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# HUNTING BEHAVIOR, PREY SELECTION, AND ENERGETICS OF SNAIL KITES IN GUYANA: CONSUMER CHOICE BY A SPECIALIST

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**ABSTRACT.**—The hunting behavior, snail size selection, and time-activity patterns of non-breeding Snail Kites (*Rostrhamus sociabilis sociabilis*) were studied in Guyana rice fields. Kites spent 62% of the photoperiod perching, 19% foraging, 13% in maintenance activities, and 6% flying. As the day progressed, the percentage of daylight hours spent perching increased significantly, while foraging decreased significantly. Kites successfully captured and ingested *Pomacea* snails in 78% of the foraging bouts observed. The mode of hunting was evenly split between coursing (50.7%) and still-hunting (49.3%). Searching and returning times were related to time of day, as significantly more coursing hunts and still-hunts occurred in mornings and late afternoons, respectively. Prey handling time was the most time-consuming component of a foraging bout. Time spent searching for prey, returning, or handling prey was not related to snail size. The size distribution of captured snails differed significantly from that of available snails; kites selected more medium snails and fewer small snails and took large snails in equal frequency to that at which large snails were available. Kites captured the same-sized snails when coursing as when still-hunting. As rice grew, kite utilization of rice fields declined, and the frequency of still-hunting decreased while course-hunting attempts increased. The daily caloric intake of kites was estimated to be 104.2 kcal, the daily energy expenditure 85.7 kcal. Results are discussed in relation to consumer choices of specialists. The most important decision a foraging Snail Kite may make is what patch to search in and how long to search before abandoning patches. *Received 14 January 1982, accepted 28 June 1982.*

LITTLE is known about the hunting behavior and foraging ecology of the Snail Kite (*Rostrhamus sociabilis*). Long recognized as an extreme diet specialist, the Snail Kite feeds almost exclusively on *Pomacea* snails (Haverschmidt 1962, Snyder and Snyder 1969, Voous and van Dijk 1973; for exceptions see Sykes and Kale 1974, Beissinger in prep.). A kite captures a snail by flying over a marsh, extending a foot, and grabbing the mollusc with long toes near the water surface. It then perches in order to extract the body from the shell with its thin, sharply hooked bill. Two modes of hunting have been observed (Snyder and Snyder 1969, Haverschmidt 1970): "still-hunting" kites visually search from a perch and capture a snail near that perch after a short flight; "course-hunting" kites fly 3–5 m above a marsh, usually facing into the wind, visually searching until a capture occurs. Snyder and Snyder (1969) and Voous and van Dijk (1973) described in

detail how kites extract and consume snails, but there is no quantitative information on the behavior and energetics of kite foraging. In this paper, I describe the foraging ecology of the Snail Kite (*R. s. sociabilis*) on the basis of field observations of hunting behavior, activity patterns, and prey selection in rice fields in Guyana, South America.

## STUDY AREA AND METHODS

Studies were conducted from July–August 1977 at the Rice Research Station and surrounding rice fields on the coastal lowlands (1.4 m below sea level) at the Mahaicony and Arbarly Rice Development Scheme (MARDS), Burma, Guyana, South America (6°28'N, 57°45'W). The freshwater marshes or mangroves that once covered this region have been almost totally replaced by rice cultivation (6,721 ha in 1976; Kennard pers. comm.), with few fields remaining fallow. There are two rainy and two dry seasons (Cummings 1965). Rainfall during the study period totaled 14.76 cm in July, the end of the long rainy season, and 3.84 cm in August, the onset of the short dry season. Daily minimum and maximum temperatures ranged from 22–31°C. For a more detailed description of the study area, see Giglioli (1959), Osborne and Bourne (1977) and Bourne and Osborne (1978).

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A 26-ha study site of seven fields was selected for behavioral observations of kites. Strip censuses of Snail Kites and Limpkins (*Aramus guarana*) were made one to five times weekly from 0700 to 0800. Fieldwork was initiated near the time of sowing. Rice had reached full height by the end of the study 6–8 weeks before harvest.

I marked 14 fence posts on the border between two fields and cleared the surrounding area of old snail shells so that I could sample the size of snails selected by kites. As many as 14 kites were observed foraging from these posts during strip censuses but four was the average. Posts were selected because of easy accessibility and use by foraging kites. Fence posts ranged from 7 to 17 cm in diameter and 1 to 1.5 m high. Empty snail shells were collected from beneath each post on 14 occasions with periods of 24–48 h between collections. Aperture length was measured to the nearest millimeter, and after one week three size classes were delineated: small (11–24 mm), medium (24–28 mm), and large (29–36 mm).

I attempted to estimate the relative abundance of the three size classes of snails in the two fields from late July through early August. Because water turbidity was great, I could not detect snails visually. I collected snails by walking or crawling a transect through the field, tactily searching the mud and plant surfaces with both hands. A total of 20 h was spent sampling snails in kite feeding areas. Thirty-four of these snails (13 large, 9 medium, and 12 small) were collected for caloric analyses. After extraction from the shell, albumen glands were discarded (as kites do not generally ingest them; see Snyder and Snyder 1969), and each snail was oven dried for 28 h at 100°C, when dry weight became constant. Ten snails were individually ground in a Wiley Mill, and caloric determinations were made on 40-mg samples of each through use of a Phillipson Microbomb calorimeter.

I monitored Snail Kite activities by observing focal individuals (Altmann 1974) chosen at random for 15-min periods from 20 to 75 m away through spotting scope and binoculars. As there was no breeding colony of kites in the vicinity and kites that were observed extracted and ate snails in the study area, none of the focal individuals was assumed to be breeding during the time of the study. Activities were recorded directly into a tape recorder and later timed to the nearest second with a stop watch. Three time periods were chosen a priori to homogenize air temperature trends within periods (morning: from sunrise at 0630 to 1100; midday: from 1100 to 1500; and late afternoon: from 1500 to 1830, just before sunset). A total of 60 focal samples was distributed almost evenly throughout the daylight hours (morning 19, midday 21, late afternoon 20). I tried not to sample the same kite more than once a day by sampling during only one time period a day.

Activities were categorized as follows. (1) Perched

birds were sitting upon a fence post, vegetation, or mudflat. It was not possible to determine reliably whether perched birds were engaged in searching activities (i.e. still-hunting), and no attempt was made to separate perched birds into those searching or those not searching for snails. Thus, still-hunting kites visually searching for prey while perched were included in this category. (2) Maintenance activities included preening, scratching, feather ruffling, wing stretching, wing drying, and bill cleaning. (3) Flying was defined as movements for the purpose of changing location of perches or hunting areas, as well as flights to or from roosting areas. (4) Aggression was observed mainly in the form of the supplanting of one individual by another or by active chasing of another kite. Finally, (5) foraging included all activities associated with the capture and ingestion of snails. A foraging bout was composed of searching (flight in the pursuit and capture of snails, including both coursing and still-hunting), returning (flight from the point of capture to any perch where the prey was consumed), and handling (the extraction of a snail from its shell and ingestion). The time between foraging bouts ("between") was calculated as the amount of time that elapsed between ingestion of a snail and the initiation of the next searching flight. For each capture clearly observed (79% of the captures), I visually estimated the snail size class. From experience gained while measuring over 1,000 snail shells, I usually was able to estimate the aperture length within 1 mm. A comparison of my estimate of the distribution of snail size classes that kites fed upon during periods of behavioral observation and the distribution of snails collected beneath feeding perches revealed no significant difference ( $\chi^2 = 0.94$ ,  $df = 2$ ,  $0.50 < P < 0.70$ ). This supported my ability to assign captured snails correctly to the three size classes.

Statistical analyses were conducted using parametric procedures on the Statistical Analyses System (S.A.S.) at Miami University and Wayne State University. Assumptions of normality and homoscedasticity of parametric models were tested by inspecting scatter and residual plots, skewness and kurtosis coefficients, and comparing sample variances. Non-parametric statistics were used when assumptions were violated. Because percentage data were not normally distributed and often outside the 30–70% interval, they were arcsine transformed before analyses. Differences were designated as significant if  $P < 0.05$ .

## RESULTS AND DISCUSSION

*Daily activity.*—Snail Kites usually arrived individually at foraging stations, presumably from a communal roost to the north, between dawn (0630) and 1100, with occasional arrivals or departures during the course of the day.

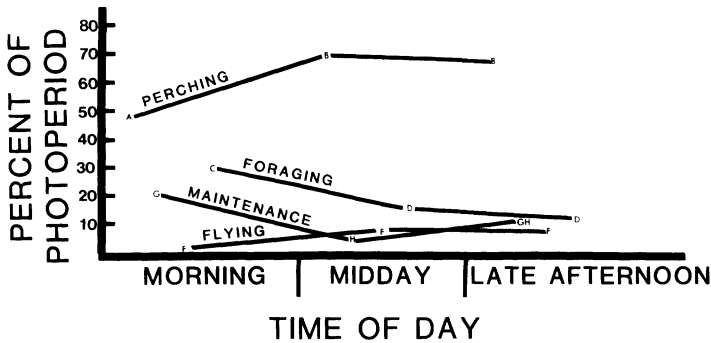


Fig. 1. The activity pattern of Snail Kites in Guyana rice fields relative to time of day. Different letters within activity types indicate significant differences between time period means as tested by Duncan's Multiple Range test.

Twice, I observed group movements away from the study area during the day. It appeared, however, that most of the individuals foraging in the area remained there for the entire day until departing for the roost again 0.5–1 h before sunset. Although kites were not individually marked, certain fence posts were consistently occupied during some periods of the study, perhaps by the same individual.

The diurnal activity pattern of Snail Kites is presented in Fig. 1. Kites spent the majority of the daylight hours perching (62%), followed by foraging (19%), maintenance (13%), and flying (6%). Less than 0.1% of the photoperiod was spent in aggressive behavior, which was observed only twice during the 60 sampling periods. Although aggression associated with feeding territories has been occasionally observed in Florida (Snyder and Snyder 1970), I saw no evidence of this in Guyana. Because aggressive behavior was a minor proportion of Snail Kite activities, it was excluded from the remainder of the analyses in this paper.

Activity patterns changed with time of day: the percentage of photoperiod spent perching increased significantly from morning to midday and late afternoon, while foraging decreased significantly during this time (Fig. 1). As it was not possible to determine reliably whether a perched kite was searching visually for prey (still-hunting) or simply resting, all perched kites were assumed to be resting, which resulted in lower foraging and increased resting values. This bias does not apply to energy budgets constructed later from these data, however, as the energetic cost of perching and

perching while visually searching are nearly identical (King 1974).

Despite fluctuations during the day in the amount of time spent in maintenance and flying activities, no statistically significant trends were noted (Fig. 1). Maintenance was highest in the morning, most likely in response to frequent morning rainstorms. Morning values for flying were lowest but would have been higher if flights from the roost to the foraging grounds could have been observed.

*Hunting behavior.*—I observed 74 foraging bouts by kites, and 82% of these were successful. All food items were *Pomacea* snails. In only 78% of the bouts was the snail completely ingested, however, as kites dropped snails three times during the process of handling them on a perch. On one of these occasions, a young-of-the-year kite (identified by plumage characteristics; Haverschmidt 1968) had difficulty perching with the snail in its talons, a behavior often seen in young kites in Florida (pers. obs.). I do not know in the other two cases whether the snails were rejected purposely (e.g. a capture of an empty shell) or dropped accidentally. In summary, Snail Kite predatory efficiency was similar to the mean value of 73% that Collopy (MS) noted for other invertebrate-eating birds, the most successful avian predators, but much higher than he found for fish-eaters (45%) and those hunting primarily mammals (27%) or birds (8%). When snails were available, kites had little trouble capturing them.

Both hunting modes were equally employed by kites: 50.7% of the foraging bouts observed were coursing hunts and 49.3% were still-

TABLE 1. Descriptive statistics for the components of a Snail Kite foraging bout.

Foraging components	Number of observations	$\bar{x} \pm SD$ (s)	Range (s)	$\bar{x}\% \pm SD$ (s) of complete bouts
Coursing				
Searching	36	88 $\pm$ 69	16–303	44 $\pm$ 13
Returning	28	17 $\pm$ 15	1–79	11 $\pm$ 8
Handling	27	73 $\pm$ 27	32–150	45 $\pm$ 12
Still-hunting				
Searching	35	4 $\pm$ 4	1–13	5 $\pm$ 5
Returning	30	4 $\pm$ 3	1–12	7 $\pm$ 5
Handling	33	66 $\pm$ 34	21–200	88 $\pm$ 7
All hunts				
Searching	71	47 $\pm$ 64	1–303	24 $\pm$ 21
Returning	58	11 $\pm$ 12	1–79	9 $\pm$ 7
Handling	60	69 $\pm$ 31	21–200	67 $\pm$ 23
Between	43	146 $\pm$ 172	10–710	—

hunts. In Florida, young kites have been observed to still-hunt, but adults rarely do so except in times of food stress during regional drought, when kites are forced to forage along woody lake margins or along canals (Snyder and Snyder 1969, Beissinger in prep.). Snyder and Snyder (1969) attribute the high incidence of still-hunting by kites in Guyana to the availability of more suitable perches along rice fields and canals. The hunting success of both methods was similar, as 81% of 36 coursing-hunt attempts and 83% of 35 still-hunt attempts were successful.

Descriptive statistics associated with the components of a Snail Kite foraging bout are summarized in Table 1. The mean searching time for coursing hunts was 22 times more than for still-hunts, but this was partly due to the manner in which these parameters were measured, concealing still-hunt searching time within perching time and thus disproportionately lowering searching times for still-hunts. In comparison to the other components of a foraging bout, prey handling was the most time consuming. For all hunts, handling constituted an average of nearly 68% of a bout. Even the handling time for coursing hunts (45.2%), which may be the most meaningful value because searching time is totally measured, indicated that handling a snail is as time consuming as finding one.

The amount of time spent searching and returning by kites was related to the time of day (Table 2). When observations of both hunting modes were pooled, mean searching and re-

turning times decreased significantly throughout the day. Searching times for coursing hunts showed a similar but not significant trend. Decreased search times probably were related primarily to the proportion of still-hunts and coursing hunts that occurred in the three time periods: 58% of the coursing hunts occurred in the morning, while 46% of the still-hunts occurred in the late afternoon (from Table 2). The distributions of still-hunts and coursing hunts throughout the three time periods were significantly different ( $\chi^2 = 9.38$ ,  $df = 2$ ,  $P < 0.01$ ). Three explanations could account for this shift in foraging mode: (1) as ambient air temperature increased during the day, the costly exertion of long coursing flight was avoided because the energetic requirements for flight increase proportionally with increases in ambient air temperature (Kendeigh et al. 1977); (2) by coursing in the morning, Snail Kites may have been investing time exploring the prey base of the chosen foraging patch, a tactic reported for other avian predators (Smith and Sweatmen 1974, Davies 1977); and/or (3) with increasing water temperature, snails become more active (McClary 1964) and inspire near the water surface more often, increasing the encounter rate (and still-hunting success) for perching kites. Neither handling time nor time between captures (a measure of feeding rate) showed any significant trends in relation to time of day (Table 2).

No significant differences were found in the amount of time required for foraging-bout components in relation to snail size (Table 3).

TABLE 2. Variation in the components of a Snail Kite foraging bout during three time periods.

Foraging component	Mean $\pm$ SE ( <i>n</i> ) s by time of day			<i>p</i> <sup>a</sup>
	Morning	Midday	Late afternoon	
<b>Coursing</b>				
Searching	95 $\pm$ 16 (21)	94 $\pm$ 27 (8)	60 $\pm$ 14 (7)	0.628
Returning	17 $\pm$ 2 (20)	24 $\pm$ 14 (5)	8 $\pm$ 4 (3)	0.245
Handling	69 $\pm$ 5 (19)	70 $\pm$ 11 (5)	101 $\pm$ 25 (3)	0.462
<b>Still-hunting</b>				
Searching	4 $\pm$ 2 (9)	6 $\pm$ 1 (11)	2 $\pm$ 1 (15)	0.107
Returning	4 $\pm$ 1 (8)	6 $\pm$ 1 (9)	4 $\pm$ 1 (13)	0.282
Handling	57 $\pm$ 4 (10)	90 $\pm$ 19 (9)	58 $\pm$ 5 (14)	0.708
<b>All hunts</b>				
Searching	68 $\pm$ 14 (30)	43 $\pm$ 15 (19)	21 $\pm$ 7 (22)	0.020
Returning	13 $\pm$ 2 (28)	12 $\pm$ 5 (14)	4 $\pm$ 1 (16)	0.003
Handling	65 $\pm$ 4 (29)	83 $\pm$ 13 (14)	65 $\pm$ 7 (17)	0.734
Between	122 $\pm$ 66 (21)	160 $\pm$ 55 (10)	175 $\pm$ 66 (12)	0.448

<sup>a</sup> Significance levels based on Kruskal-Wallis test (Chi-square approximation).

Searching and returning times decreased relative to snail size, but this was not statistically significant. The trend of decreased search times for larger snails seems to run counter to the potential encounter rate, which would be lower for the less common, larger snails (Fig. 2). The possibility that kites foraged by searching for larger snails but took smaller snails after a time without capture in order at least to stay even with energy expenditures might account for the shorter searching times observed for less common, larger snails. For all hunts, handling time was very consistent, with a mean for the three size classes of 67 s. Because the cost in

time (and presumably energy) required to find a snail, return to a perch, and extract and ingest the snail did not differ significantly for snails of different sizes, the profitability of a snail can be defined merely by its total energetic value (Krebs 1978, Schoener 1979).

An interaction between time of day and snail size might have been responsible for the outcome of the above results. Despite not meeting the assumption of normality, a two-way analysis of variance (ANOVA) model was constructed to test for interaction. One-way ANOVA models were examined simultaneously with the Kruskal-Wallis tests previously re-

TABLE 3. Variation in the components of a Snail Kite foraging bout in relation to the size class of snail captured.

Foraging component	Mean $\pm$ SE ( <i>n</i> ) s for snail size			<i>p</i> <sup>a</sup>
	Small	Medium	Large	
<b>Coursing</b>				
Searching	78 $\pm$ 15 (8)	54 $\pm$ 9 (10)	53 $\pm$ 21 (2)	0.402
Returning	15 $\pm$ 3 (8)	17 $\pm$ 3 (10)	7 $\pm$ 2 (2)	0.336
Handling	60 $\pm$ 6 (8)	65 $\pm$ 11 (10)	93 $\pm$ 6 (2)	0.168
<b>Still-hunting</b>				
Searching	6 $\pm$ 2 (8)	3 $\pm$ 1 (9)	3 $\pm$ 1 (6)	0.245
Returning	6 $\pm$ 1 (8)	4 $\pm$ 1 (9)	4 $\pm$ 1 (6)	0.507
Handling	72 $\pm$ 16 (10)	71 $\pm$ 9 (10)	58 $\pm$ 4 (6)	0.440
<b>All hunts</b>				
Searching	42 $\pm$ 12 (16)	30 $\pm$ 8 (19)	16 $\pm$ 9 (8)	0.340
Returning	10 $\pm$ 2 (16)	11 $\pm$ 2 (19)	4 $\pm$ 1 (8)	0.200
Handling	66 $\pm$ 9 (18)	68 $\pm$ 7 (20)	67 $\pm$ 6 (8)	0.604
Between	131 $\pm$ 51 (10)	145 $\pm$ 52 (12)	259 $\pm$ 119 (6)	0.444

<sup>a</sup> Significance levels based on Kruskal-Wallis test (Chi-square approximation).

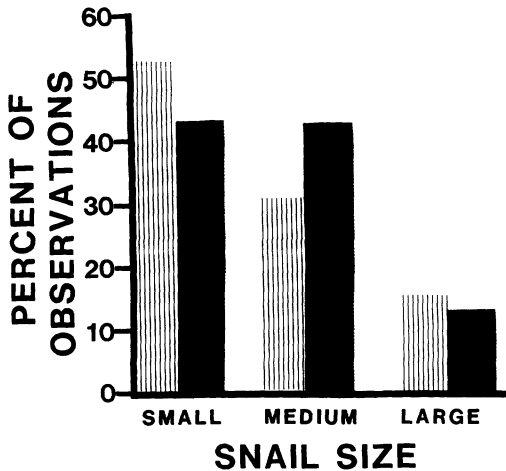


Fig. 2. The sizes of *Pomacea dolioides* potentially available (striped bars) to Snail Kites and sizes taken (dark bars).

ported (Tables 2, 3), and in all cases parametric and nonparametric tests yielded similar values. From the two-way ANOVA model, there was no evidence that a time of day and snail size interaction occurred for searching ( $F = 0.70$ ,  $P = 0.596$ ) or returning times ( $F = 0.07$ ,  $P = 0.991$ ).

*Snail size selection.*—I collected 959 *Pomacea* shells that had been eaten by kites. Over 99% of the snails were *Pomacea dolioides*; *P. glauca* composed the remainder of the sample. Snyder and Snyder (1969) also noted Snail Kites in Guyana feeding heavily on *P. dolioides* near the water surface and rarely upon *P. glauca*, a less abundant and more aquatic bottom dweller.

From transect searches, I collected 155 *P. dolioides* to serve as a sample of the size distribution of snails potentially available to kites. Figure 2 compares the sizes of snails available and those chosen by kites. There was a significant difference between the frequency of size classes available to kites and those selected ( $\chi^2 = 7.632$ ,  $df = 2$ ,  $P = 0.022$ ). It appears that Snail Kites avoided the more abundant small snails, preferred the medium sized snails, and took the large snails in approximately equal frequency with those that were available.

Because snails are captured by kites on the wing, snail availability is a function of: (1) snail density; (2) snail depth below the water surface; (3) the effects of water temperature and dissolved oxygen on *Pomacea* inspiratory and surfacing behavior (McClary 1964, Freiburg

and Hazelwood, 1977); and (4) the density of vegetation covering the water surface. I sampled snail availability in a manner that assumed that factors affecting availability act similarly on all sizes of snails. If not, then the size distribution of snails that was collected from the field might not be the same as that available to kites. For instance, large snails may be less vulnerable to predation, because they may have respiratory rates that are less affected by changing water temperatures, causing them to surface less often, or they may frequent dense vegetation more often than small snails.

The choice of snail size could be affected by one other factor—snail parasite loads. Grossman and Hamlet (1964) state that kites are infected by "lung flukes" carried by *Pomacea* snails but offer no direct evidence of parasitism or references. At least eight trematode species are described from *Pomacea* snails, and birds are definitive hosts in all three cases where life histories are known (Nasir and Rodriguez 1969; Nasir et al. 1969a, b; Nasir and Silva 1972; Gascon 1975; Hanning and Leedom 1978). Gigantism, increased shell thickness, and shell abnormalities in molluscs sometimes result from parasitism (Cheng 1971, Hanning 1978) and might offer kites a mechanism to reject highly parasitized individuals. Because parasitic loads do increase with snail size in *Pomacea paludosa* (Hanning 1978), kites may not have taken large snails more often in order to avoid higher infection rates.

Coursing hunts require far more flying, a very energetically expensive activity (Table 4), than do still-hunts. Course-hunting Snail Kites would be expected to choose larger snails in order to gain a greater energetic payoff to offset increased costs (Schoener 1969, 1979), especially as searching time is unrelated to snail size. No differences in the distributions of snail size classes selected by coursing or still-hunting kites occurred when all three size classes were considered ( $\chi^2 = 1.85$ ,  $df = 2$ ,  $0.60 < P < 0.70$ ) or when medium and large size classes were combined and tested against small ( $\chi^2 > 0.750$ ,  $df = 1$ ,  $P > 0.750$ ).

*Effects of rice growth.*—Figure 3 illustrates the declining use of rice fields by Snail Kites during the study period. When rice fields were drained, kite numbers were highest. As irrigation and rice growth commenced, kite use significantly declined, until no birds were observed in mid-August. A highly significant

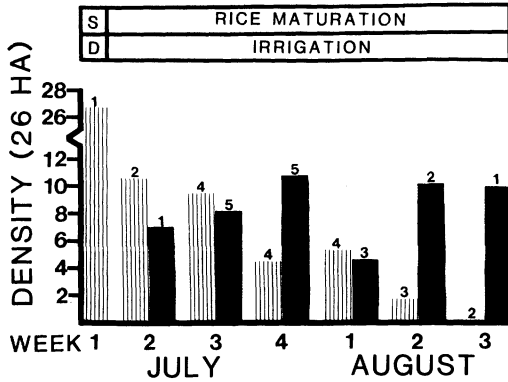


Fig. 3. Weekly mean density of Snail Kites (striped bars) and Limpkins (dark bars) determined by strip censuses in Guyana rice fields. The number of weekly counts appears above each bar. Upper horizontal bars indicate the duration of sowing (S), rice growth and maturation, drainage (D), and irrigation.

( $P = 0.002$ ,  $r^2 = 0.747$ ,  $n = 20$ ) linear correlation between daily counts and week was found for Snail Kites but not for Limpkins ( $P = 0.620$ ,  $r^2 = 0.125$ ,  $n = 18$ ). As rice grows, foraging becomes more difficult for kites because: (1) the area of water surface that a kite can visually scan while hunting decreases and (2) to make a capture, a kite's descent to the water must be unhindered by vegetation. For effective foraging, Snail Kites need sizeable patches of open water with floating but not tall emergent vegetation. Limpkins are able to search tactilely for *Pomacea* snails while wading (Snyder and Snyder 1969) and can forage successfully in heavily vegetated areas. In the study area, they utilized fallow fields until rice reached approximately a 0.5-m height.

Assuming relatively stable snail populations, snail availability should decrease as rice grows, and the encounter rate of still-hunting kites should decrease. In response, Snail Kites should course-hunt more often to increase encounter rates by searching a greater area. To test this, I examined the proportion of still-hunts that occurred during the first 2 weeks of behavioral observations, when rice was absent or low, and the last 3 weeks, when rice was highly emergent. Because hunting mode was related to time of day, I used only the 24 hunts that occurred in the late afternoon, when still-hunting was most frequent for this analysis. The proportion of coursing hunts increased

TABLE 4. A simplified energy budget for nonbreeding Snail Kites. Equation 10 from Koplín et al. (1980) was used to calculate energy cost, assuming an average daily air temperature of 27°C (pers. obs.) and a mean body weight of 367.6 g, the mean of seven observations from Haverschmidt (1968, 1970), and specimens from the Museum of Zoology, University of Michigan.

Activity	Proportion of 24-h day	Energy cost (kcal)
Nonflight	0.945	59.1
Flight	0.055	26.6
Total	1.000	85.7

significantly ( $\chi^2 = 5.93$ ,  $df = 1$ ,  $P < 0.025$ ) from 0% ( $n = 9$ ) in the first 2 weeks to 47% ( $n = 15$ ) in the last 3 weeks. These results are opposed to predictions from models by Norberg (1977) that predators should employ less energy-consuming hunting methods as prey density decreases.

*Energy budget.*—The daily food intake of Snail Kites was calculated by proportionately reducing the distribution of the three size classes for the 68 snails consumed during the 15 h of time-activity observations to that which would have occurred in a 12-h Guyana photoperiod. Caloric values per gram dry weight for *P. dolioides* were relatively constant ( $\bar{x} \pm SD = 4.04 \pm 0.09$ ,  $n = 10$ ). Using mean dry weights for each snail size class and assuming an assimilation efficiency of 0.9, a value chosen because snail tissue is almost entirely digestible and raptor assimilation efficiencies peak near this value (Sarker and Naulleau 1981), I calculated the daily energy intake by Snail Kites to be 104.2 kcal.

An average daily energy expenditure for Snail Kites was calculated in the following manner. As kites spent 12 h a day roosting, means from the 60 time-activity samples (Fig. 1) were pooled to determine the mean percentage of each daily activity for a 24-h period. Because Snail Kites spent less than 20% of the photoperiod in flight activities, equation 10 from Koplín et al. (1980) was used to compute the daily energy budget (Table 4). Daily energy expenditure for Snail Kites was estimated to be 85.7 kcal (Table 4).

My calculations indicate that kites easily utilized rice fields to meet their daily energy needs, realizing a daily net energy gain of 18.5 kcal. The high proportion of snails captured by energetically inexpensive still-hunting probably



accounted for this large net energy gain. During the study period, I saw no evidence that kites were ever stressed to find food or that any were malnourished. On the contrary, the small proportion of time spent flying by kites in rice fields (Table 4) may indicate that this was a very profitable patch to exploit.

*Consumer choice by a specialist.*—Snail Kites are a classic example of a "specialist." Preying almost solely on one genus of freshwater snails (often one species in some portions of its range), kites need not distinguish among a number of different items to be included in the diet. Under most conditions a kite may need only to choose among food items by size as it relates to the energetic benefit of caloric intake and the energetic cost of searching and handling times.

In this study, no increased cost was associated with the pursuit, capture, handling, and ingestion of prey in relation to prey size. No additional energetic benefit in terms of calories per capture was accrued during costly coursing hunts as compared to still-hunts. Snail Kites avoided capture of smaller snails, selectively preyed on medium-sized ones, and did not take large snails more frequently than they were encountered. In addition, patch use and hunting mode were affected by rice growth. Rice fields proved to be an easy place for kites to meet their energetic needs.

MacArthur (1972) partitioned the process of food gathering into four phases: (1) where to search; (2) how to search and what to look for; (3) whether to pursue or ignore a food item; and (4) the capture attempt and ingestion. Kite morphology is so specialized (Snyder and Snyder 1969) that, in order to maximize snail capture and ingestion proficiency (4), the decision of what foods to search for (2) has already been determined. A Snail Kite need only decide on where to search (1), how to search (2), and (3) whether or not to include an item in its diet on the basis of size. These decisions may be based on the encounter rate within a given patch.

In the choice of hunting modes, kites might be expected to still-hunt exclusively if they could find enough food. When insufficient numbers of snails per unit time are available from a perch, kites should shift to coursing. Thus, the effectiveness of still-hunting may be primarily controlled by the snail-encounter rate within the patch as a function of the distance

from the still-hunting perch. Factors that affect snail-encounter rates can cause a shift in hunting mode: the vegetative structure of a patch may be a prime determinant, as still-hunting increased with rice growth during the 2 months of study, and environmental factors (e.g. air and water temperature, dissolved oxygen, and wind speed) that affect both snail-encounter rates and kite metabolic costs probably accounted for the diurnal shift by kites in the mode of hunting that was observed.

Because Snail Kites selectively avoid small snails, a kite might be expected to prefer large snails. The diet should vary from patch to patch, however, depending upon the distribution of size classes available and the energetic costs of capture, which are both functions of the encounter rate and hence of patch choice. Patches do vary greatly in snail density and size distribution (Bourne and Berlin 1982). Thus, the most important decision a foraging Snail Kite must make is what patch to search in and how long to search before abandoning one patch for another.

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