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Source: *The Auk*, Vol. 107, No. 2 (Apr., 1990), pp. 327-333
Published by: University of California Press on behalf of the American Ornithologists' Union
Stable URL: http://www.jstor.org/stable/4087616
Accessed: 12/03/2009 17:59

ALTERNATIVE FOODS OF A DIET SPECIALIST, THE SNAIL KITE

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ABSTRACT.—Although Snail Kites (*Rostrhamus sociabilis*) in Florida and Venezuela fed mostly on *Pomacea* snails, I documented three alternative foods. In Florida, kites fed on five species of small turtles, but especially on *Sternotherus odoratus* and *Kinosternon bauri*. During the height of a drought, one kite in Florida fed on a small aquatic snail (*Viviparus georgianus*) for 5 weeks. In Venezuela, freshwater crabs (*Dilocarcinus dentatus*) made up on average 10% of the Snail Kite's diet, but more than 25% during September and October. Kites consumed alternative foods with techniques that resemble snail-eating behavior, such as entering a turtle's body cavity by piercing the only leg shaped like a snail operculum. Handling times for turtles (76 min) and crabs (5.4 min) were much longer than for *Pomacea* snails (1.5 min). *Viviparus* snails required approximately one-third less handling time but contained one-fifth less body mass than *Pomacea* snails. Handling time (30 s) for *V. georgianus* did not differ between the Snail Kite and the Boat-tailed Grackle (*Quiscalus major*), a diet generalist.

These findings are related to the factors that reinforce diet specialization and the ecological conditions that promote diet diversification in specialists. Like *Pomacea* snails, alternative foods have shells or carapaces and move relatively slowly. Alternative foods are probably less profitable than *Pomacea* snails, except for large crabs. Although crabs were regularly eaten by kites in Venezuela, turtles and *Viviparus* snails were eaten in Florida only during times of food scarcity. *Received 9 June 1989, accepted 6 November 1989.*

DEPENDENCE on a single prey type is unusual among vertebrates, but may be more common in invertebrates (Bristow 1988). A notable exception, the Snail Kite (*Rostrhamus sociabilis*), feeds almost exclusively on one genus of freshwater snails (*Pomacea*). In Florida the kite eats only *Pomacea paludosa* (Howell 1932, Snyder and Snyder 1969, Sykes 1987), while in Central and South America several *Pomacea* species are eaten (Haverschmidt 1962, 1970; Beissinger 1983; Snyder and Kale 1983; Bourne 1985). Alternative foods are taken on rare occasions. These include turtles (Sykes and Kale 1974, Woodin and Woodin 1981, Takekawa and Beissinger 1989) and a small mammal (Sykes and Kale 1974). Other less carefully documented observations of nonsnail foods include a "small yellowish serpent" (Slud 1980), a ring-necked snake (*Diadophis punctatus*), and a dead American Coot (*Fulica americana*) (Sykes 1987). In Venezuela and Colombia, kites fed on freshwater crabs and *Marisa* snails for short periods (Mader 1981, Snyder and Kale 1983).

The evolutionary pathway to specialization is often difficult to identify from ecological studies (Futuyma and Moreno 1988). However, some understanding of the factors that promote and maintain diet specialization may emerge by examining the causes and consequences for specialists when they select alternative foods. For instance, two morphological specializations allow Snail Kites to efficiently catch and eat snails (Snyder and Snyder 1969). These are a long, slender, hooked bill to sever the snail's columellar muscle and detach the snail's body from its shell, and long toes for seizing the snail by the shell. These morphological specializations could be expected to carry a cost of reduced efficiency for feeding on alternative foods (MacArthur 1972, Benkman 1988).

Here I document alternative foods regularly eaten by Snail Kites in Florida and Venezuela. I report behavior associated with diet generalization by a specialist and the ecological conditions that favored diet diversification.

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The Auk 107: 327–333. April 1990

METHODS

I observed the food habits of Snail Kites in Florida during studies of their reproductive behavior (1979–1983). Studies were conducted on Lake Okeechobee (Glades, Hendry, and Okeechobee counties), State Water Conservation Areas 2 and 3 (Dade and Broward counties), and Lakes Tohopekaliga and Kissimmee (Osceola County). Beissinger (1986) and Beissinger and Snyder (1987) described the study areas and climatological conditions. Fieldwork was conducted from January to August each year, except 1980 (July to August) and 1983 (March to June). Additional observations were made during February and April 1986.

In Venezuela, studies were conducted in the llanos at the ranch "Fundo Pequario Masaguaral" (8°34'N, 67°35'W), 45 km south of Calabozo in Guarico, and on other ranches along the main highway 30 km to the north and south. I observed food habits of kites from July to December 1985, and from July to November 1986 and 1987, usually by watching food delivered to nestlings by parents. No observations were made during the dry season (January–May) when most kites leave the llanos. Eisenberg (1979) and Beissinger et al. (1988) described the study areas and climatological conditions.

I observed behavior with 10× binoculars and 15–60× spotting scopes. When kites were feeding, their behavior was described and timed to the nearest second. *Handling time* is defined as the time required by a kite to extract and consume completely a food item after perching with it. Whenever possible, remains of nonsnail foods were recovered, identified, and measured. During this process, I often collected other food items beneath perches where kites had eaten snails or nonsnail foods.

Data were analyzed by SYSTAT microcomputer programs. As the data were normally distributed and variances were equal, I used Student's t-tests to compare handling times between *Pomacea* snails and various alternative foods. Means ($\bar{x}$) are reported with standard deviations (SD).

RESULTS

Selection and occurrence of alternative foods.—Small turtles were the alternative food most frequently eaten by kites in Florida (Table 1). I watched kites eat 9 turtles and found 39 turtles dead under perches that kites used regularly for extracting snails. Musk turtles (*Sternotherus odoratus*) accounted for 58.3% and mud turtles (*Kinosternon bauri*) 31.3% of the turtles eaten. Soft-shelled turtles (*Trionyx ferox*), and peninsula and Florida cooters (*Chrysemys nelsoni* and *C. floridana*) made up the remainder. Most turtles eaten by kites were smaller than full-sized adults, especially the larger species (Table 1).

Turtles were eaten most frequently when water levels were low during drought (n = 34 turtles; 71%) or in years following drought (n = 10 turtles; 21%). Kites also ate turtles in winter months (n = 4 turtles; 8%) during or just after the passage of cold fronts. The seasonal distribution of turtle predation was as follows: 2 in January, 4 in February, 9 in March, 28 in May, and 5 in July.

During the height of a drought in Florida in 1981, one banded 2-year-old male Snail Kite (#230) fed almost exclusively on a very small aquatic snail (*Viviparus georgianus*) at Lake Okeechobee. The kite was observed 300–500 m north of the Clewiston locks on six different days during a 5-week period (11 June–13 July). Lake levels were so low (ca. 3.0 m above mean sea level) that *V. georgianus* snails, normally found on the bottom of lakes and streams (Snyder and Snyder 1969), lay exposed on a shallow mudflat. During 5 hours of observations, male #230 rapidly ate 46 *Viviparus* snails and captured 12 others that he discarded, possibly because they were empty shells. Although no *Pomacea* snails were captured during these observation periods, he caught one *Pomacea* snail during the five weeks that he foraged along the mudflat. Remains of 170 *Viviparus georgianus*, 4 *Pomacea paludosa*, and 1 unopened freshwater mussel were under male #230's extraction perch on 3 July.

During this same period, another kite foraged near the mudflat on four occasions. Although this other kite frequently had difficulty finding *Pomacea* snails, it never fed on *Viviparus georgianus* even though it watched male #230 feed on *Viviparus* snails.

On one other occasion (during the 1981 drought), kites fed on *Viviparus georgianus* on Lake Okeechobee. Twelve empty snail shells were found under an extraction perch used exclusively by kites.

In the llanos of Venezuela, Snail Kites augmented their diet with freshwater crabs (*Dilocarcinus dentatus*). Of 3,866 food items captured by kites, 82.9% were positively identified. Freshwater crabs made up 10.3% of the diet and *Pomacea doliodes* the remainder; but, the consumption of crabs by Snail Kites varied seasonally (Fig. 1). Crabs were rarely eaten from July through early August, the first half of the wet season. The frequency of crabs in the diet increased in September and October, and crabs constituted more than one fourth of the food items in some months. Crab-eating declined in

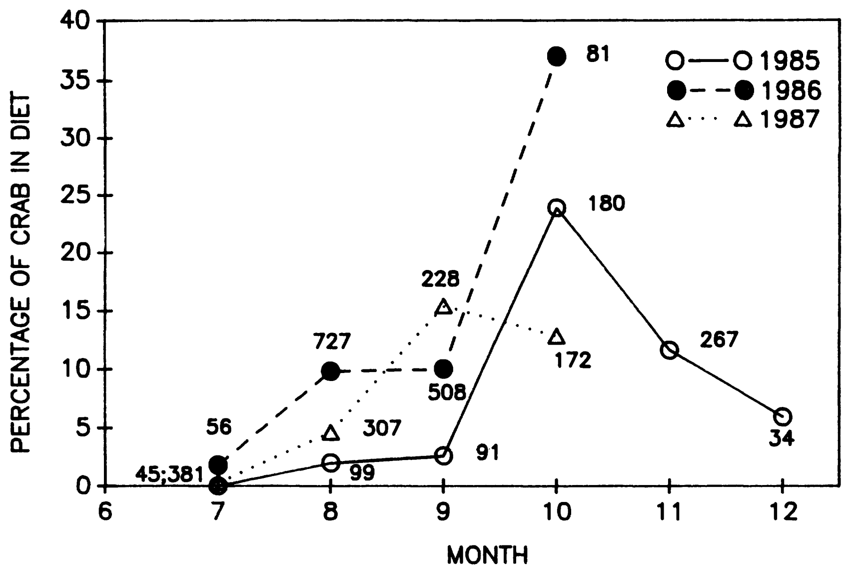

Fig. 1. Seasonal variation in the diet of Snail Kites in the llanos of Venezuela during three years of study. Only two foods were identified: *Pomacea doliodes* snails and freshwater crabs (*Dilocarcinus dentatus*). The percentage of crabs in the diet and the total number of food items identified are given for each month that >20 food items were identified.

November and December in 1985, the only year with sufficient sample sizes to characterize kite diets during these months.

Methods of catching and consuming alternative foods.—Snail Kites consumed turtles with techniques that resembled snail-eating behavior (Snyder and Snyder 1969, Beissinger 1988). After arriving at a perch, the turtle was placed on its back with its head near the branch and its posterior away (Fig. 2). Then the kite would grip the loose skin around a leg and pull, in an attempt to break the skin and enter the turtle's body cavity. From its position looking down on the turtle, the kite could choose which appendage among the four legs and neck it should attack. In all instances (direct observations: $n = 3$; and recovered carcasses: $n = 3$), kites attacked the turtle's right-rear leg. From a ventral view, the turtle's right-rear leg is the only appendage that is oriented in a manner which resembles the sickle shape of a *Pomacea* snail operculum and shell when positioned in a kite's talons for extraction (Fig. 2).

Often a kite had trouble gripping both the turtle and the perch, and on two occasions kites dropped an uneaten turtle prematurely. One kite required 5–8 min to tear away enough flesh from the turtle's right-rear leg to enter the body cavity. Once the right-rear leg was pierced, the kite pulled small pieces of meat from inside the turtle's body cavity with its bill and swallowed them.

Snail Kites rarely completely consumed a turtle. Often organs in the anterior part of the body cavity (heart and lungs) were not eaten and intact eggs remained in 4 turtles. In only one third of the freshly discovered turtle bodies were the internal parts completely eaten; in nearly half of the turtles, more than two thirds of the internal parts were eaten; and in one fifth of the turtles, only half was eaten ($n = 15$). Usually the head and front legs (40%), or these anterior external body parts and the left-rear leg (33%) were not eaten ($n = 15$); but in 20% of the cases all limbs and the head were gone, and once only the front legs remained intact.

Viviparus snails were captured and eaten somewhat differently than *Pomacea* snails. First, as *V. georgianus* was quite abundant and especially visible in shallow water, male #230 captured them quickly using short flights (14.6 ± 10.8 s, $n = 27$). In the Everglades, capturing *Pomacea* snails commonly required flights of 90–180 s (pers. obs.). Second, male #230 frequently extracted *Viviparus* snails while standing on the exposed mudflat instead of flying to a perch, the usual substrate for extraction of *Pomacea* snails. Third, to eat *Viviparus,* male #230 simply

TABLE 1. Species composition and size of turtles eaten by Snail Kites in Florida. Adult size ranges (Conant 1975) are in parentheses.

		Carapace length (mm)	
Species	*n*	$\bar{x} \pm SD$	Range
Sternotherus odoratus	28	62.8 ± 12.5	30.0–76.8 (80–115)
Kinosternon bauri	15	82.5 ± 5.1	69.8–89.8 (75–100)
Chrysemys floridana	3[a]	65.3 ± 1.8	64.0–66.5 (320–330)
C. nelsoni	1	57.2	— (200–305)
Trionyx ferox	1	45.0	— (150–498)
Totals	48	68.8 ± 14.1	30.0–89.8 (75–498)

[a] Only two carcasses were measured.

pulled on the snail's operculum until both the operculum and body separated from the shell. *Viviparus* snails cannot close themselves tightly in their shells and only moderate force is required to pull the snail's body from its shell. In contrast, before a *Pomacea* snail's body can be removed from its shell, kites must first remove the operculum and then cut the columellar muscle (Snyder and Snyder 1969).

Crab extraction techniques resembled those used for turtles. First, the crab was pinned to a perch (usually by holding one foot on the carapace and the other on a claw). Crabs were usually positioned dorsal side down with the head toward the perch. Then the carapace was lifted from the ventral side and pulled off. Very small bits of meat and organs were eaten from under the abdomen, near the head, and inside the carapace. Kites usually ate most of the soft parts in the crab's body cavity, but the legs and claws were never eaten and often were not removed.

When feeding crabs to nestlings, kites often removed the carapace and most of the appendages before carrying the crab to the nest. Kites frequently made two or more trips to the nest with pieces from the same crab. The feeding process, which usually required only one trip to the nest lasting 1–2 min for snails, frequently required 6–8 min for crabs.

Handling times of alternative foods.—Exact handling times for turtles often could not be measured because the kites were already in the process of eating when I found them. In three cases, however, I encountered the kite shortly after it

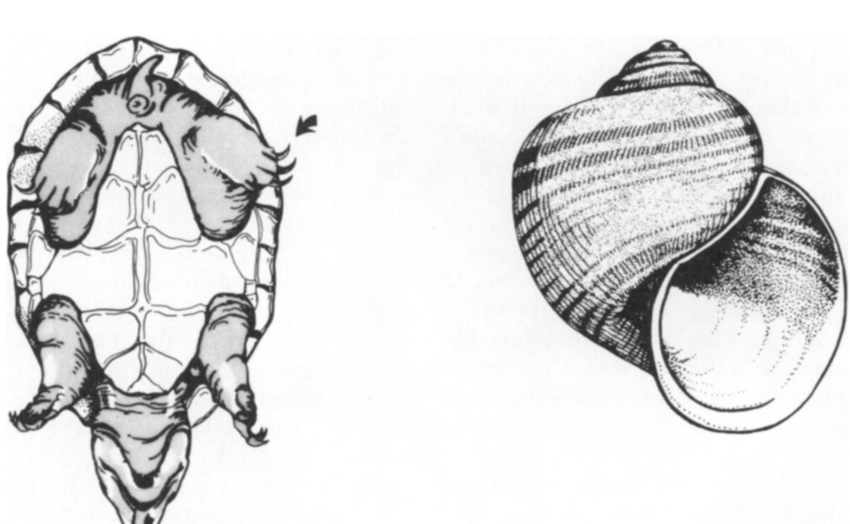

Fig. 2. The orientation of a turtle and *Pomacea* snail as viewed by a kite when positioned on a perch for extraction. Note how only the fleshy area around the turtle's right-rear leg, indicated by the arrow, has the same sickle shape of the aperture opening of the *Pomacea* snail. Kites always began extracting turtle meat by piercing the right-rear leg to enter the body cavity.

TABLE 2. Comparison of the time required to extract and eat (handling time) *Pomacea* snails and alternative foods by Snail Kites in Florida (FL) and Venezuela (VZ).

Diet/food item	Area	n	Handling time (s)
Preferred			
Pomacea paludosa	FL	197	95.7 ± 37.3
P. doliodes[a]	VZ	248	93.0 ± 48.0
Alternative			
Small turtles[b]	FL	3	4,579.8 ± 864.0
Viviparus snails	FL	46	31.3 ± 15.5
Dilocarcinus crabs	VZ	14	329.1 ± 119.0

[a] Data from T. Donnay and S. Beissinger (unpubl.).
[b] Minimum handling times for *Sternotherus odoratus* and *Kinosternon bauri*. (See text for explanation.)

began to eat. Handling times for turtles averaged >60 min (range: 63–85 min) compared with just 1.5 min for *Pomacea paludosa* (Table 2).

Extracting and eating crabs was also relatively time consuming (Table 2). Handling times for crabs were significantly longer than for *Pomacea doliodes* ($t = 7.4$, df = 260, $P < 0.01$). Although kites usually were able to begin eating crabmeat within 30 s, additional time was required to remove and eat the small bits of meat from the body.

Viviparus snails required approximately one-third less handling time ($t = 11.5$, df = 241, $P < 0.001$) by kites than *Pomacea* snails (Table 2). However, the average wet weight of extracted *Pomacea* snail bodies (2.9 ± 0.6 g, $n = 15$) on Lake Okeechobee was more than 5 times greater ($t = 12.1$, df = 24, $P < 0.001$) than *Viviparus* extracted wet weights (0.5 ± 0.2 g, $n = 11$).

Boat-tailed Grackles (*Quiscalus major*) also fed on *Viviparus* snails on the mudflat with kite #230. The grackles captured snails by walking, hopping, and sometimes making short flights. Kite #230 usually captured snails more quickly than the grackles (14.6 ± 10.8 s, $n = 27$ vs. 22.9 ± 20.4 s, $n = 19$), but the difference was not quite statistically significant ($t = 1.8$, df = 44, $P = 0.08$). Also, there was no difference in the length of time required for the Snail Kite (Table 2) or the grackles (33.0 ± 15.4 s, $n = 42$) to extract and eat *Viviparus* snails ($t = 0.5$, df = 86, $P = 0.61$).

DISCUSSION

Snail Kites fed mostly on *Pomacea* snails, but small turtles and another species of snail in Florida, and freshwater crabs in Venezuela, served as alternative foods. Alternative foods resemble *Pomacea* snails in several ways. First, all have shells or carapaces, which permit kites to utilize extraction procedures similar to those used for eating *Pomacea* snails. For example, the technique of extracting turtle meat closely resembled the methods that kites use to remove a snail from its shell (Fig. 2). Second, alternative foods, like *Pomacea* snails, move relatively slowly in the water and cannot struggle vigorously to escape once caught. Because kites descend slowly to the water surface rather than dive on prey during capture (Snyder and Snyder 1969), prey that move rapidly would probably be difficult for a kite to capture. Also, kites might find it difficult to grip a struggling fish, frog, or snake with their long, thin toes and weak talons.

The specializations that enable kites to extract and eat *Pomacea* snails so efficiently appear to make it difficult for kites to extract and eat some alternative foods (Table 2). Handling times for small turtles were >60 min compared with just 1.5 min for *Pomacea* snails. Although a small turtle probably provides more energy than a snail, it might not provide more energy than 3 or 4 snails. The inability of Snail Kites to reach all of the meat in the anterior portion of a turtle body cavity, compared with other turtle-eating raptors (e.g. Auffenberg 1981, Woodall 1982), suggests that the kite's hooked bill may not be able to penetrate deeply enough into the turtle's body cavity. Kites presumably selected relatively small turtles (Table 1) possibly because of the difficulty in manipulating and eating larger ones.

Although kites had no difficulty eating crabs, handling times were 3–4 times longer than for *Pomacea* snails. The time-consuming portion of extraction was the removal of the small bits of meat from the crab's exoskeleton. The kite's strongly decurved bill did not appear to hinder this process.

Kites are preadapted to extract and eat *Vivip-*

arus snails. But apparently little morphological specialization is required to feed on these mollusks because the Boat-tailed Grackle, a diet generalist (Snyder and Snyder 1969), extracted and ate *Viviparus* as efficiently as did kite #230. This kite required approximately one-third less time to extract and eat *Viviparus* snails compared to *Pomacea* snails. However, the profitability (energy consumed/handling time) of *Pomacea* snails should be ca. 1.4 times greater than *Viviparus* because they are approximately one-fifth the size of a *Pomacea* (assuming the energy and water content of snail tissue to be equivalent). Feeding on such a small snail may have been an act of desperation for kite #230. Another kite nearby continued to search for *Pomacea,* even though they were apparently difficult to find, rather than eat *Viviparus* snails.

Alternative foods in Florida were eaten only during times of apparent food scarcity caused by regional drought or the passage of a winter cold front. *Pomacea* snails estivate in response to drying conditions, which causes kites to disperse from the Everglades throughout the Florida peninsula to search for food (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989). Cold fronts cause water temperatures to fall rapidly, and snails become inactive. Both situations result in snails becoming temporarily unavailable to kites. Diet diversification under such circumstances is in accordance with optimality models of diet choice (Stephens and Krebs 1986). These models predict that food items should be included in the diet, not on the basis of their abundance, but dependent upon their profitability and the abundance of more profitable food items already being eaten.

Freshwater crabs were the only alternative food regularly included in the diet of kites. Crabs made up more than 25% of the diet during some months in Venezuela (no freshwater crabs are found in Florida), but the percentage of crabs eaten by kites varied seasonally (Fig. 1). Because handling times for crabs are 3–4 times longer than *Pomacea* snails, crabs would have to yield significantly more energy to be included in the diet on the basis of profitability alone. Large crabs become big enough that they can be more profitable than snails (S. Beissinger and T. Donnay unpubl. data). Crab size increases greatly throughout the wet season in the llanos (Taphorn and Lilyestrom 1984) and this could account for the increase in crab-eating by kites during these months (Fig. 1).

Crabs might also be included in the diet if they contained some nutrient which snails lacked. Because kites in Florida have no nutritional or growth problems on strictly a *Pomacea* diet (Beissinger 1987, Beissinger and Snyder 1987), nutrient needs seem an unlikely explanation for crab-eating. If snail abundance fluctuated seasonally, this might also account for the switch to include crabs in the diet. Low snail abundance in Venezuela is suggested by lower food delivery rates to nestlings and smaller brood sizes compared with Florida (Beissinger 1990).

Natural selection should favor increased efficiency in food handling. If efficiency is gained through morphological specialization, diet breadth may contract (MacArthur 1972, Futuyma and Moreno 1988). I suggest that even severe diet specialists with strong trophic adaptations can be somewhat flexible. Specialists can feed on alternative foods if the foods structurally resemble preferred food, but efficiency in handling alternative foods may be low. Although diet diversification by specialists occurs most often during times of food scarcity, specialization may not preclude regularly eating some alternative foods that may be profitable and can be processed with extraction techniques already mastered.

ACKNOWLEDGMENTS

This study was supported by grants from the Smithsonian Institution, the U.S. Fish and Wildlife Service, and a National Science Foundation Postdoctoral Fellowship in Environmental Biology. Señor Tomas Blohm graciously allowed me to live and work on his ranch. Russell Thorstrom, Manuel Felipe Rodriguez, David Jickling, and Kirsten Silvius assisted with field observations. Tim Donnay kindly allowed me to use unpublished data. Peter Meylan identified Florida turtles and placed them in the Florida State Museum collection (catalog numbers 54089-54120, 54174-54183). John Anderton drew Fig. 2. Craig Benkman, Tim Donnay, Russell Greenberg, Mickey Hetmeyer, Noel Snyder, and Steve Zack made helpful comments on the manuscript.

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