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Habitat structure effects on size selection of snail kites (*Rostrhamus sociabilis*) and limpkins (*Aramus guarauna*) when feeding on apple snails (*Pomacea* spp.)

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ABSTRACT

Consumer density can influence foraging patterns such as prey-size selection, but few studies have evaluated its effects in field conditions. Here we evaluate the hypothesis that habitat structure influences forager density, and that this in turn influences the size of prey consumed by two avian predators. The sizes of two apple snail species available to, and consumed by, snail kites and limpkins were determined at sites with high and low densities of snail kite foraging perches. Sites with more perches had higher densities of snail kites, but not of limpkins. Both predators consumed prey larger than those available in the marshes, but habitat structure influenced the probability of consumption of different prey sizes. Limpkins consumed larger prey at low-density sites when compared with high-density sites, in contrast to other studies that found no size selection. Thus, limpkins can present prey-size selectivity but the presence of other predators can influence the range of prey sizes consumed. When a wider range of prey sizes is available, limpkins can select larger prey; alternatively, higher densities of other predators can result in higher foraging risk, favoring the capture of smaller, easier to handle prey. Snail kites incorporated smaller prey to their diet at low-density sites than at high-density ones, probably due to the higher costs of carrying large prey, differential age distribution, or lower foraging risks. Thus, habitat structure can influence consumer density and foraging patterns in complex ways, influencing predator–prey interactions in natural systems.

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1. Introduction

Size-selective predation can have large effects on predator–prey dynamics and food web organization (Fryxell and Lundberg, 1998; Goss-Custard, 1996; Turesson et al., 2002). It is

generally predicted from optimal foraging models, in which foragers should maximize net energy gain in relation to energetic costs such as searching and handling times (Sih and Christensen, 2001). Net energy per prey captured can vary with different handling times, which in turn can vary with prey types (Stephens and Krebs, 1986), changes in prey profitability during foraging bouts (Hirvonen and Ranta, 1996), risk of predation (Lima and Dill, 1990), and presence of conspecifics (Nilsson et al., 2000; Triplet et al., 1999). For example, interactions among conspecifics can influence both foraging rates (Stillman et al., 1996, 1997; Triplet et al., 1999) and size preferences of consumers. In the latter case, models predict that interactions with competitors are generally costly,

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and smaller prey should be favored to minimize handling times (Nilsson et al., 2000). These authors found that distinct consumer species may differ in their responses to risk of intraspecific interactions, so that in the presence of competitors the predators could either select smaller prey to reduce handling times, or larger prey to reduce the number of foraging excursions, minimizing the risk of interactions. Thus, different patterns of prey-size capture in the presence of competitors can be found, but few studies addressed this issue.

Neotropical wetlands are an ideal system to study species interactions because species that occur in distinct regions are exposed to similar variations in resource availability, as a result of marked wet and dry periods and resulting flood pulses (Junk and Silva, 1999). One example of such a resource are apple snails (*Pomacea* spp.), abundant herbivores which are consumed by predators such as birds, fish, and caymans (Donnay and Beissinger, 1993). Apple snails have a wide distribution range, with different species occurring in different American regions, such as *Pomacea paludosa* in Florida (Darby et al., 1999), *Pomacea flagellata* in Costa Rica (Reed and Janzen, 1999), *Pomacea doliodes* in Guyana and Venezuela (Bourne, 1993; Donnay and Beissinger, 1993), *Pomacea lineata*, *Pomacea canaliculata* and *Pomacea scalaris* in the Brazilian Pantanal (Bezerra et al., 1997; Callil and Junk, 2001). Although different *Pomacea* species occur in these regions, their main avian predators are the same, the snail kite *Rostrhamus sociabilis* Vieillot and the limpkin *Aramus guarauna* Linnaeus (Beissinger, 1983; Beissinger et al., 1994; Bourne, 1993; Reed and Janzen, 1999; Sick, 1997; Snyder and Snyder, 1969). These predators consume apple snails of a wide range of sizes, but have distinct prey-size preferences possibly due to differences in foraging behavior (Bourne, 1993; Snyder and Snyder, 1969).

Snail kites occur from Florida and Mexico to Argentina and Uruguay. This visual hunter feeds almost exclusively on apple snails, although it may sometimes consume other prey (Beissinger, 1990; Sick, 1997). It has two basic capture strategies: (1) still-hunting by visually searching for prey from a feeding perch and capturing it after a short flight, and (2) course-hunting by slowly flying 3–5 m above the marsh, visually searching for prey (Snyder and Snyder, 1969). After finding and capturing a prey, it returns to the perch to consume the soft parts, discarding the empty shells that accumulate in piles on the ground (Sick, 1997). The limpkin is distributed from Florida and Mexico to Argentina and Bolivia. Its main food items are freshwater snails of the genus *Pomacea* and *Marisa* (Sick, 1997; Snyder and Snyder, 1969). The choice of food items seems determined by size and availability, and four basic strategies are used for prey capture: (1) visual search on land, (2) visual search in clear waters, (3) tactile search on the vegetation surface, (4) tactile search on the bottom of marshes (Snyder and Snyder, 1969). Strategies 3 and 4 tend to be used where apple snails are abundant, because snails tend to stay on the vegetation surface and on the bottom in shallow waters, only moving to the surface to breathe. When finding a prey item, the limpkin takes it immediately to a dry site or in shallow water to consume it, leaving a pile of empty shells (Snyder and Snyder, 1969).

Studies carried out in different geographical areas have evaluated prey-size selection by both predators and the results generally agree with predictions from optimal foraging models (Beissinger, 1983; Bourne, 1993; Reed and Janzen, 1999). Working in Guyana, Bourne (1985a) showed that snail kites first select habitat patches with high densities of apple snails and, within patches, select those snails that are larger than expected by chance. Active selection for larger apple snails was observed in Costa Rica (Collett, 1977), Guyana (Beissinger, 1983; Bourne, 1993), and Brazil (Magalhães, 1990), a pattern generally interpreted as size optimization in cost-benefit analyses. On the other hand, limpkins tend to select average-sized snails, as observed in Costa Rica (Collett, 1977; Reed and Janzen, 1999) and Guyana (Bourne, 1993). Reed and Janzen (1999) suggested that the lower handling costs for small snails would compensate for the loss of energetic gain when compared to larger prey. Larger snails may have effective avoidance behavior or may be more difficult to handle, as suggested by the presence of holes in larger shells, made when limpkins fail to open the operculum and have to puncture the shell.

Most studies of the interaction between avian predators and apple snails have been carried out at the same broad spatial scale, without considering whether habitat components could influence prey-size selection. An exception is the study by Bourne (1993), who compared size selection by limpkins and snail kites in Guyana. He showed that in deeper marshes, snail kites selected larger snails while limpkins selected smaller ones, whereas in shallow marshes the distribution of snail sizes consumed by the two species did not differ from those available. Bourne (1993) suggested that these differences could be ascribed to the snails' behavior, because larger individuals would have larger parasite loads, stay for longer on the surface, and be more easily found by snail kites, whereas in the shallow marsh there would be no vertical size stratification of the snails. However, the possible influence of habitat structure was not investigated.

As the snail kite uses feeding perches both to select and consume prey, it is expected that the availability of such perches should influence the local densities of foraging kites. On the other hand, limpkins do not need perches and thus their local density should be less influenced by this habitat characteristic. Thus, we predicted that at sites with higher predator densities there would be a higher probability of interactions with competing foragers, influencing the size of prey consumed.

In this study, we evaluate whether (1) habitat structure influences the densities of limpkins and snail kites. We show that higher densities of foraging kites were found at sites with higher availability of perches, and thus asked two further questions: (2) does the availability of prey differ between areas with distinct kite densities? and (3) does the size of prey consumed by these predators change between areas with distinct habitat structure, and therefore distinct predator densities? For the limpkin, an important energetic cost is handling larger apple snails, resulting in empty shells with holes. Thus, we asked a further question (4) can we test for differences in the difficulty of handling differently sized snails by comparing the sizes of shells with and without

holes, as suggested by Reed and Janzen (1999)? To answer these questions, we evaluated prey-size selection by both predators on two species of apple snail, *P. canaliculata* and *P. scalaris*, through a field study in the Brazilian Pantanal.

2. Materials and methods

2.1. Study area

The Brazilian Pantanal is located in the central part of South America, and is part of the Paraguay River catchment with about 140,000 km². The landscape is heterogeneous, with marshy areas largely covered by small lakes, abandoned meanders, and old river beds partly or completely covered by vegetation, as well as areas intermittently flooded by rivers or precipitation (Carvalho, 1986). The study was carried out in the southern part of the floodplain, in the subregions Miranda and Nabileque (Adámoli, 1982), Corumbá district, near the Base de Estudos do Pantanal from Universidade Federal de Mato Grosso do Sul (19°34'S, 57°01'W). The climate is tropical, with mean annual temperatures between 20 and 28 °C and a marked rainy season, resulting in relatively low annual precipitation values, between 1000 and 1400 mm. There is a flood peak due to precipitation between December and February, and a second peak due to drainage of waters from the northern region, peaking between June and July (Adámoli, 1986).

The study sites were located along about 25 km of MS-325, a secondary road that crosses a large area seasonally flooded by the Corixo Mutum, which is part of the Miranda River catchment, with the water slowly moving through the area for several months (Boock et al., 1994). The landscape is dominated by monospecific stands of *Copernicia alba* Morong, a palm tree with 8–20 m high which may cover 60% of the substrate in dense areas (Boock et al., 1994). In this area, *C. alba* is used as feeding perch by snail kites. Thus we considered a priori that areas with high densities of snail kites would be the ones with dense *C. alba* trees (generally more than 20 trees at the sampling site), whereas areas of low snail kite density would be those with rare occurrence of *C. alba* (fewer than three trees at the sampling site).

To verify whether snail kite densities corresponded to areas previously considered as high- or low-density areas, the numbers of individuals at the study sites were estimated. At each site, all individuals observed in the morning during a period of 15 min in a circle with a 100 m radius were counted, resulting in a sampling area of 3.14 ha. All limpkins present in the sampling areas were also recorded.

2.2. Data collection

This study was carried out between March and May 2002. Six sites were studied, three sites with a high-density of *C. alba* and another three with a low-density, which were randomly selected from the available ones. Each site was located at least 2 km from each other. Thus, there was one treatment

with two levels (high or low densities), each level with three replicates. To determine the prey available to the predators, we sampled marginal vegetation areas at each site, where water depths varied between 0.2 and 0.6 m. At each site, four 1 m² quadrates were marked and, within each quadrate, all snails found were removed. In the laboratory, all the snails were identified to species and measured with a dial caliper to the nearest 0.1 mm. The following measures were obtained: shell length and width, and aperture length and width (for details, see Estebenet, 1998).

To determine the distribution of apple snail sizes consumed by snail kites and limpkins in areas with high or low *C. alba* density, two sites with high-density and another two with low-density were sampled. At each site, all shells found in piles near feeding areas of each species were collected. Piles made by limpkins were found on the margins of water-courses, with no trees nearby, whereas those made by snail kites were found under trees. All shells were identified and measured as described above, and we noted whether shells discarded by limpkins had holes in them.

2.3. Data analysis

Predator densities between high- and low-density areas of *C. alba* were compared with Student's t-test. The same tests were used to compare densities of *P. canaliculata* and *P. scalaris*, using mean densities per site as replicates. Density values were previously transformed to logarithms, to obtain homogeneity of variances, and residuals were analyzed graphically to check the effectiveness of the transformations. To compare the size distributions of available and consumed *Pomacea*, data from all measures were analyzed with principal components analysis (PCA). The first PCA axis of both species explained more than 99% of the variation, and all measured variables correlated highly with this axis, with coefficient values in excess of 0.99. Thus we chose to use only shell length data, to facilitate comparison of the data with other studies. Available size distributions between high- and low-density areas were compared with a Kolmogorov–Smirnov test (Sokal and Rohlf, 1995). The probability of consumption by predators (π) in relation to shell length (l) was evaluated from simple logistic regression models as follows:

$$\pi(l) = \frac{e^{\beta_0 + \beta_1 l}}{1 + e^{\beta_0 + \beta_1 l}}$$

where β_0 is a constant and β_1 is the slope of the logistic curve. The logit for this model is:

$$g(l) = \beta_0 + \beta_1 l$$

We estimated the shell length at the inflection point ($P_{50} = -\beta_0/\beta_1$) of the curves to evaluate the differences in the size of snails selected by the predators. The inflection point indicates the shell length where the chances of being captured is 50%; thus, snails larger than those at P_{50} are selected by the predators.

The curves of high and low *C. alba* density areas were compared by adjusting a model containing the factor density

(d), the covariable shell length (l), and their interaction; the logit for this model is (Hosmer and Lemeshow, 1989):

$$g(d, l) = \beta_0 + \beta_1 l + \beta_2 d + \beta_3 dl$$

where β_2 is the density coefficient and β_3 is the coefficient of the interaction (density vs. shell length). When the interaction was not significant, we adjusted a model without this term to estimate the effect of density (Hosmer and Lemeshow, 1989).

3. Results

3.1. Predator and prey densities

Sites with high densities of *C. alba* perches were confirmed to influence the density of snail kites, resulting in predator densities 2.6 times higher than at sites with low densities (Table 1). On the other hand, the density of *C. alba* did not influence limpkin densities, with no significant differences between both areas (Table 1). On the other hand, densities of snails did not differ significantly between areas with high and low densities of *C. alba*, both for *P. canaliculata* and *P. scalaris* (Table 1).

3.2. Distribution of prey sizes available and consumed

Although snail densities did not differ significantly between sites with high and low *C. alba* densities, the size distributions of snails available differed both for *P. canaliculata* (KS = 0.435, $P < 0.001$) and *P. scalaris* (KS = 0.487, $P < 0.001$). For both species, larger individuals were more frequent at low *C. alba* density sites (Figs. 1 and 2). Size distributions of available *P. canaliculata* and *P. scalaris* were bimodal, due to the presence of both juveniles and adults in the population (Figs. 1 and 2).

Almost all the snails eaten had a shell length greater than 25 mm, the size of adult individuals (Estebenet and Martín, 2002). The shell lengths of *P. canaliculata* captured by limpkins ranged between 23.8 and 90.2 mm, whereas those captured by snail kites ranged between 24.0 and 86.0 mm. For *P. scalaris*, shell lengths of captured snails varied between 29.4 and 57.9 mm for limpkins and 37.5–59.5 mm for snail kites.

Table 1 – Mean densities (\pm 95% CI, $N = 3$) of predators (numbers per ha) and prey (numbers per m^2) at sites with high and low densities of *C. alba* in the Brazilian Pantanal

	High-density	Low-density	t
Predators			
<i>R. sociabilis</i>	15.7 \pm 2.8	6.1 \pm 2.8	3.20 *
<i>A. guarana</i>	4.1 \pm 3.8	6.9 \pm 1.9	-1.47 ^{ns}
Prey			
<i>P. canaliculata</i>	21.4 \pm 42.9	22.4 \pm 2.8	-0.053 ^{ns}
<i>P. scalaris</i>	12.7 \pm 9.0	41.2 \pm 4.4	-1.921 ^{ns}

Values were back-transformed from log-transformed data; results of Student's t-tests ($df = 4$) are also shown; * $P < 0.05$, ^{ns} $P > 0.05$.

Thus, selection for larger snails was statistically significant in all cases (Table 2). However, the slopes of the regression curves differed between the high and low *C. alba* density sites in most cases (Table 3 and Fig. 3).

Limpkins responded differently to shell length increases of *P. canaliculata* between the high and low *C. alba* density sites (Table 3). Limpkins respond faster to increases in shell length at high-density sites, as indicated by the differences in β_1 (Table 2). On the other hand, the interaction was not significant for *P. scalaris* (Table 3), and the chances of predation with increases in shell length were similar between both areas. The model without the interaction term showed that the effect of density was highly significant ($\beta_2 = 1.910$, $P < 0.001$), so that snail sizes at P_{50} in the low-density sites were 66% larger than those at high-density ones (Table 2).

Limpkins made holes selectively in different sized shells for *P. canaliculata*, with larger shells more likely to be damaged both in areas of high (KS = 0.335, $P < 0.001$) and low *C. alba* density (KS = 0.143, $P = 0.048$) (Fig. 4). On the other hand, smaller shells of *P. scalaris* had more holes in high *C. alba* density sites (KS = 0.273, $P < 0.001$), but no differences were found at low-density sites (KS = 0.288, $P > 0.30$).

Snail kites responded faster to shell length increases of both *P. canaliculata* and *P. scalaris* individuals at high *C. alba* density sites when compared to areas with low-density of *C. alba* (Fig. 3 and Table 2). Thus, there was a significant interaction between adjusted logistic regression curves for these sites (Table 3). However, the results for *P. canaliculata* should be examined with caution, because of the weak fit of the logistic regression for the low-density sites ($Rho^2 = 0.27$; Table 2).

4. Discussion

In the wetlands studied, sites with high availability of perches, represented by high densities of *C. alba*, allowed a higher density of foraging snail kites, with almost three times more kites than at sites where few perches were available due to low *C. alba* densities. Snail densities did not differ between areas with high and low *C. alba* densities, and both areas should be equally selected by foraging snail kites. In a study carried out in Guyana, Bourne (1985a) showed that snail kites choose foraging patches by first selecting patches with more prey, and then selecting those with the largest individuals. Thus, the main determinants of foraging strategy and success of these predators must be directly related to habitat structure due to the availability of feeding perches, or indirectly by different densities of foraging kites. The snail kite uses two different hunting strategies, course-hunting or still-hunting, but the latter strategy is more frequently used when perch availability is high (Snyder and Snyder, 1969). When there is a low availability of feeding perches, still-hunting is more used by young birds (Beissinger, 1983). Thus, the availability of appropriate perches can influence the local density and foraging behavior of snail kites. Although the importance of habitat structure and consumer density on predator-prey interactions is recognized (e.g. Nilsson et al.,

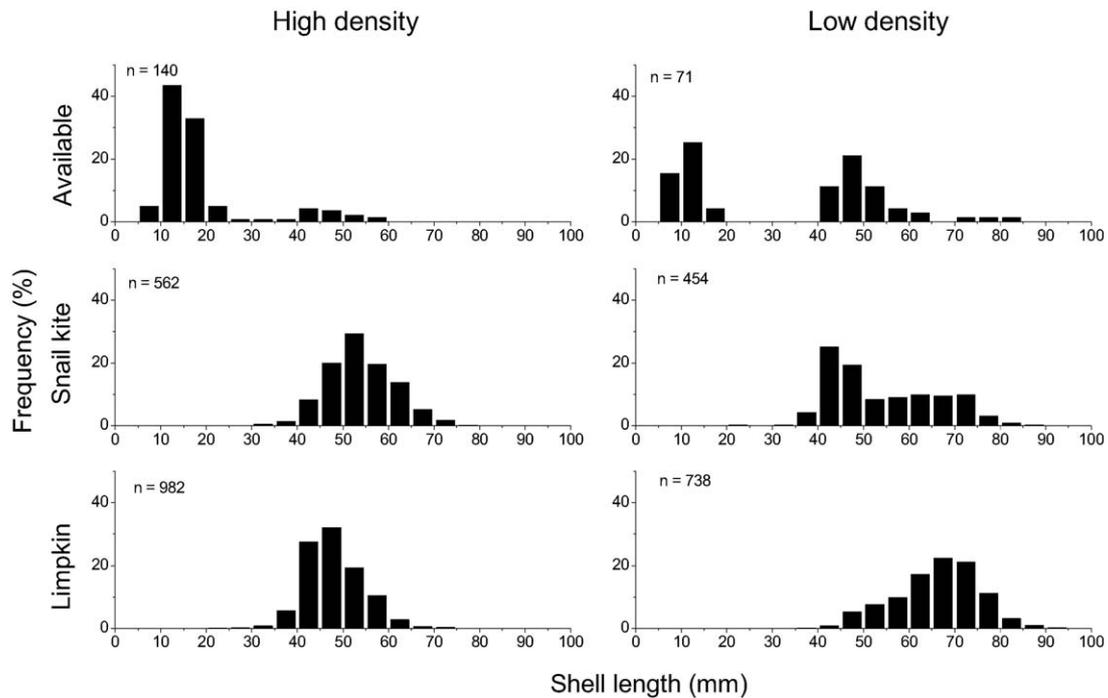


Fig. 1 – Distribution of shell lengths of *P. canaliculata* available in the meadows and found in piles made by foraging snail kites and limpkins, at sites with high and low densities of *C. alba*.

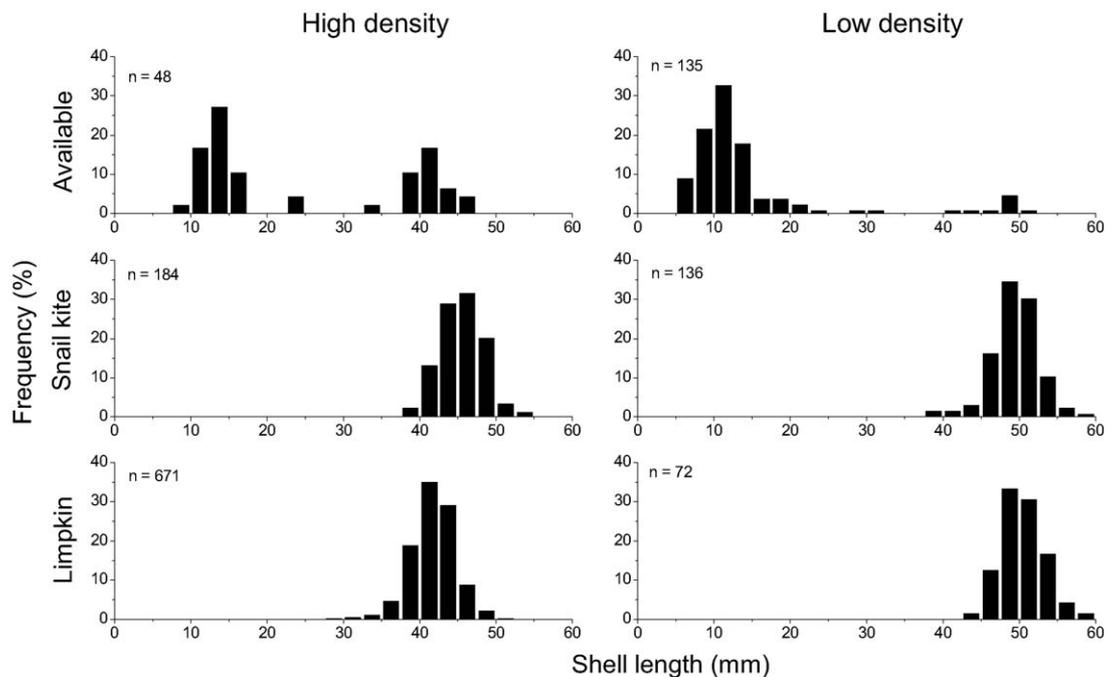


Fig. 2 – Distribution of shell lengths of *P. scalaris* available in the meadows and found in piles made by foraging snail kites and limpkins, at sites with high and low densities of *C. alba*.

2000; Triplet et al., 1999), their influence on foraging strategies of snail kites and limpkins has been overlooked.

Both species of predator showed differences in the size of prey consumed in areas with high and low densities of *C. alba*. However, prey-size distributions also varied between

areas, with larger *P. canaliculata* and *P. scalaris* available at low *C. alba* density sites. Consumer density and habitat structure influenced the foraging behavior of limpkins, although they selected larger individuals of both species in both areas. At low *C. alba* densities limpkins consume a greater range of

Table 2 – Logistic regression analysis for the effect of shell length of two *Pomacea* species on the probability of predation by limpkins and snail kites in areas with high and low-density of *C. alba*. β_1 is the parameter estimate, P_{50} is the shell length where the probability of consumption by predators is 50%, G is the estimate of the likelihood ratio test, Rho^2 is McFadden's statistic

	β_1	SE (β_1)	P_{50} (mm)	G	P	Rho^2
<i>P. canaliculata</i>						
Limpkin						
High-density	0.244	0.019	28.81	625	< 0.001	0.74
Low-density	0.183	0.123	41.97	260	< 0.001	0.54
Snail kite						
High-density	0.228	0.023	34.19	549	< 0.001	0.78
Low-density	0.098	0.012	26.13	113	< 0.001	0.27
<i>P. scalaris</i>						
Limpkin						
High-density	0.251	0.033	26.83	169	< 0.001	0.48
Low-density	0.474	0.163	44.48	219	< 0.001	0.82
Snail kite						
High-density	0.588	0.125	39.37	147	< 0.001	0.62
Low-density	0.273	0.060	38.53	307	< 0.001	0.82

Table 3 – Comparison of logistic regression curves for the effect of shell length of two *Pomacea* species on the probability of predation by limpkins and snail kites between areas with high and low-density of *C. alba*

	<i>P. canaliculata</i>		<i>P. scalaris</i>	
	Limpkin	Snail kite	Limpkin	Snail kite
Constant	-7.678 ***	-2.558 ***	-21.080 **	-10.516 ***
Shell length (l)	0.183 ***	0.098 ***	0.474 **	0.273 ***
Density (d)	0.650 ns	-5.226 ***	14.338 ns	-12.644 *
Interaction (ld)	0.061 *	0.130 ***	-0.223 ns	0.315 *

***P < 0.001; **P < 0.01; *P < 0.05; nsP > 0.05.

P. canaliculata sizes by incorporating larger snails when compared to high-density sites, probably because of the higher availability of larger prey at low-density sites. On the other hand, limpkins did not present differences in prey-size selectivity for *P. scalaris* (as suggested by the non-significant interaction term), but these predators captured larger *P. scalaris* at low *C. alba* density areas when compared with higher density areas. These results differ from the patterns of prey-size selection described in other regions, where limpkins showed preferences for small and medium sizes of other *Pomacea* species (Bourne, 1993; Collett, 1977; Reed and Janzen, 1999). Thus, this study shows for the first time that limpkins select larger prey when large individuals are available. Bourne (1993) suggested that prey sizes selected by limpkins could be related to resource partitioning with snail kites, with limpkins selecting medium-sized apple snails and snail kites selecting large snails. On the other hand, Reed and Janzen (1999) suggested that large snails would incur greater handling costs, as evidenced by the presence of holes in larger shells of consumed snails, a pattern also recorded in the high *C. alba* density areas of our study. Our data suggest that there may be no differences in energetic costs when consuming different sized prey at low *C. alba* density areas, because there was no significant difference between shells of *P. scalaris* with or without holes, and a marginal value was found for *P. canaliculata*. Thus, when faced with different sized prey at low *C. alba* density sites, limpkins would have a greater energetic return when selecting larger individuals,

since handling costs would be equivalent. Alternatively, the higher density of foraging snail kites at high *C. alba* density areas could result in a higher frequency of interactions between both predator species, resulting in capture of smaller prey due to lower handling costs. Snail kites can influence limpkin foraging due to kleptoparasitism, a behavior observed in Belize when prey availability was very low (Miller and Tilson, 1985).

On the other hand, snail kites presented different responses to the differences in habitat structure provided by *C. alba* perches. As previously found in other systems, snail kites selected individuals that tended to be larger than those available in both *Pomacea* species (Bourne, 1993; Collett, 1977; Magalhães, 1990), but our results suggest that the probability of capturing smaller snails differs between areas. At low *C. alba* density areas, snail kites incorporate smaller prey in their diet when compared to high-density sites, resulting in a greater range of apple snail sizes. Although the model fit was weak for *P. canaliculata* at low-density sites, the pattern was similar to the found for *P. scalaris*, where the fit was much better (Table 2). The selection for smaller prey at low *C. alba* density areas is not related to differential availability. As there are fewer perches per unit area, it is possible that the snail kites have to fly further with the prey compared to high *C. alba* density areas, and thus expend more energy when carrying large prey rather than smaller ones. The largest snail captured in the high-density sites had a total mass of 159 g, whereas the corresponding value in low *C. alba* density areas was 111 g, a 40% difference [calculated using equations in Guedes et al. (1981)]. Considering that snail kites have an average body mass of 394 g for males and 446 g for females (Sykes et al., 1995), the maximum size of *P. canaliculata* at high *C. alba* density areas would represent 40% of the body mass of male snail kites and 35% of the females, whereas at low *C. alba* density areas the corresponding values would be of only 28% and 25% of the snail kite body mass, respectively. Since the predominant strategy is still-hunting at sites with high availability of feeding perches (Beissinger, 1983; Snyder and Snyder, 1970), there should be an interaction between the availability of adequate perches and the optimal size of selected prey. The existence of more

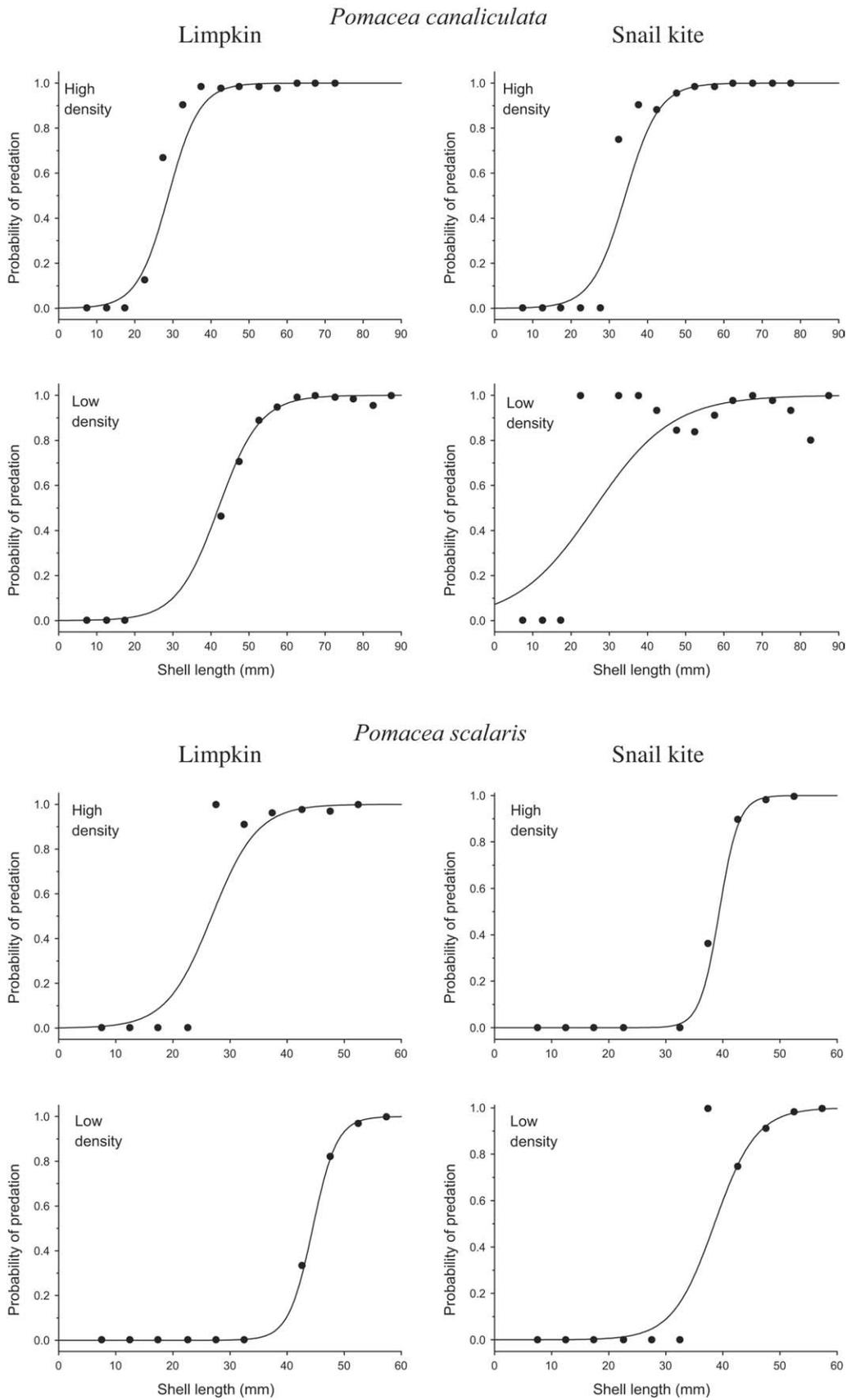


Fig. 3 – Probability of predation by limpkins and snail kites at sites with high and low densities of *C. alba* in relation to shell length of *P. canaliculata* and *P. scalaris*. Circles indicate the midpoint of 5 mm classes, lines were fitted by logistic regression models.

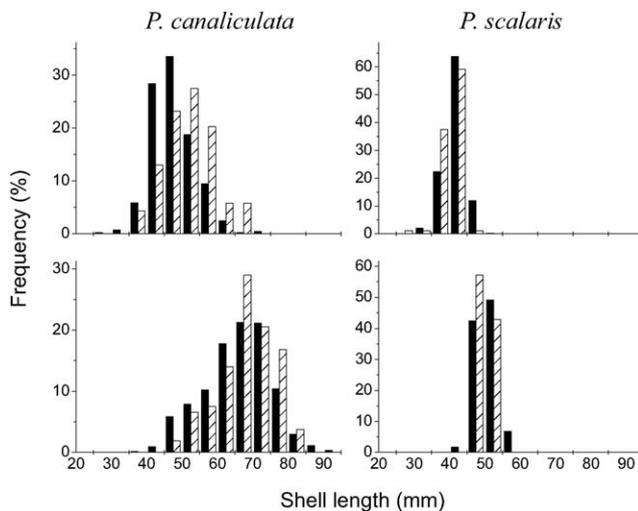


Fig. 4 – Distribution of shell lengths with (hatched bars) and without (black bars) holes of *P. canaliculata* and *P. scalaris* consumed by limpkins, at sites with high (upper panels) and low densities of *C. alba* (lower panels).

perches could allow smaller return times, enabling the capture of larger prey. Two alternative hypotheses to explain the capture of smaller *P. canaliculata* by snail kites at low *C. alba* density areas can also be proposed, although they are not mutually exclusive. First, areas with higher availability of feeding perches could be higher quality sites to locate and manipulate prey. Thus, adult snail kites could concentrate in these areas, excluding younger individuals to lower quality areas. Young kites may have lower energetic needs and hunt less efficiently than adults, so that their optimal prey-size could be smaller, as found by Bourne (1985b). Second, the higher density of foraging kites could result in higher energy expenditure per individual because of increased aggressive interactions in disputes for prey and perches, so that more energy per captured prey is needed (Beissinger, 1983). Snyder and Snyder (1970) observed aggression in feeding territories in Florida, where adequate perch availability was high, and Beissinger (1983) verified that in an area that apparently had a lower availability of perches, less than 0.1% of snail kite daily activities were aggressive. Thus, at low *C. alba* density sites, where competition is lower, energetic costs would be related only to foraging activities, enabling the exploitation of smaller prey, which are more easily found around the few available perches. In this situation, the energetic return when capturing smaller prey would compensate for the low energetic requirements of other activities when compared to high *C. alba* density sites (Stillman et al., 1997).

Prey-size preferences of predators in natural systems have been studied mainly in relation to changes in prey availability (Tyrrell and Hornbach, 1998; Ward, 1991), whereas the effects of consumer density were evaluated mainly in laboratory studies (Nilsson et al., 2000) or evaluating total prey consumed (Stillman et al., 1996, 1997). Although differences in prey-size selection and hunting behavior between snail

kites and limpkins have been recognized (Beissinger, 1983; Bourne, 1993; Reed and Janzen, 1999), our study is the first to suggest that habitat structure and forager density can influence the decisions taken by these predators when foraging. The variation in patterns of prey-size selection described in other studies could possibly reflect differences in predator densities at distinct temporal and spatial scales. The variation in predator densities, together with the distribution of available prey sizes, can influence the decisions of the predators when foraging at different places. The flexibility of prey-size selection in relation to predator density and habitat structure suggests that this system could be of great value to understand the factors that influence foraging decisions in natural systems, and the consequences of this variation to predator and prey distribution.

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