.7, P = 0.0001; Fig. 2). Proportion of time away from the nest also correlated with Julian date, a rough measure of the breeding stage (r_{360} = 0.62, P = 0.0001). Regression analysis with AIC model selection showed that a different combination of predictor variables provided the best explanation for the observed variation in each nest-activity category. Many predictor variables appear in the final AIC models for several nest-activity categories (Table 1).

Food-Provisioning Intervals

Four adult Snowy Egrets were captured in 2009 and five in 2010. Mean (±SE) body

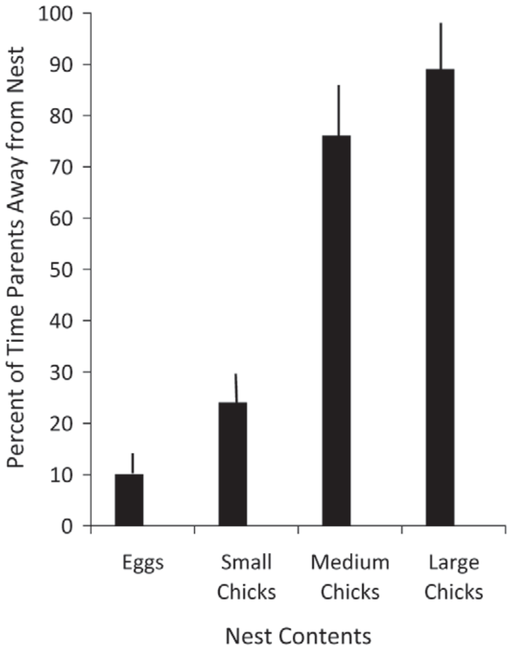

Figure 2. Mean (±1 SE) percentage of time that a nest was left unattended during different nesting stages. Percentages are based on 68 h of scan samples at 34 random study nests, which yielded 11,228 instantaneous records. The overall difference in nest-attendance rates is significant, as determined by one-way ANOVA (P < 0.0001).

Table 1. Results of stepwise multiple regression that examined the effects of six independent variables (columns) on the proportion of time that adult Snowy Egrets were engaged in different nest activities (rows). Independent variables that accounted for a significant proportion of the variation in nest activity are shown. Minimum AIC values indicate the most appropriate model for each nest activity.

	Independent Variables (F-value)									
	Julian Date	Nest Number	Stage	Time of Day	Study Year	Nest Content	Min AIC	F-value	dfs	P-level
Intercept	612.8	50.4	23.7	3.29	—	—	3.38	136.4	4,927	0.0001
Standing	—	—	4.6		19.3	107.7	2.75	44.7	3,928	0.0001
Sitting	28.9	5.9	823.8	—	7.0	29.9	3.23	192.1	5,926	0.0001
Preening	20.7	—	—	18.7	11.9	—	1.93	17.4	3,928	0.0001
Nest Maintenance	33.7	54.3	—	8.3	3.4	—	1.51	25.6	4,927	0.0001
Feeding Chicks	7.0	4.2	4.4	—	—	—	1.22	7.6	2,929	0.0005

weight for the nine birds was 518 ± 8 g (range = 425-590 g). Eight birds outfitted with leg-mounted transmitters were followed for a total of 219 bird-days. During the egg and small-chick stages, one parent departed the colony, often at first light. The mean departure time of 35 first-provisioning trips was 5.5 ± 3.4 min before sunrise. When a bird returned from a trip during the early stages of the breeding season, it remained in the colony for several hours before it departed again. We assume that its mate left to forage at this time. Later in the breeding season when both parents were away from the nest for most of the day, a bird that returned from a food-provisioning trip spent a mean of only 4.6 ± 1.0 min (n = 16) at the nest before it departed again.

The durations of 57 food-provisioning intervals ranged from 53-539 min, with mean (242 ± 22 min) and median (230 min) durations similar (Fig. 3). Mean provisioning intervals differed significantly by radio-tagged bird ($F_{6, 50}$ = 4.94, P = 0.001) and ranged from 140 ± 18 min to 321 ± 73 min. The durations of provisioning trips initiated during the morning (228 ± 16 min; N = 37), at midday (296 ± 41 min; N = 13), and in the late afternoon (211 ± 20 min; N = 7) did not differ ($F_{2, 54}$ = 2.12, P = 0.13). Although the proportion of time that both parents were away from the nest increased steadily with chick stage, the durations of individual food-provisioning trips did not change during the breeding season (r_{55} = -0.07, P = 0.61). Overall mean round-trip flight distance between the colony and the foraging site was 16.1 + 3.2 km (range = 6-49 km). The mean round-trip distances to foraging sites also differed significantly by radio-tagged bird ($F_{6, 66}$ = 7.92, P = 0.0001), and ranged from 6.7 ± 0.3 km to 33.0 ± 9.9 km. Mean food-provisioning intervals did not correlate with mean distances to foraging sites (r_6 = 0.25, P = 0.66).

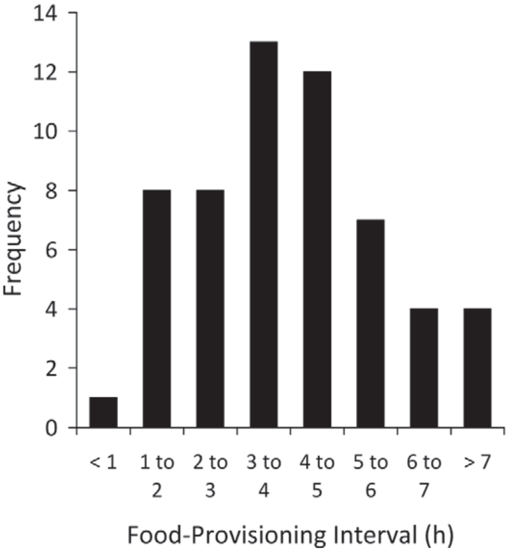

Figure 3. Frequency distribution of 57 food-provisioning intervals for eight radio-tagged Snowy Egrets. Intervals were recorded in 2009 and 2010 between May-July at random times of day. Durations of provisioning intervals ranged from 52-539 min, had a mean duration of 242 ± 22 min and a median of 230 min.

Foraging Activities

Flight velocities measured for 16 trips averaged 12.4 ± 2.0 m/sec (range = 10.8-14.1 m/sec) over distances of 3-27 km. The mean velocity was similar to the 11.7 m/sec obtained previously for Snowy Egrets at this colony (Maccarone *et al.* 2008). Table 2 summarizes energy inputs and expenditures related to food provisioning. Birds were observed for 27 h, during which prey capture efficiency was significantly higher at nearby sites (43%) than at distant sites (33%) (χ^2_1 = 9.4, P < 0.01). However, the mean size of prey captured at nearby sites (32 ± 10 mm; n = 299) was significantly smaller ($F_{1, 8}$ = 7.71, P < 0.02) than prey captured at distant sites (51 + 10 mm; n = 102). Because the weight of a fish (or frog) increases as an exponent of its length (Denlinger and Hale 2006), the mean power input for egrets which used distant sites (34.7 W) was 5.4 times higher than for birds which foraged nearer the colony (6.4 W). The frequency of aggression and chases for birds that used nearby sites was 5.2/h, which reduced their potential total foraging time by 5%. By contrast, birds that flew to distant ponds experienced much lower rates of intraspecific aggression (0.7/h), and diverted <1% of their foraging time to defending patches.

DISCUSSION

The ability to identify individual birds through radio-telemetry illuminated both a

Table 2. Foraging parameters, energy input and costs and rates of intraspecific aggression for eight radio-tagged Snowy Egrets who flew to nearby (3 km from the colony) and distant (>18 km) sites. Based on 16 h of observation at nearby sites and 11 h at distant sites.

	Weir, River (<3 km)	Ponds (>18 km)
Energy Input		
Capture Efficiency (captures/strikes)	299/688 (43%)	102/308 (33%)
Mean Prey Capture Rate (n/min)	0.31	0.15
Mean Prey Length (mm)	32	51
Mean energy gain (Joules)	1,984.3	9,833.9
Mean power gain (Watts)	6.4	34.7
Energy Costs		
Mean Round-trip Distance (km)	6	42
Mean Round-trip Flight Time (min)	8.5	61.0
Cost for Round-trip Flight (Joules)	13,388.8	87,864.0
Total Aggressions/Aggression Rate (n/h)	83/5.2	8/0.7
% Foraging Time Spent in Aggression	5	<1
Comparisons		
Energetic Efficiency (Input/Cost)	0.24	1.45
Foraging Time Needed to Recoup Flight Costs	34.9 min	42.1 min

seasonal pattern and pronounced individual differences in nesting activity and foraging decisions. These differences were most evident in the durations of food-provisioning flights, the distances flown to feeding sites, and rates of net energy intake. The decision of where to hunt for prey had consequences in terms of both time and energy. Birds that used nearby sites invested little time or energy for the 4-min flight from the colony, and could devote more time to prey capture. The energy expended to reach the weir could be recouped after about 30 min of typical foraging activity at the weir. Birds that used the weir typically stood atop exposed rocks and struck at fish from a fixed position. Kent (1987) showed that Snowy Egrets have a higher foraging efficiency while standing rather than walking, which might explain their attraction to the weir microhabitat. The decision to exploit nearby sites was not without its drawbacks. The short flight from the colony combined with high prey-capture rates attracted both Snowy Egrets and Great Egrets. However, there were few exposed rocks to serve as feeding spots, and high levels of aggression to defend a rock prevented most birds from remaining at the weir. Birds that lost encounters often flew to uncontested sites, which required additional time and energy. Kent (1986) showed that when Snowy Egrets engage in aggression with Little Blue Herons and Tri-colored Herons (*E. tricolor*), they incur reduced foraging efficiencies. The present study suggests that the same process might also operate on Snowy Egrets at the intraspecific level. Prey were captured at a higher rate at the weir and adjacent river but were about half as large and contained much less energy than prey caught at distant ponds. As a result, birds which foraged close to the colony had average rates of power input only about 20% that of birds that used distant sites.

Compared with birds which used the weir and river, Snowy Egrets who flew to distant ponds needed to forage for 20% longer just to recoup the energy expended for the flight (Brzorad *et al.* 2004; Maccarone and Brzorad 2007). However, once a bird reached a remote site, it encountered little competition and was able to attend to prey capture for the entire time. Despite the greater costs in time and energy associated with exploiting distant sites, egrets which used them had substantially higher rates of energy intake. We assume that an egret's foraging bout ends when its crop becomes full, or when some internal clock indicates it is time to return to the colony. Therefore, the fact that the distance to a site was not related to the length of a food-provisioning interval suggests that a short flight to a site with smaller prey and higher rates of aggression is less optimal than a longer flight to an uncontested site that yields more energy per unit time. Because reproductive success in waterbirds is tied closely to food-delivery rates (Burger 1982; Erwin *et al.* 1996; Bryan *et al.* 2005), intraspecific differences in habitat use, prey-capture rates, and energy gain might express themselves in nestling growth rates and chick survival.

Regression analysis detected a year-effect in all nest-activity categories except the time spent feeding chicks, which in both years accounted for <1% of the activity budget. Although the year-effect might be explained by the one-week difference between 2009 and 2010 in the schedule for nest observations, we believe that the difference reflected weather conditions during the breeding season. Records obtained from NOAA (www.crh.noaa.gov/ict/?n=records) show that the 2009 breeding season averaged about 2°C cooler and was more than 40% drier than in 2010. Ambient temperature has been shown to influence incubation patterns in different birds (Beintema and Visser 1989; Gresswell *et al.* 2002). In addition, heavy precipitation in 2010 during the early nesting season kept water levels elevated in the nearby rivers and streams for long periods. Rivers are a mainstay of egret foraging activity in this area (Maccarone 1993; Maccarone and Brzorad 2007). Water levels have been shown to affect foraging patterns in Snowy Egrets and other waterbirds (Frederick and Collopy 1989; Bryan *et al.* 2005).

In general, nest-activity patterns changed after eggs hatched and adults began to spend less and less time at the nest as food demand increased. Similar nest-activity patterns have been observed in other waterbird species such as White-naped Cranes (*Grus vipio*; Bradter *et al.* 2007), Wood Storks (*Myteria americana*; Bryan *et al.* 1995), Common Loons (*Gavia immer*; Evers 1994) and Great Egrets that nest in a nearby colony (Maccarone *et al.* 2010). Larger chicks may be less vulnerable to predation, can better maintain their body temperature and place much greater food demands on their parents. This combination of attributes might have selected for similar responses across different species.

Snowy Egrets engaged in low-cost activities such as incubating and sleeping while at the nest, but more energy-intensive activities such flying and foraging while away from the nest. Low-cost activities comprised about 15 h in a 24-h period, or 60%. When BMR (Paynter 1974) is multiplied by 1.3 to estimate energy costs (Kushlan 1977), nest activities accounted for only about 30% of daily energy costs. Because the duration food-provisioning trips varied widely, the median time of 230 min was used. A radio-tagged bird typically made two foraging trips per day, which would require it to spend about 8 h away from the nest. At a mean foraging distance of 16.1 km and at a mean velocity of 12.4 m/sec, provisioning trips would require 43 min of flight time each day and would cost about 65.4 kJ. Thus, when compared with low-cost nest activity, food-provisioning accounts for much less of the daily time budget, but on a per-unit basis is much more expensive. Although it was shown that Snowy Egrets continue to increase their time away from the colony as chicks grow, we were not able to support the prediction that adults respond to increased food demand by making briefer trips so that more trips can be made each day.

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