FORAGING STRATEGIES AND ENERGETIC COSTS OF FORAGING FLIGHTS BY BREEDING WOOD STORKS[1]

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Abstract. Wood Storks (*Mycteria americana*) were followed (*n* = 269) from their colony in east-central Georgia to foraging sites to examine the foraging travel strategies of these birds. Most sites were relatively close to the colony (median distance = 8.8 km) requiring short travel times (median time = 22.52 min). Directness ratios (total distance flown/direct distance) for 89 mapped foraging flights suggested that storks flew relatively straight paths to feeding areas. Comparison of flight (air) speeds determined from this data with speeds determined from energetics models suggested that storks minimized flight energy costs rather that maximized range during foraging travel. Estimated energetic costs of flapping and soaring modes of flight were 204.8 W and 18.1 W, respectively.

Seasonal analyses indicated that storks employed soaring flight more frequently in the latter half of the breeding season when they traveled to more distant sites. Energetic costs did not vary seasonally due to the increase in use of the energetically conservative soaring mode of travel on the longer flights. Observations at the colony indicated that foraging trip durations were constant throughout the season and that parents met increased nestling food demand by increasing the frequency of foraging trips.

Key words: Energetics; foraging strategies; flight; flapping; Mycteria americana; soaring; Wood Stork.

INTRODUCTION

For many avian species, travel to foraging sites can be an important component of an individual's time and energy budgets, particularly during the breeding season (Drent and Daan 1980). Distance to feeding areas and the selection of foraging sites can directly affect foraging travel time. Attendance requirements at the nest can also constrain travel time for breeding birds. However, parents must meet the increasing energetic demands of their growing young.

Wood Storks (*Mycteria americana*) are large wading birds that may fly as far as 130 km from their colonies to foraging sites (Kahl 1964, Ogden et al. 1978), although most sites were generally within 56 km of colony sites (Ogden 1986). The cost of travel can be energetically expensive for such large birds employing powered (flapping) flight (Pennycuick 1975, 1989). However, storks

may conserve energy by employing soaring/gliding flight when atmospheric conditions are suitable (Kahl 1971, Pennycuick 1975).

In an earlier study of Wood Stork foraging flights from a breeding colony in east-central Georgia, Bryan and Coulter (1987) noted that most flights were relatively short in distance and duration. Annual and seasonal differences in the use of flapping versus soaring modes of flight were also documented. To better understand foraging travel strategies of this species, we continued the initial study (1984–1986) through 1989. Also, recently developed models by Pennycuick (1989) were applied to these field observations (1984–1989) to estimate the energetic costs of the observed foraging flights. Finally, the number and duration of foraging trips for breeding storks, determined by observations of breeding pairs in the colony, were examined in relation to observed foraging travel characteristics.

The Wood Stork was declared an endangered species in February, 1984, due to population declines resulting from the loss or degradation of wetland habitats where storks forage (USFWS 1986). Wetland losses continue, perhaps at a level as high as 182,000 ha annually (USFWS 1989). The determination of foraging flight character-

istics, travel strategies, and estimated energetic costs of travel can provide important information necessary to assess the impact of wetland loss on the energetic costs associated with successful reproduction in this endangered species.

METHODS

STUDY AREA

The Birdsville Colony is located in a 540 ha Carolina Bay (Big Dukes Pond) in Jenkins County, Georgia (32°52′N, 82°03′W) (Coulter 1987). Wood Storks were followed in a fixed-wing airplane (Piper Supercub or Cessna 172) from the colony to foraging areas on 269 occasions from 1984 through 1989 by methods described by Bryan and Coulter (1987). During the flight, the amount of time (min) the stork used flapping and soaring modes of flight was recorded. The minimum direct distance from the site to the colony was determined with a Loran C navigational device. Total flight time (colony departure until the bird landed at a wetland) and the number of storks and other wading birds already present at the site when the followed stork arrived were also recorded. Many of these foraging sites ($n = 192$) were later sampled to determine the types, densities, and biomasses of prey available for storks. Sampling methods and characteristics of these foraging sites have been described by Coulter and Bryan (1993). Densities and biomasses of stork prey (primarily fish), or potential prey (Depkin et al. 1992), were considered in this study.

To determine average air speed for flapping and soaring modes of flight, wind speed and direction data from an airport in Augusta, Georgia (65 km NE of colony) were used to convert ground distance traveled to air distance. Air distances of complete flights and intervals of mapped flights in which >90% of the total flight time was either flapping or soaring flight were plotted against total flight time (or interval time) and the slopes of the regressions for both modes of flight were used as their average air speeds.

Computer programs available in Pennycuick (1989) were used to estimate a minimum power speed (V_{mp}) and a maximum range speed (V_{mr}). V_{mp} was the air speed at which the least amount of work was done (or fuel consumed) per unit time. V_{mr} was the air speed at which the least amount of energy was expended per unit distance (or fly as far as possible before the fuel was exhausted). These speed calculations were based,

in part, on morphological measurements from a single stork carcass: body mass (2.90 kg), wing span (1.78 m), and wing area (0.439 m²) (Museum No. SMNH 93-17, Scheile Museum, Gastonia, NC).

Energetic costs per unit air distance ($J \cdot m^{-1}$) were also estimated for flapping and soaring modes of flight by these programs (programs 1 and 2, respectively, in Pennycuick 1989). Both programs were run with default values of variables, as published. Flapping and soaring costs ($J \cdot m^{-1}$) were multiplied by the average speed ($m \cdot sec^{-1}$) of each mode to convert each cost to Watts ($W = J sec^{-1}$). For each flight to a foraging site, the costs were then multiplied by the number of seconds of each mode of flight, and the costs of both modes were added to calculate an estimated total cost (J).

DIRECTNESS OF TRAVEL

From 1986 through 1989, 89 foraging flights were mapped at 5-min intervals with Loran C to examine the directness of the paths storks take to their feeding areas. The combined lengths of these intervals was our estimate of the actual distance flown, or *total flight distance*. A *directness ratio* was calculated for each flight by dividing the total flight distance by the minimum direct distance between the colony and the foraging site. Flight modes used (flapping, soaring/gliding), total flight time, and site characteristics (direct distance, prey density, and the number of birds previously present) were recorded for these flights and related to the directness ratios.

FEEDINGS AT THE NEST

To assess how feeding visits to the nestlings were related to travel to sites, the duration of foraging trips and the number of such trips per hour were determined for storks tending nestlings in 1986–1989. Foraging trip duration from colony observations was defined as the amount of time an adult stork was away from a nest after an observed departure that later resulted in food being brought to the nestlings. Therefore, each trip would include travel time (outbound and inbound) as well as the time actually spent foraging and performing other activities. Foraging trip duration and number of trips per hour were compared between seasons (see below). Observations of parent storks were made from mid-March through mid-August from an 18 m tower in the

TABLE 1. Variation of Wood Stork foraging flight and site characteristics throughout the breeding season at the Birdsville Colony.

	April–May			June–July			
	n	Median	Range	n	Median	Range	Prob > Z[a]
Direct distance (km)	150	7.7	0.3–43.9	119	14.9	0.8–63.1	0.0001
Flight time (min)	150	18.8	1.3–121.0	119	30.5	2.6–181.6	0.0001
% Flapping flight[b]	150	52.4	0.0–100.0	119	21.8	0.0–100.0	0.0003
Estimated energetic cost (kJ)	150	87.5	15.6–895.0	119	102.2	9.6–645.5	0.0765
Number storks present	150	1.0	0–87	119	1.0	0–170	0.2614
Number other wading birds present	150	0.0	0–30	119	0.0	0–95	0.0163
Density of potential prey (items/m²)	109	2.7	0.07–79.50	77	2.8	0.07–249.8	0.6773
Biomass of potential prey (g/m²)	109	9.2	0.33–165.65	77	8.6	0.14–479.4	0.4487

[a] Comparison by Wilcoxon rank sum tests.
[b] Percent flapping values were arcsine transformed prior to analysis.

colony, approximately 11 hr/day, 5 days/week, during each of the four annual breeding seasons.

DATA ANALYSES

Flight characteristics examined included total flight time, flight speed, mode of flight, and estimated energetic cost of travel. Flight modes compared included *predominantly flapping* (flapped >90% of total flight time), *predominantly soaring* (flapped <10% of total flight time), and *intermediate* (all flights in-between). Foraging site characteristics examined included minimum direct distance from the colony, the number of storks and other wading birds already present at the site when the followed stork arrived, and the estimated density of potential prey.

Seasonal aspects of foraging travel and feedings at the nest were examined by comparing flight and foraging site characteristics in April–May with those in June–July. The April–May period represented the interval when most parents were either incubating eggs, or brooding young nestlings (< 4 weeks old). A minimum of one parent remains in attendance at the nest during this period (Kahl 1964). During the June–July period, a majority of the nestlings (> 4 weeks old) were generally left unattended by their parents.

Many of the flight and foraging site characteristics were not normally distributed, so nonparametric tests were used for all analyses. Kruskal-Wallis tests and Wilcoxon Rank Sum tests, calculated with PROC NPAR1WAY of SAS (1985), were used for comparisons. Spearman rank correlation coefficients (r_s) were used to determine the degree of relatedness of certain variables. Medians and ranges were presented for all characteristics. Means were presented ±1 standard deviation (SD) for some variables to allow for comparisons with other studies.

RESULTS

FLIGHT AND FORAGING SITE CHARACTERISTICS

The median flight time (outbound from colony) was 22.5 min ($\bar{x} = 31.8 \pm 29.4$ min, $n = 269$) in duration and ranged form 1.3 to 181.6 min. The median direct distance from the colony to stork foraging sites was 8.8 km ($\bar{x} = 12.0 \pm 10.6$ km, $n = 269$) and ranged from 0.3 to 63.1 km. Minimum direct distances were significantly correlated ($r_s = 0.887$, $P < 0.0001$) with flight times. Annual differences for flight time and minimum direct distances to sites were not significantly different ($P > 0.05$). Total flight times and minimum direct distance were either greater in June–July than April–May, or were not significantly different (Tables 1 and 2).

Seventy-six foraging trips (28%) were classified as predominantly flapping. Predominantly soaring flights ($n = 72$) made up 27% of all foraging flights and intermediate flights ($n = 121$) made up the remaining 45% of the flights. Storks using predominantly soaring flight visited foraging sites that were significantly further from the colony than sites visited after intermediate or predominantly flapping flights (Table 3). Predominantly

TABLE 2. Seasonal within-year trends of foraging flight characteristics of Wood Storks of the Birdsville Colony.[a]

Year	Direct distance (km)	Flight time (min)	Percent flapping[b]
1984	JJ > AM	JJ > AM	AM > JJ
1985	NS	NS	JJ > AM
1986	NS	NS	AM > JJ
1987	JJ > AM	JJ > AM	NS
1988	JJ > AM	JJ > AM	AM > JJ
1989	NS	NS	AM > JJ

[a] AM > JJ = values in the April–May period were significantly greater than values in June–July ($P < 0.05$); JJ > AM = values in the June–July period were significantly greater than values in April–May ($P < 0.05$); NS = no significant differences were found between values in April–May and June–July ($P > 0.05$).
[b] Percent flapping values were arcsine transformed prior to analysis by Wilcoxon rank sum tests.

soaring flights were also longer in duration than either intermediate or predominantly flapping flights.

Annual differences in the use of either flapping or soaring mode of flight were determined. Storks used flapping flight more frequently in 1985 and 1988 than in 1986 and 1987, and storks used flapping flight more frequently in 1989 than in 1987 (Table 4). The use of flapping flight in 1984 did not differ significantly ($P > 0.05$) from the use observed in the other five years. Seasonal differences were also determined, as storks generally used flapping flight more frequently in April–May than June–July (Table 1). Only in 1985 was the frequency of flapping flight greater in June–July than April–May (Table 2).

Storks or other wading birds were already present at 55% ($n = 146$) of the 269 sites visited by storks. However, numbers of storks (median = 1, range: 0–171) and other waders (median = 0, range: 0–94) found at these foraging sites were very small. Seasonal differences were determined for the number of other wading birds already present at the site (Table 1). In June–July, storks traveled to sites with greater numbers of other wading birds already present than in April–May.

Densities of potential prey at foraging sites were relatively low (median = 2.67 items/m²; $n = 168$), and ranged from 0.07–249.75 items/m² (see also Coulter and Bryan 1993). The median value for biomass of potential prey at sites was 12.3 g/m² (range: 0.28–479.43). Densities and biomass determined for sites found in April–May were not significantly different ($P > 0.05$) from sites found in June–July (Table 1).

DIRECTNESS OF TRAVEL

The median of the directness ratio (actual distance flown/direct distance) for 89 mapped foraging flights was 1.1 ($\bar{x} = 1.3 \pm 0.8$) (Fig. 1), indicating that storks generally fly direct routes to foraging sites.

Directness ratios were positively correlated with flight time ($r_s = 0.51, P < 0.0001$) and direct distance ($r_s = 0.24, P < 0.05$). Ratios were negatively correlated with the percent flapping flight ($r_s = -0.47, P < 0.05$) and number of storks already present at the site when the followed stork arrived ($r_s = -0.21, P < 0.05$). Directness ratios in April–May were not significantly different from those in June–July ($P > 0.05$).

FLIGHT SPEEDS AND ESTIMATED ENERGETIC COSTS

The average air speeds of Wood Storks, as determined from actual flights, using flapping and soaring modes of flight were 12.8 ± 0.6 m·sec⁻¹ ($n = 34, r^2 = 0.94$) and 9.5 ± 0.7 m·sec⁻¹ ($n = 72, r^2 = 0.71$), respectively. Pennycuick's (1989) model predicted that the minimum power speed (V_{mp}) for flapping Wood Storks was 12.1 m·sec⁻¹ and the maximum range speed (V_{mr}) was 19.7 m·sec⁻¹.

The estimated cost of flapping flight with no payload (additional weight attributed to food be-

TABLE 3. Direct distances from the colony and flight times of Wood Storks traveling to foraging sites in relation to modes of flight.[a]

	Predominantly flapping ($n = 76$)		Intermediate ($n = 121$)		Predominantly soaring ($n = 72$)		Prob > Z[b]
	Median	Range	Median	Range	Median	Range	
Direct distance (km)	5.3	0.3–34.5	8.9	0.9–51.1	15.2	0.9–63.1	0.0001
Flight time (min)	9.6	1.3–79.0	23.1	2.7–127.5	40.7	7.8–181.6	0.0001

[a] Modes of flight include: predominantly flapping (>90% of flight time), intermediate (flapped ≥10%, but ≤90% of flight time), and predominantly soaring (>90% of flight time).
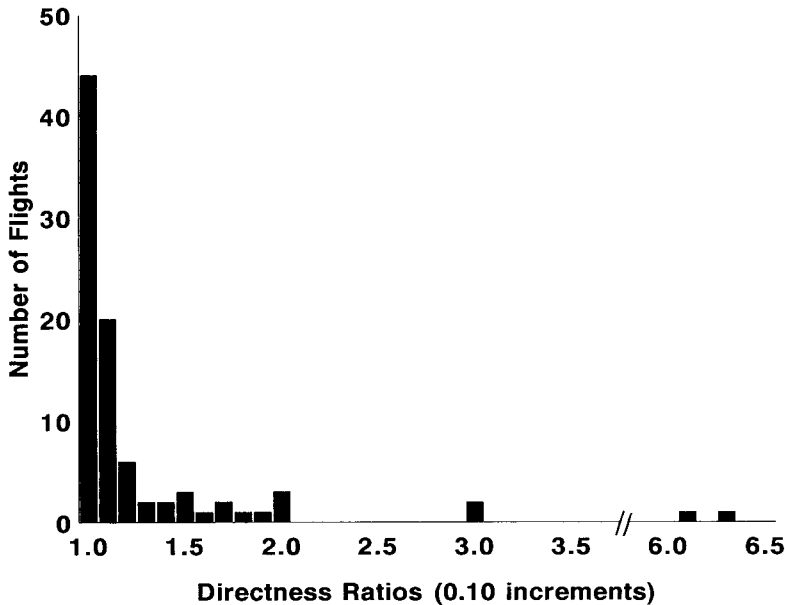[b] Comparison by a series of Wilcoxon rank sum tests.

FIGURE 1.   Directness ratios (actual distance flown/direct distance) of mapped Wood Stork foraging flights ($n = 89$) from the Birdsville Colony.

ing carried) was $16.0\,\mathrm{J\cdot m^{-1}}$ (air distance), or 204.8 W during flapping flight. Estimated soaring costs were $1.9\,\mathrm{J\cdot m^{-1}}$, or 18.1 W during soaring flight.

The application of these estimated costs of flapping and soaring flight to the entire dataset ($n = 269$) suggested that the median energetic cost of an outbound leg of a foraging trip was 96.6 kJ and ranged from 9.6 to 895.0 ($\bar{x} = 132.6 \pm 120.9$ kJ). The maximum cost occurred when a stork flew 79 min to a site 34.5 km from the colony using flapping flight 91.4% of the time. There was no significant difference ($P > 0.05$) in the amount of energy expended per foraging flight (outbound leg) in April–May as compared to flights in June–July (Table 1).

Interyear differences in estimated energy expenditure for foraging flights were determined (Table 4). Energetic costs per trip were significantly higher in 1984 and 1985 than in 1986, 1987, and 1988. Costs estimated for foraging trips in 1989 were not different from other years.

FEEDINGS AT THE NEST

The median duration of a foraging trip was 3.9 hr ($\bar{x} = 4.0 \pm 1.4$ hr; $n = 1{,}198$). Foraging trip durations in April–May were not significantly different from durations in June–July ($P > 0.05$; Table 5). The median number of feeding trips/ hr by individual storks to their nestlings was 0.09 ($\bar{x} = 0.11 \pm 0.06$; $n = 2{,}446$), or one foraging

TABLE 4.   Flapping flight utilization and estimated energetic costs of Wood Stork foraging flights from the Birdsville Colony.

Year	n	Percent flapping				Energetic cost (kJ)/trip			
		Median	$\bar{x} \pm$ SD	Range	Tests[a,b]	Median	$\bar{x} \pm$ SD	Range	Tests[b]
1984	52	27.8	45.1 ± 39.68	0.0–100.0	ABC	106.2	171.6 ± 156.0	21.3–645.5	A
1985	39	76.5	61.2 ± 40.07	0.0–100.0	A	156.5	183.3 ± 163.8	21.2–895.0	A
1986	48	21.7	37.3 ± 36.22	0.5–100.0	BC	86.6	105.3 ± 93.6	9.6–443.7	B
1987	44	20.5	33.0 ± 33.48	0.8–100.0	C	80.6	93.6 ± 69.4	20.3–390.6	B
1988	39	79.3	59.7 ± 41.40	1.8–100.0	A	105.7	101.4 ± 62.0	26.6–352.0	B
1989	47	47.9	52.2 ± 39.18	0.6–100.0	AB	94.0	136.5 ± 107.2	15.6–587.2	AB

[a] Percent flapping values were arcsine transformed prior to analyses with series of Wilcoxon rank sum tests.
[b] Years with the same letter were not significantly different.

TABLE 5. Seasonal comparisons of foraging trip duration[a] and number of foraging trips/hr of Wood Storks as determined by observations in the Birdsville Colony.

	April–May				June–July				Prob $> Z$[b]
	n	Median	$\bar{x} \pm SD$	Range	n	Median	$\bar{x} \pm SD$	Range	
Foraging trip duration (hr)	401	3.9	4.0 ± 1.56	0.5–8.7	797	3.9	3.8 ± 1.53	0.5–9.2	0.4087
Number of foraging trips/stork/hour	811	0.09	0.08 ± 0.053	0.0–0.42	1,782	0.09	0.11 ± 0.068	0.0–0.42	0.0001

[a] The duration of a foraging trip was defined as the amount of time an adult stork was away from the nest after an observed departure that resulted in food being brought back to the nestlings.
[b] Comparison by Wilcoxon rank sum texts.

trip every 11 hours. Storks made a significantly greater ($P < 0.05$) number of feedings trips/hr in June–July than in April–May (Table 5).

DISCUSSION

Breeding Wood Storks in east-central Georgia generally traveled to foraging sites near the colony which required relatively short travel times. Overall, both flapping and soaring modes of flight were utilized an equal amount of the time; however, in a single flight a stork tended to use one mode predominantly. Storks traveling to more distant sites used soaring flight more frequently than flapping flight. In the latter half of the breeding season, storks traveled to more distant sites, had longer flight times, and used soaring flight more often than in the early half of the breeding season.

Few annual differences were found among flight and site characteristics. In all years except 1985, the amount of flapping flight utilized either decreased as the season progressed or remained the same. Atmospheric conditions for the development of convective currents used by soaring birds are generally better in the late summer months (Critchfield 1974) so an increase in the use of soaring might be expected. However, in 1985 the amount of flapping flight was greater in the latter half of the season. Atmospheric conditions resulting in fewer late-season thermals were not apparent that year, but the occurrence and strength of thermals was not studied. Bryan and Coulter (1987) suggested that the late season increase in flapping flight in 1985 was due to storks using flapping flight to return to previously used sites. There was a drought-related shortage of foraging areas in 1985. However, 1988 was also a drought year in which many storks were followed to the same sites, but flapping flight was not found to increase seasonally that year.

Foraging travel can be affected by the prox-

imity of the foraging areas to the colony. Satellite imagery analyses of the region surrounding the Birdsville Colony indicated that at least 20% of that region was shallow wetland and, therefore, potential foraging habitat (Coulter et al. 1987). The short travel distances reported in this study could be a result of this abundance of potential habitat. Storks breeding in southern Florida have been documented foraging at sites 130 km from their colony (Ogden et al. 1978).

Attendance and feeding requirements at the nest could limit the amount of time parent storks can spend on a foraging trip. One might expect the durations of foraging trips to increase as nestlings grow and require more food. However, foraging trip durations did not increase significantly from April–May to June–July. Later in the season, most nestlings were ≥ 4 weeks old and were left unattended. It appears that parents met the increased demand for food by foraging simultaneously and by individual parents increasing the number, rather than the duration, of foraging trips.

The travel time to foraging sites increased seasonally even though foraging trip duration, as observed in the colony, did not. This suggests that the storks were spending less time actually foraging for prey later in the season. Doubling the median one-way flight time to foraging sites to roughly estimate total travel time for a single trip indicated that travel consumed approximately 16% of the time used during a foraging trip in April–May, compared with 26% in June–July. Kahl (1964) stated that the Wood Stork breeding season in southern Florida coincides with a period of decreasing water levels and prey items should be concentrated in smaller-sized wetlands later in the season. Less time would therefore be needed to acquire prey later in the season. However, while the breeding season in east-central Georgia also coincides with the sum-

mer drawdown of wetlands (Coulter 1987), prey densities and biomasses at foraging sites visited in June–July were not greater than at sites visited in April–May.

Wood Storks using flapping flight flew near the minimum power speed, which required the least amount of energy per unit time, and implied that the birds were willing to sacrifice travel time to save energy. Pennycuick and DeSanto (1989) suggested that birds searching for food would occasionally fly at, or below, the minimum power speed. Storks employing soaring flight used only one-tenth the amount of energy of flapping, but also at the expense of time. Even though the direct distance flown to foraging sites increased seasonally, the total energetic cost per trip did not. This was a result of the increase in soaring flight used as the season progressed. Annual differences in median cost per foraging trip were significantly different, but the greatest difference (1985 and 1987, Table 4) was equivalent to only 76 kJ, or 2 g of pure fat (Pennycuick 1989), per trip.

Kahl (1964) conservatively estimated that Wood Storks must ingest 2,390 kJ daily to maintain their free-flying metabolism. Doubling the median energetic cost (96.6 kJ) for an outbound leg of a foraging flight to approximate a round-trip cost suggests that storks expend only 8.1% of their daily intake on a foraging trip. The estimated energetic cost of travel to foraging sites is thus relatively low, due to the availability of foraging areas close to the colony, the stork's ability to choose their mode of flight when atmospheric conditions are suitable, and their ability to use convective current soaring to minimize the energetic costs of travel. Although the energetically conservative method of flight increases the time spent in travel, the time lost is not costly if it allows the storks to choose "better" sites with either more prey which can be captured in a shorter period of time, or less competition for the available resources at the site.

The energetic estimates were based only on the measurements of a single stork carcass. These measurements were within the range of measurements for wing span (165–179 cm) and mass (2.05–3.30 kg) listed by Hancock et al. (1992). Energetic costs associated with flapping flight for the smallest and largest storks listed were estimated (Program 1, Pennycuick 1989) to be 125.97 W (0.0032 g fat·sec⁻¹) and 240.79 W (0.0062 g fat·sec⁻¹), respectively. Soaring costs for the smallest and largest storks listed were estimated as 12.75 W (0.0003 g fat·sec⁻¹) and 18.71 W (0.0005 g fat·sec⁻¹), respectively (Program 2, Pennycuick 1989). Wing areas used in these estimates were calculated under the assumption that wing area and wing span were directly proportional. Smaller, lighter storks should be able to fly with less energetic cost than larger, heavier storks, although the estimated energy expenditure by even the largest Wood Stork is probably just a minute portion of its total energy budget.

Approximately 50% of the foraging sites selected by followed Wood Storks had storks or other wading birds already present, although these birds were usually present in low numbers. Wading bird use of social, or aggregate, foraging is well documented as a method of efficient utilization of ephemeral food resources (see review in Kushlan 1981). The low amount of social foraging observed here could be another result of the abundance of potential foraging areas near the colony, where foraging in large flocks may not be the most efficient method (Coulter and Bryan 1993).

Wood Storks generally travelled a relatively direct path to their foraging areas, implying that a straight-line path was the best method for searching for a site, the nearness of the foraging sites reduced the likelihood of circuitous travel, or perhaps that these storks were returning to previously used foraging areas. The few circuitous flights observed tended to be to more distant sites, had long durations, used more soaring flight, and visited sites with fewer storks already present. It is possible that these storks either were not breeding birds with the time constraints associated with nestlings in the colony, were birds searching for strong convective currents for soaring, or were willing to deviate from a straight-line route in order to gain more altitude in strong thermals.

Foraging travel strategies of Birdsville Colony Wood Storks appear to conserve energy through the utilization of locally abundant wetlands, to utilize convective current soaring whenever atmospheric conditions are suitable, and to meet the increasing need for food by nestlings by increasing the frequency of foraging trips as the breeding season progresses and nest attendance requirements decrease. Potential foraging areas around this inland colony are sufficiently close to allow the parents to conserve energy at the expense of travel time. The energetic cost of for-

aging travel from the Birdsville Colony was generally so low that occasionally flying less direct paths was probably not an energetic liability for these birds. However, in areas where storks must consistently travel greater distances to acquire food for their nestlings, such as southern Florida, the continued loss of local wetland food sources could disrupt the time and energy budgeting for this endangered species and possibly result in increased stress on breeding storks and reduced reproductive success.

ACKNOWLEDGMENTS

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