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The influence of energy, nutritional value and noxiousness of prey in sex- and size-biased predation by Snail Kites in southern South America

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ABSTRACT

Snail Kites (*Rostrhamus sociabilis*) feed almost exclusively on Apple Snails (*Pomacea* spp.). While field observations indicate they discard the noxious albumen gland (AG) when feeding on female snails, there is no information on the energy lost by this behaviour, the gland composition, or whether there are associated snail sex preferences. We addressed, for the first time, these aspects for Snail Kites foraging on *Pomacea canaliculata* in southern South America. The whole snail's biochemical composition exhibited significant differences between sexes. Proteins and carbohydrates were the major energy-providing components. Soft parts provide $\sim 2.91 \pm 0.16$ and 2.50 ± 0.14 Kcal g⁻¹ dry weight (dw) for male and female without the AG, respectively, while the AG accounts for 15% of available energy. The size and sex of prey consumed, determined at foraging perches sampled monthly, showed that Snail Kites preferentially fed on the largest snails available throughout the sampling period. Even though the remains of the female body without the AG have less energy than males, sex preferential predation towards females was observed. Our study demonstrates, for the first time, the optimal foraging trade-off between prey size/sex and nutrition/energy in Snail Kites. After discarding the AG, male and female snails of equivalent size provide different nutrients and energy, though Snail Kite foraging is generally biased towards females mostly as a result of their larger size, suggesting that Snail Kites are unable to distinguish between the sexes.

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Introduction


Specialised predators are more extinction-prone than generalists (Owens and Bennett 2000) and may be particularly sensitive to environmental effects on subtle aspects of predation behaviour. Snail Kites (*Rostrhamus sociabilis*; Accipitridae) feed almost exclusively on Apple Snails (Ampullariidae). Snail Kite distribution demonstrates a marked dependence on *Pomacea* species and results in a nomadic behaviour, migrating in response to changes in snail availability and distribution (Bennetts and Kitchens 2000). Snail Kites are one of the main avian predators of Apple Snails (Hayes *et al.* 2015) and their interaction provides an excellent predator-prey model for examining nutrient and energy transfer.

The foraging and hunting behaviours of Snail Kites have been studied for some of the northern

species of Apple Snails (Beissinger 1983; Snyder and Kale 1983). After finding and capturing a snail, they carry them to feeding perches to consume the soft parts, leaving the operculum and the shell intact, which accumulate below the perches (Snyder and Kale 1983; Sykes 1987). They usually consume the largest available snails (Beissinger 1983; Tanaka *et al.* 2006), but there are, however, no reports analysing the sex of the ingested prey. Some field reports state that Snail Kites also discard a bulky accessory reproductive organ called the albumen-capsule gland complex or pallial oviduct, commonly referred to as the albumen gland (AG), when feeding on female snails (Snyder and Kale 1983). The AG synthesises the egg perivitelline fluid providing nutrients, protective compounds, and the calcareous eggshell (Catalán *et al.* 2006; Hayes *et al.* 2015). However, its biochemical composition is unknown for *Pomacea* species.

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Interestingly, several *Pomacea canaliculata* egg proteins are toxic, anti-nutritive and anti-digestive for different animals (Dreon *et al.* 2013). These defensive proteins are already active within the AG, and are the most probable reason for the rejection of the AG by predators (Cadierno *et al.* 2017).

In their southern distribution limit (Southern Pampas, Argentina), the staple prey of the Snail Kite is *P. canaliculata* (Lamarck, 1822), the most conspicuous and abundant snail in lentic waterbodies (Martín *et al.* 2001). In this temperate region *P. canaliculata* remains active and available for Snail Kites during the reproductive season from October to March (Estebenet and Martín 2002). This snail exhibits a marked sexual dimorphism in size and age at maturity; females are bigger and mature later than males (Estebenet *et al.* 2006). Few studies have focused on *P. canaliculata* as Snail Kite prey in this region, reporting the size of preyed or living snails (De Francesco *et al.* 2006; Mapelli and Kittlein 2011).

We hypothesise that consumption of female snails represents a disadvantage from nutritional and energetic viewpoints. We expect that females' edible parts would have a lower energy content compared to males of an equivalent size and that the Snail Kite behaviour of discarding the AG would be reflected in prey selection by sex.

Methods

Biochemical composition and energy content

Pomacea canaliculata were collected from a pond (La Plata, Argentina) during the reproductive season. Nine copulating couples were captured. Soft parts from males and females and the AG were removed and weighed. The biochemical composition of the whole male body, female body (without the AG) and the AG was determined in three pools of three individuals/organs each. Analysis was performed and energy conversion factors were determined as described previously (Heras *et al.* 1998).

Snail body weight and caloric content

To compare the energetic content of female and male snails according to their size, we estimated the dry biomass for snails measuring 20–80 mm using the shell length-dry weight relationship published by Estebenet (1998) as $dw = a * size^b$ (common slope for both sexes: $b = 3.164 \pm 0.086$; male $\log(a) = -2.151$; female $\log(a) = -2.034$). We then calculated the values for females without the AG by

determining the AG dry weight percentage related to the whole soft parts of 34 females. This was considered constant along the size range of interest for calculations. Applying the model and relationships in Estebenet (1998) and the AG data from this study, we estimated the average dry weight and caloric content for male and female as a function of shell length.

Snail Kite preferences for snail sizes and sexes

To know what is actually consumed by Snail Kites as a function of prey sex and size, we undertook a study at Piedras Moras reservoir, Argentina, during the snail reproductive season.

Each month we conducted a snail population census by standardised wading (Burela and Martín 2014). Collected snails were sexed on the basis of operculum shape (Estebenet *et al.* 2006) and their shell length was registered, from apex to the opposite aperture end, to the nearest tenth of a millimetre. With the use of this method we were able to register snails >20 mm, which was appropriate considering Snail Kites are not able to manipulate smaller prey items. Additionally, empty snail shells were collected from five Snail Kite feeding perches which were easily recognised because of their distinctive features, particularly by the near absence of shell damage which contrasts with those shells discarded by other predators (De Francesco *et al.* 2006). Feeding perches were cleared of any shells before the beginning of the study. Shells were sexed based on aperture shape differences (Estebenet *et al.* 2006; Tamburi and Martín 2013), and their length measured and analysed using size classes.

Statistical analysis

Biochemical composition was analysed by *t* tests. For prey selection by size and sex, the forage ratio index (Manly *et al.* 2002) was employed. This is defined as $W_i = U_i/A_i$, where W_i = the forage ratio for item *i*, U_i = the proportion of item *i* in the diet (perches), and A_i = the proportion of item *i* available in the environment (snail population); the statistic $(W_{i-1})^2/ES (W_i)^2$ was calculated and compared with a critical chi-square value ($df = 1$). W_i was calculated for males and females of different size classes (pooled for all the sampling period) and for both sexes for each sampling date (pooling all the size classes to estimate W_i using U_i from a given month and A_i from the previous month). The degree of sexual bias in the prey selection in each month was estimated as the difference between the W_i of both sexes. Intersexual size differences were analysed by means of Mann-Whitney's two-sample rank test; the degree to which females oversize males or vice

versa was estimated monthly as the difference in the mean rank of both sexes.

Results

Biochemical composition and energy content of snail tissues

The major nutrients of the soft parts in the male and female were proteins, followed by carbohydrates and lipids (Table 1). Only protein levels differed between sexes, with females having less protein than males ($P = 0.038$). The average caloric content of male and female edible tissues, 2.9 ± 0.2 and 2.5 ± 0.1 Kcal g^{-1}

dw, respectively, was significantly different ($P = 0.029$) (Table 1). Likewise, the biochemical composition of the AG showed that proteins and carbohydrates were also the major components (Table 1).

Female and male biomass and caloric content as a function of snail size

The AG represents up to $28 \pm 6\%$ of female dry weight, indicating that Snail Kites discard nearly one-quarter of the whole snail dry biomass. The average whole dry weight and caloric content for male and female (with and without the AG) as a function of snail size are shown in Figure 1(A, B), respectively. For any given

Table 1. Comparison among the energetic and nutritional content of soft parts of *Pomacea* Apple Snails.

	Snail species				
	<i>P. canaliculata</i> ^a			<i>P. maculata</i> ^b	<i>P. paludosa</i> ^c
	Male	Female ^d	AG		
Kcal g^{-1} dw	2.9 ± 0.2	2.5 ± 0.1	1.6 ± 0.02	3.3 ± 0.1	4.6 ± 0.2
Total glucids	10.8 ± 2.7	6.9 ± 1.6	4.7 ± 0.6	11.0 ± 5.6	NA
Proteins	47.6 ± 1.0	41.7 ± 3.2	16.6 ± 0.9	63.6 ± 6.3	36.3
Lipids	5.4 ± 0.3	5.4 ± 0.4	3.3 ± 0.2	2.9 ± 0.2	3.4
Polysaccharides	4.7 ± 1.7	2.4 ± 1.6	4.0 ± 0.6	NA	NA
Soluble glucids	6.0 ± 2.7	4.6 ± 1.6	0.7 ± 0.2	NA	NA
Ashes	NA	NA	NA	22.5 ± 2.5	32.1
Moisture	81 ± 1.0	81 ± 2.1	57.9 ± 5	86.6 ± 2.4	85.5

Biochemical composition is expressed as percentage dry weight (dw) \pm SD. NA: not available.

^a Determined in this study.

^b Cattau *et al.* (2010).

^c Sykes (1987).

^d Female without albumen-capsule gland complex (AG).

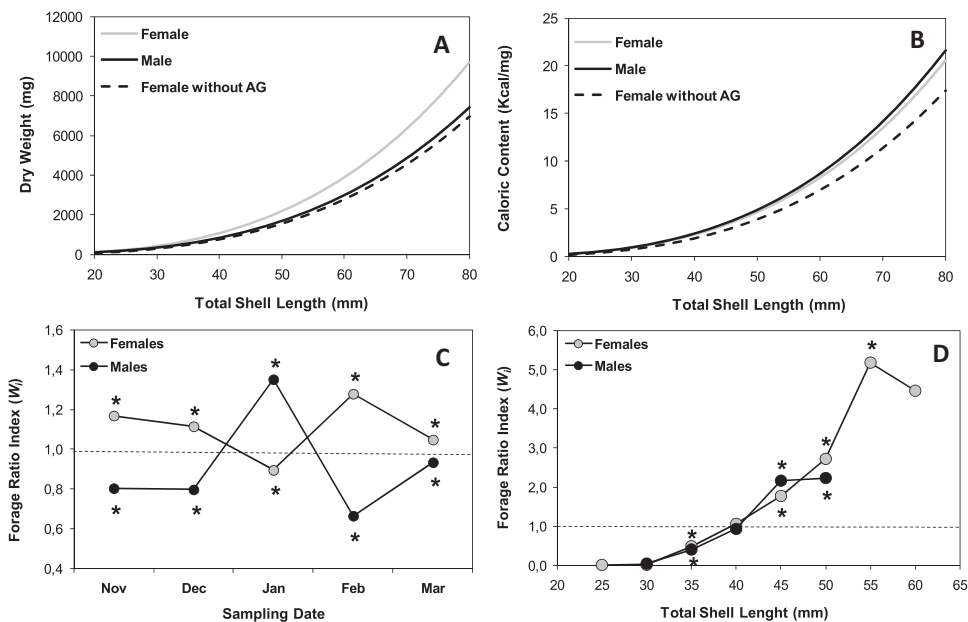


Figure 1. Prey characteristics and Snail Kite prey selection. (A) Allometric relationship for the snail biomass (dry weight, mg) and (B) energy provided by *P. canaliculata* (caloric content, Kcal mg^{-1}). Scatterplot of dry weight values vs. total shell length. Estimated values were based on Estebenet (1998) together with data generated in the present study. (C) Forage ratio index (W_i) for male and female snails during the sampling period and (D) different sizes. The index considers the proportion of the item in the diet and its availability in the environment (determined from a snail population census). Values <1 and >1 indicate negative and positive selection, respectively. * Significant departure from no-selection ($W_i = 1.0$).

size, females are significantly heavier than males. The remains of the female body after discarding the gland showed an average biomass roughly equivalent to that of a male of the same size; they are only 6% lighter than male soft parts (Figure 1(A)). However, the remains of female soft parts effectively eaten have nearly 19% less energy than those of a male of equivalent size (Figure 1(B)).

Kite preferences for snail size and sex

Living snails showed a mean shell length of 36.11 ± 6.11 mm while those consumed by Snail Kites had a mean size of 40.80 ± 4.72 mm ($n = 1571$ living snails and 2564 empty shells). The average sex ratio in the population and Snail Kite perches was biased towards females (61.8% and 67.4%, respectively).

The forage ratio index (W_i) showed that Snail Kite predation was significantly female-biased in all months except for January (Figure 1(C)); in both sexes sizes >40 mm were positively selected whereas those <30 mm were negatively selected or not preyed at all (Figure 1(D)). The comparison of the mean rank in shell length of both sexes in the population showed that the size distribution of females oversizes significantly that of males in October ($P = 0.018$) and January ($P = 0.001$), whereas males oversize females only in December (chi-square = 26.7, $P = 0.001$); the distributions were not significantly different in November and February ($P = 0.83$ and $P = 0.45$, respectively). There was a significant correlation ($r = 0.96$, $P = 0.008$) between the degree to which females oversize males in a given month and the degree of predation bias towards females in the same month (see supplemental material Figure S1).

Discussion

Energy content and nutritive value of Apple Snails and the albumen-capsule gland

The biochemical analysis of snails' macronutrients indicates that there are significant intersexual differences in the edible tissues regarding both the main carbon sources and their energy content, mainly as a result of the higher protein content of male tissues. Thus, despite its equivalent biomass content, at a similar snail size, a Snail Kite preying on a female and discarding the noxious AG incorporates less energy than preying on a male. Furthermore, the energetic cost of transporting and the time spent handling females to discard the gland may further decrease its fitness, though this action has been

considered energetically not relevant compared to the energy required for hunting (Beissinger 1983). The AG composition was hitherto unknown for the genus, and, not surprisingly, it was rich in carbohydrates and proteins and similar to that of *P. canaliculata* eggs (Heras *et al.* 1998). The energy content of *P. canaliculata* tissues is somewhat lower than that reported for other *Pomacea* species (Beissinger 1983; Sykes 1987; Cattau *et al.* 2010), perhaps owing to differences in the methodology applied (Sykes 1987). The somewhat low energetic content of Apple Snails may be compensated by the high densities and biomasses and large adult sizes (Hayes *et al.* 2015) which may ensure the availability of enough biomass to sustain Snail Kite populations.

Prey selection by sex and by size

The energetic results indicated that selection on the snails consumed should be biased towards males. However, the forage ratio index showed that females were preferentially selected during most of the sampling period. Snails Kites are probably not able to differentiate between the Apple Snail sexes and hence other traits overcome sex as the cue to obtain prey with the highest profitability. The nomadic migratory behaviour of Snail Kites (Bennetts and Kitchens 2000) drives them to forage on different species of Apple Snails which may differ in their secondary sexual dimorphism (Estebenet *et al.* 2006; Hayes *et al.* 2015) or the noxiousness of the AG, probably precluding the evolution of a more selective predation towards males.

The female-biased predation observed herein is likely a by-product of the preference for big snails because females were generally bigger. On the whole, sex bias in predation depends on which sex is bigger at a given time. A preference to forage on larger snails has been observed along the whole range of Snail Kite distribution (present paper; Beissinger 1983; Tanaka *et al.* 2006; Mapelli and Kittlein 2011) and has a firm basis in energetic profitability (Beissinger *et al.* 1994); the positive size selection towards adult snails could also reflect that Snail Kite talons and bill are better suited for larger snails or that larger snails are easier to spot. As *Pomacea* females are generally bigger than males in most populations (Estebenet *et al.* 2006; Hayes *et al.* 2015), this evidence indicates that predation biased to females is probably a common feature of the interaction between the Snail Kite and Apple Snails in most of their geographical range. However, Snail Kite prey selection by sex was not studied before precluding further comparisons.

Conclusion

The fitness of individual Snail Kites and the viability of their populations depend primarily on the abundance of Apple Snails but also on their population structure, distribution, behaviour and somatic composition (Beissinger *et al.* 1994; Darby *et al.* 2007). Our research provides evidence that the behaviour of discarding the AG does have an impact on the energy and nutrients taken by Snail Kites, although this is not reflected in a sex preferential predation. However, the impact it may have on their fitness and the viability of their populations could also rely on the Apple Snail sex ratio which is known to be variable among populations and during the reproductive season. Further studies are needed to evaluate this issue in Snail Kite populations from the northern range of distribution where *P. canaliculata* is a major invasive species and provides a critical resource for native Snail Kites (Cattau *et al.* 2010).

Geolocations: La Plata pond 34°54'38" S; 57°56'17" W; Piedras Moras reservoir 32°10'23" S; 64°14'57" W, Argentina.

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Ethics statement

This research was conducted in compliance with the *Guidelines to the Use of Wild Birds in Research*.

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