MOLLUSK PREDATION BY SNAIL KITES IN COLOMBIA

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Abstract—Snail Kites (*Rostrhamus sociabilis sociabilis*) observed along the lower Río Magdalena in northern Colombia fed heavily on *Pomacea chemnitzi* but also took *Marisa cornuarietis*, a smaller species. The kites captured *Pomacea* preferentially over *Marisa* and had difficulties extracting *Marisa* from its shell. They also failed to extract some large specimens of *P. chemnitzi*. Failures with both species were apparently related to problems in removing opercula. These observations indicate that *R. sociabilis* can no longer be considered a strict specialist on *Pomacea*. *Received 21 August 1979, resubmitted 8 April 1982, accepted 15 October 1982.*

Mollusks are a major dietary component for a surprisingly diverse assemblage of birds, including various ducks, shorebirds, rails, storks, and raptors (Snyder 1967). Of particular interest, because of its endangered status in the United States, is the Snail, or Everglade, Kite (*Rostrhamus sociabilis*), a species renowned for its dependence on fresh-water snails of the genus *Pomacea*. Snyder and Snyder (1969) discussed some of the peculiar anatomical and behavioral specializations of the Snail Kite that enable it to feed on *Pomacea paludosa* in Florida. Here, we present information on interactions of the species with snails of northern Colombia, as observed 28 April to 5 May 1978, the start of the rainy season.

Our study area was a backwater of the Río Magdalena next to the Barranquilla airport. Two large snails of the family Pilidae were found in abundance here, *Pomacea chemnitzi* and *Marisa cornuarietis*. *Pomacea chemnitzi*, with its shallow spire, closely resembles *P. paludosa* in shape, but, at least in this locality, it commonly reaches a size considerably larger than typical individuals of the Florida species. *Marisa cornuarietis* is coiled in a plane and looks like a giant ramshorn snail, but, like *Pomacea*, it possesses a hard operculum with which it can close off the entrance of the shell.

Results

Snail Kites characteristically bring their prey to conspicuous feeding perches for extraction procedures, and the shells accumulating underneath give a record of the foods eaten. We soon learned, however, that some shell piles in the study area yielded biased representations of kite diet because of differential losses of shells after deposition. Shell piles under perches standing in water retained their *Marisa* shells well but lost most of their *Pomacea* shells, apparently because the former are heavily calcified and tend to sink, while the latter readily float and can drift away on water currents. Thus, for example, we found only 28 *Pomacea* shells among 699 *Marisa* shells at one perch that obviously had been inundated recently.

In contrast, we found a preponderance of *Pomacea* over *Marisa* in shell piles above the water line. The overall *Pomacea* to *Marisa* ratio at four such perches was 3.0, and it varied from 1.8 to 7.2 among the perches (Table 1). The four perches were located within 100 m of each other in an area of mixed brushy swamp and flooded pasture immediately adjacent to an active kite nesting colony. Using the perches were a minimum of three brown-plumaged kites (females and/or young males).

Under all four of the above perches we were surprised to find evidence that the kites were failing to extract some *Pomacea* and *Marisa*, as we found whole uneaten individuals of both species, some still alive and others in various stages of decay. In addition, an inspection of the shells revealed that many of the snails were

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TABLE 1. Shells found under active perches of Snail Kites in Colombia.[a]

	Perch number				Total shells
	1	2	3	4	
Pomacea chemnitzi					
Empty shells	35	35	28	28	126
Shells with viscera	5	15	2	5	27
Whole snails	6	1	6	1	14
Total shells	46	51	36	34	167
Marisa cornuarietis					
Empty shells	5	1	0	5	11
Shells with viscera	7	7	1	8	23
Whole snails	5	6	4	6	21
Total shells	17	14	5	19	55
Pomacea/*Marisa* ratios	2.7	3.6	7.2	1.8	

[a] All shell piles above the water line.

only partially eaten (Table 1). The failure rates for the two snail species were highly significantly different ($\chi^2 = 25.47$, df = 1, $P < 0.001$). Of 167 *Pomacea* shells only 14 (8%) still contained whole, uneaten snails, compared to 21 of 55 *Marisa* shells (38%).

In the cases of uneaten *P. chemnitzi*, failure appeared to be related to snail size (Fig. 1A), as uneaten snails (averaging 57.2 mm in greatest length) were significantly different in length from eaten snails (averaging 52.8 mm), as shown by a Mann-Whitney *U*-test ($t_s = 3.182$, $P < 0.005$). Opercula of the uneaten specimens were scratched with the usual bill marks one finds on kite-extracted *Pomacea*. Apparently, the kites had tried to extract the uneaten *Pomacea* but had failed to grasp the opercula or had been unable to pull the opercula free from the snails. In watching several unsuccessful attempts, we saw no signs that the birds might have been deliberately rejecting individual snails that were noxious to them. The kites simply worked away at these snails with their bills in the usual fashion, appeared to lose interest after a few minutes, and eventually allowed the snails to fall from the perches.

The failure of the kites to extract all *P. chemnitzi* bears further comment. With *P. paludosa* in Florida we have never, in many hundreds of direct observations, seen an adult kite fail, and only very rarely have we found evidence of less than complete extractions of softparts. For example, of 529 *P. paludosa* shells collected from beneath a perch being used exclusively by adult and subadult kites on Lake Okeechobee in February 1979, only four still contained small fragments of snail viscera. On the other hand, recently fledged Florida Snail Kites do fail occasionally in extractions of *P. paludosa*. For example, on 21 May 1979 we collected shells from a screen installed below a perch being used almost exclusively by banded kites less than 2 months beyond fledging age. Of the 114 shells collected, 9 (7.9%) contained whole, unextracted snails. The uneaten snails did not differ significantly in size from eaten snails ($t_s = 1.524$, $0.10 < P < 0.20$; Mann-Whitney *U*-test), and, in the cases in which we directly observed young kites dropping whole snails at perches, the cause was quite clearly nothing more than clumsiness. The birds had obvious difficulties holding the snails properly in their feet and sometimes lost control of the shells in attempting to position them.

Whether the failures of Colombian Snail Kites in extraction of *P. chemnitzi* might similarly be related to the age of the kites is conjectural. The kites we observed at the perches were all brown-plumaged and none appeared to be mated—characteristics consistent with youth. All were fully independent, however, and none was clumsy in its snail-extraction efforts. These factors, together with the size-dependence of their failures with *P. chemnitzi*, suggest that their difficulties may have resulted from more than just inexperience. In any event, we believe it would be unwise to assume that the few birds we observed were representative of the kite population as a whole.

Failures with *M. cornuarietis*, like failures

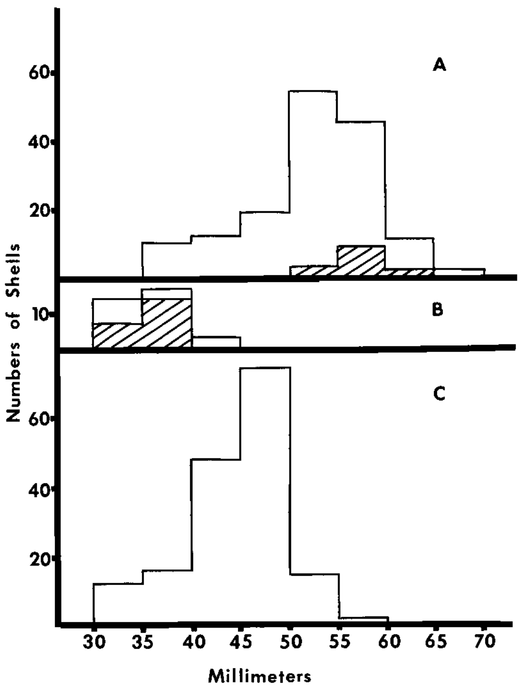

Fig. 1. Size distributions of *Pomacea chemnitzi* and *Marisa cornuarietis* shells found under active perches of Snail Kites: A, greatest length of eaten (clear) and uneaten (shaded) *Pomacea chemnitzi*; B, greatest diameter of eaten (clear) and uneaten (shaded) *Marisa cornuarietis*; C, greatest diameter of all *Pomacea chemnitzi*.

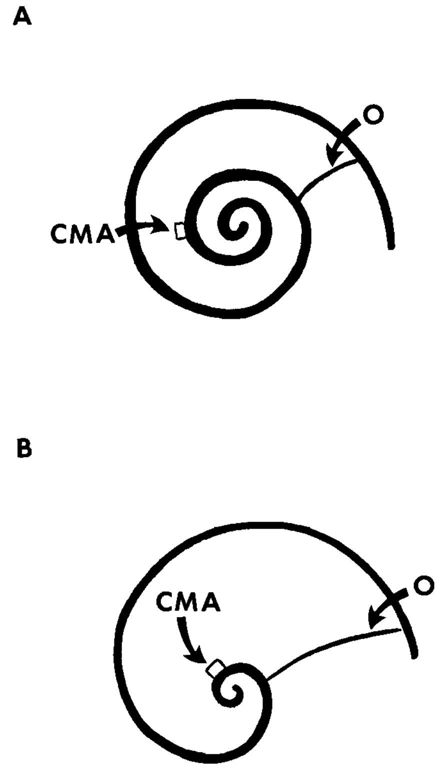

Fig. 2. Diagrammatic representation of position of columellar muscle attachment (CMA) and operculum (O) of: A, *Marisa cornuarietis*; B, *Pomacea chemnitzi*.

with *P. chemnitzi*, appeared to be caused by an inability of the kites to remove opercula, as the opercula of whole, uneaten snails under perches showed clear scratch marks. The high frequency of failure may have been due to this snail's ability to pull far back into its shell: in *Pomacea* the operculum usually forms a tight fit just inside the aperture; in *Marisa* the operculum can be withdrawn for a considerable distance inside where it is difficult to grasp. Failure with *Marisa* was not a function of snail size, as unextracted snails did not differ significantly in maximum diameter from extracted snails ($t_s = 0.468$, $P > 0.5$; Mann-Whitney *U*-test).

Even when kites were able to remove the opercula of *Marisa*, they commonly failed to get more than the foot of the snail out of the shell, probably because the columellar muscle attachment of this snail is about as far inside the entrance as the long hooked bill of the birds can reach (Fig. 2A). This muscle attachment, which must be severed to allow a complete extraction of the softparts, lies much closer to the entrance in *Pomacea* (Fig. 2B). The great majority of *P. chemnitzi* from which kites were able to remove opercula were fully extracted (126 of 153 cases). By comparison, only 11 of 34 *Marisa* from which the opercula had been removed were fully extracted, a highly significantly difference ($\chi^2 = 33.0$, df $= 1$, $P < 0.001$). Generally, the softparts of *Marisa* snails were broken near the columellar muscle attachment, and all of the viscera remained in the shells. Breakage probably resulted from the kites' pulling on the softparts from the shell entrance after failing to sever the columellar muscle.

Direct observations of the snail-extraction behavior of the minimum of three kites using the active perches listed in Table 1 confirmed a higher success rate with *Pomacea* than with *Marisa*, although the success rates were not significantly different ($\chi^2 = 1.13$, df $= 1$, $0.25 < P < 0.50$) for the two snails, probably due to small sample size. Of six cases of the kites attempting to extract *Marisa*, only two were successful to the point of the birds' getting some meat out of the shell. With *Pomacea* the success rate was eight of 11 attempts.

Not only were the kites failing more frequently with *Marisa* than with *Pomacea*, they were also receiving much less reward from this snail when successful. The wet weight of a *Marisa*'s softparts generally does not exceed 2 g, whereas a typical *P. chemnitzi* yields 15–20 g of meat. When the total and partial failure rates in extractions from Table 1 are included in calculations, the yield in soft tissues from an average *P. chemnitzi* runs about 15 times as great as from an average *M. cornuarietis*.

From the above comparison one might expect to find the kites selectively foraging for *Pomacea* in preference to *Marisa*. That this might be true was apparent from an inspection of foraging areas near the active feeding perches. In walking several transects through the marsh we were able to tally between 10 and 20 times as many adult *Marisa* as *Pomacea* near the water surface (where they would be vulnerable to the kites). Yet, we found a *Marisa* to *Pomacea* ratio of about 1:3 at the four feeding perches and directly observed a 6:11 *Marisa* : *Pomacea* capture ratio near the perches.

One may question why the kites were taking *Marisa* at all in view of its much inferior reward potential. Possibly, the captures of *Marisa* represented nothing more than mistakes in discrimination between the two snails. From the 3–6-m heights at which the kites generally forage, distinguishing between *Pomacea* and *Marisa* may present problems, especially when shells are covered with algae. Once a kite has gone to the trouble of capturing the "wrong species," the reward, though relatively low, may still be high enough to justify an extraction attempt rather than a rejection and a continued search for *Pomacea*. Also, assuming the observed 10–20-fold superiority in abundance of *Marisa* over *Pomacea* might apply inversely to the time and energy investment needed to locate the two snails, the net reward superiority of a typical *Pomacea* over a typical *Marisa* may be far less than that calculated above for snails already captured. Unfortunately, we did not record information on the average time it takes to capture the two snail species, so we could not evaluate this question in any direct fashion.

The size distributions of captured *Pomacea* and *Marisa* snails in Fig. 1A and B are presented in terms of maximum linear dimensions: total length from top of spire to base of aperture for *Pomacea* and greatest diameter for *Marisa*. In these terms the sizes of some *Marisa* shells fall below the sizes of all *Pomacea*. At first sight it might seem puzzling that the kites captured the smallest *Marisa*, because they were apparently rejecting *Pomacea* of similar linear extent (but much greater mass). Under field conditions, however, the maximum linear dimensions of a *Pomacea* will often be hidden from the view of a kite flying overhead, because snails near the water surface are not always oriented the same way with respect to gravity. In fact, a *Pomacea* viewed by looking down on its spire looks very much like a *Marisa*, and in this orientation its greatest visible linear dimension is a maximum diameter, not a total length. If instead of plotting *Pomacea* according to total length, we plot these snails according to greatest diameter (Fig. 1C), we find that the *Pomacea* curve now overlaps the *Marisa* curve completely. Thus, the potential ease of discrimination between the smallest *Pomacea* captured and the smallest *Marisa* captured disappears.

Discussion

The extractions of *P. chemnitzi* by Snail Kites followed the pattern described by Snyder and Snyder (1969) and supported by Voous and Van Dijk (1973). They bore no resemblance to the extraction procedures described by Lang (1924) and Murphy (1955). We have now observed kites eating three different species of *Pomacea* (including *P. dolioides*, on which Lang's description was based), and all have been handled in the same way: removal of the operculum with the bill, cutting of the columellar muscle attachment with strokes of the upper bill, and pulling of the freed softparts out of the shell with the bill. Unlike Lang and Murphy, we have not seen kites waiting for voluntary extension of snails from their shells, we have no evidence that they ever ingest opercula in the wild, and we have seen nothing to suggest that they pierce the snails in a "nerve plexus," causing the snails to release their holds on their shells. We believe that the Lang-Murphy description, while colorful, is incorrect. Unfortunately, this description has become entrenched in the popular literature on kites and may never be evicted, as there are now so many references reiterating it.

On several occasions we observed Snail Kites discarding the yolk glands of female *P. chemnitzi*, and we found discarded yolk glands of this species under kite feeding perches. Very likely the yolk and eggs of this snail are highly distasteful, as are the yolk and eggs of *P. dolioides* and *P. paludosa*, which are also commonly rejected by the kites and other predators (see Snyder and Snyder 1969, 1971). Like the orange eggs of *P. dolioides* and the pinkish-white eggs of *P. paludosa*, the yellowish-white eggs of *P. chemnitzi* are conspicuous and presumably aposematic. All three species lay their eggs out of the water on emergent vegetation. *Marisa cornuarietis*, in contrast, has aquatic eggs, which are not highly conspicuous. We did not note discarded *Marisa* yolk glands under kite perches and have no direct evidence that the yolk and eggs of this species might be distasteful.

Although with most fresh-water snails there is little evidence that opercula might serve as an effective adaptation to thwart predators (see Snyder 1967), the opercula of both *M. cornuarietis* and *P. chemnitzi* appear to have value in reducing kite predation in Colombia. Some kite perches are over water, and snails that are not successfully extracted by kites get a second chance at life if they fall back into the water on being discarded. To our knowledge, the only predators of fresh-water molluscs known to be regularly deterred by snail opercula are sciomyzid fly larvae (see Berg 1961).

Although Snail Kites have been seen taking nonsnail prey under conditions of extreme food shortage (Sykes and Kale 1974), the observations reported in this paper are the first of the species feeding on a genus of snail other than *Pomacea*. It is uncertain, however, whether or not kites are successful enough with *Marisa* to be able to exist on it alone in areas where *Pomacea* does not occur. *Marisa* was introduced into southern Florida over 20 yr ago (see Edmondson 1959) and has fairly recently spread out into regions where Snail Kites occur. It is not yet abundant there, but is widespread—we have seen shells along the Tamiami Trail and as far north as Everglades Holiday Park near Alligator Alley. To date we have not found any of its shells at kite feeding perches. As studies of *M. cornuarietis* have shown the species to have complex competitive and predatory relationships with other snail species (see Demian and Lutfy 1965, Ruiz-Tibén et al. 1969), the establishment of *Marisa* may prove to be a mixed blessing for the Snail Kites of Florida.

Acknowledgments

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