

PREY PREFERENCE AND PREDATORY BEHAVIOR OF *Aurantilaria aurantiaca* (MOLLUSCA: GASTROPODA: FASCIOLARIIDAE)

Preferência de presa e comportamento predatório de *Aurantilaria aurantiaca* (MOLLUSCA: GASTROPODA: FASCIOLARIIDAE)

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RESUMO

A família Fasciolariidae é formada por espécies carnívoras que usualmente predam outros gastrópodes e bivalves. Geralmente utilizam como estratégia de predação, o lascamento de concha, meio pelo qual o predador pode alcançar as partes moles da presa. Os objetivos desse trabalho foram determinar as possíveis presas de *Aurantilaria aurantiaca* da Praia do Pacheco (Caucaia-CE-Brasil) e a sua preferência alimentar em condições de laboratório. As presas observadas foram os gastrópodes *Pisania pusio*, *Tegula viridula* e *Stramonita brasiliensis*. O experimento de preferência de presa foi executado acondicionando um predador em um aquário de 5 litros com um indivíduo de cada presa, sendo observado durante 60 dias (replicado 10 vezes). Para a determinação do tempo de manipulação da presa, um predador foi acondicionado em uma caixa plástica mergulhada em um aquário de 80 litros juntamente com uma espécie de presa, sendo anotado o tempo de predação por duas 2 horas, durante 30 dias (replicado 10 vezes para cada espécie de presa). *Aurantilaria aurantiaca* mostrou preferência por *Stramonita brasiliensis*, o qual teve o mais baixo tempo de manipulação da presa. *Pisania pusio* e *Tegula viridula* não apresentaram resultados estatisticamente significativos ($p = 0.7235$ e 0.2499 , respectivamente). O comportamento predatório mostrou 2 estratégias: penetração direta da probóscide e sufocamento. Não houve registro de lascamento de concha. *Aurantilaria aurantiaca* apresentou-se como um predador generalista, onde a variação de tempo de manipulação da presa mostrou que o predador passou por um processo de aprendizagem.

Palavras-chave: Predação, Tempo de Manipulação da Presa, Mollusca, Gastropoda, Fasciolariidae, *Aurantilaria aurantiaca*.

ABSTRACT

Fasciolariid species are predators that prey on other gastropods and bivalves. They usually break prey shell to reach its soft parts. In this study, prey species that *Aurantilaria aurantiaca* consumes at Pacheco Beach (Ceará State, Northeast Brazil) and its prey preference in laboratory conditions were determined. Prey species observed were *Pisania pusio*, *Tegula viridula* and *Stramonita brasiliensis*. Prey preference experiment was performed placing one individual of *Aurantilaria aurantiaca* and one individual of each prey species in a 5 liters tank. It lasted 60 days and was replicated 10 times. Handling time of predation on each prey was measured by placing one predator with one prey into separate plastic containers in an 80 liters tank. Observations were made every 2 hours over a 30-day period. *Aurantilaria aurantiaca* showed preference for *Stramonita brasiliensis*, which presented the shortest handling time. *Pisania pusio* and *Tegula viridula* didn't show statistical significant results ($p = 0.7235$ e 0.2499 respectively). *Aurantilaria aurantiaca* presented 2 main predatory strategies: direct prey shell penetration and asphyxiating process. No damaged prey shells were observed. The predator showed a generalist predatory behavior. Prey handling time variations demonstrated that *Aurantilaria aurantiaca* predation act involved a training process.

Keywords: Predation, handling time, Mollusca, Gastropoda, Fasciolariidae, *Aurantilaria aurantiaca*.

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INTRODUCTION

A predator has to make decisions about what, where and when to eat (Krebs, 1977). According to optimal foraging theory (OFT), the feeding strategies presented by an organism are designed by natural selection to maximize its net rate of food intake (Krebs, 1977; Hughes, 1980).

Generalist predators have an important role in the community structure: they stabilize prey populations and affect the diversity of their communities through prey selection (Menge & Sutherland, 1976; Alford, 1989; Kurzava & Morin, 1998; Lambinet *et al.*, 2000). Few studies have quantitatively analyzed prey selection or prey composition of generalist predators (Spiller & Schoener, 1990; Wootton, 1997; Eisenberg *et al.*, 2000).

Feeding strategies may also differ with relation to the number of prey items eaten. Dietary generalists eat wider ranges of prey than dietary specialists (Curio, 1976). Specialization should be effective enough to achieve optimal hunting success but at the same time it should not be so rigid as to prevent the predator from changing from a particular and originally preferred prey species when that species becomes rare (Curio, 1976).

The food value of different food items can be compared by measuring their size, handling time (the time that a predator takes capturing, subduing, consuming, and digesting a prey) and / or caloric content (Matthews-Cascon, 1997).

The diet type and variety of mechanisms that are used in the search of food presented by members of Gastropoda are amazing if compared with other animal groups (Ankel, 1938; Graham, 1955; Owen, 1966). They show all different types of alimentary habits: herbivores, deposit-feeders, suspension-feeders, scavengers and parasites (Hughes, 1986). The main structure that allows this extensive alimentary variation is the complex formed by the radula/buccal cavity (Owen, 1966).

Some studies have been carried through evaluating aspects of behavior of gastropod predators using the optimal foraging theory (OFT) (Menge, 1978; Hughes & Dunkin, 1984a,b; Hughes & Drewett, 1985; McQuaid, 1985; Abe, 1989; Burrows & Hughes, 1989; Duarte, 1990; Palmer, 1990; Richardson & Brown, 1990; Hughes *et al.*, 1992; Richardson & Brown, 1992; Hughes & Burrows, 1994; Etter, 1996; Brown, 1997; Meirelles & Matthews-Cascon, 2003).

However, certain foraging behaviors of gastropod predators in the intertidal zone could not

have been explained by OFT (Abe, 1989; Hughes & Burrows, 1993). Sih & Christensen (2001) have concluded that the OFT could explain the prey selection if the predator feeds on sessile species. According to Yamamoto (2004) there is not enough information to explain the prey selection of predators that feed on the two types of prey species (sessile and mobile).

The biggest problem in evaluating the composition of prey in the natural environment neither is that the observation of the predatory behavior (observed diet) nor always indicates the composition of natural prey (real diet). A reason for this discrepancy is the regularity of foraging behavior in the intertidal zones (Yamamoto, 2004). Although many predators have different foraging behavior patterns between high tide and low tide, many of the studies were lead during low tide (Fairweather & Underwood, 1983; McQuaid, 1985; Moran, 1985b; Abe, 1989). Another reason is the difference in handling time in different types of prey, where those that demand a bigger time are more frequently observed (Peterson & Bradley, 1978; Fairweather & Underwood, 1983; Abe, 1989).

The gastropod family Fascioliariidae is formed by carnivorous species, usually preying on bivalves and others gastropods (Fretter & Graham, 1962; Paine, 1963; Owen, 1966; Matthews-Cascon *et al.*, 1989; Meirelles & Matthews-Cascon, 2003). It is attributed for this family, as strategy of predation, the prey shell chipping, means by which the predator can reach the soft parts of the prey (Hughes, 1986).

Paine (1963) studied the alimentary preference and the predation rate of *Triplofusus giganteus* (Kiener, 1840) in Florida, determining that this species is a generalist predator, also preying animals of the same subfamily as *Cinctura hunteria* (Perry, 1811) and *Fasciolaria tulipa* (Weisbord, 1962).

On the predation of *Aurantilaria aurantiaca* (Lamarck, 1816) two studies have been conducted: one by Schmitt (1994), that affirms its alimentary preference in laboratory conditions for *Fissurella rosea* (Gmelin, 1791) and the process of predation involves the braking of prey shell. The other Meirelles & Matthews-Cascon (2003) analyzes the relation that exists between shell size and radula size in 14 species of marine prosobranchs with different types of diet. *Aurantilaria aurantiaca* showed no significant result for this relation, demonstrating that radula size does not interfere on the prey processing.

In the present study, predatory behavior and prey preference of *Aurantilaria aurantiaca* in laboratory conditions were investigated.

MATERIALS AND METHODS

Field Studies

During the year of 2005, monthly observations of predatory activity of *Aurantilaria aurantiaca* (Figure 1) were made, during the low tides, at Pacheco Beach (3° 41'S; 38° 37'W), Ceará State, Northeast Brazil (Figure 2), to determine its possible preys.



Figure 1 - Adult individual of *Aurantilaria aurantiaca* from Pacheco Beach - Ceará State, Northeast Brazil (Shell length: 90 mm).

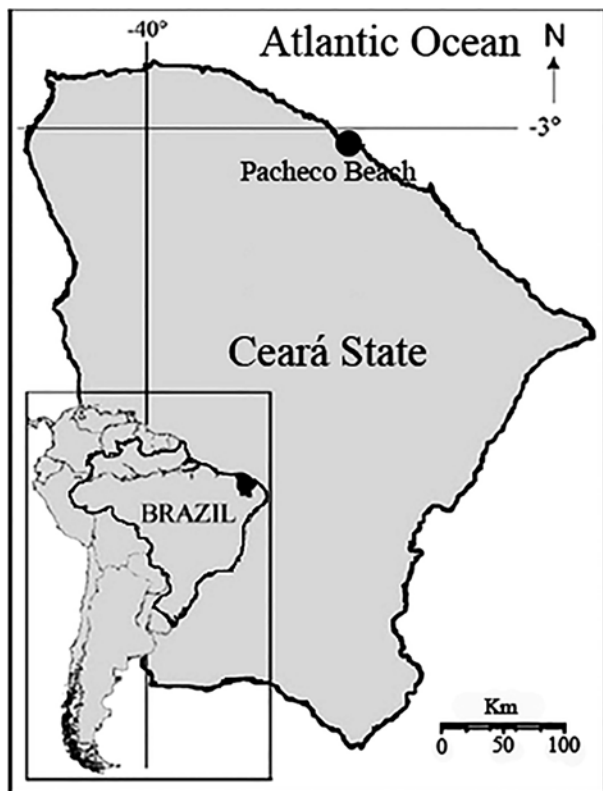


Figure 2 - Map indicating the sampling area at Pacheco Beach, Ceará State, Northeast Brazil.

Eighteen adult animals of *A. aurantiaca* were collected manually, kept in plastic boxes with constant aeration and transferred to the Laboratory of Marine Invertebrates of the Department of Biology - Universidade Federal do Ceará (UFC). Also the possible prey species available for the experiment in laboratory were collected.

Laboratory Proceeding

Five specimens of *A. aurantiaca* were anesthetized with a saturated solution of seawater + freshwater (1:1) and magnesium chloride during 3 hours. The animals were measured with a vernier caliper to 0.1 mm of precision (shell length was considered the distance from the apex to the tip of the siphonal canal) and had their stomach contents observed under optic microscope and stereoscopic microscope.

The 13 remaining specimens were kept individually in 13 tanks of 5 liters with seawater from the study area, constant aeration, temperature of 28°C and 35 of salinity. These animals remained in a period of 7 days without food before the experiments.

Prey samples for the experiments were kept separated by species in a 60 liters tank with seawater from the study area and in the same conditions of *Aurantilaria aurantiaca* tanks.

Prey Preference Experiment

Individuals of *Aurantilaria aurantiaca* were placed separately in 16 x 8 x 10 cm plastic boxes. Each *A. aurantiaca* was placed with one individual of each prey species.

During this experiment the number of consumed prey was noted and eaten individuals were replaced. This experiment lasted for 2 months and was replicated 10 times. The mean number of individuals of each species consumed was calculated per each week of the experiment. Percentage of predators that recognized each species as a prey was calculated.

Individuals of *A. aurantiaca* were placed separately in plastic boxes with 3 individuals of the same prey species and used as control group. Statistical tests were applied using program STATISTICA 7. Initially, data normality and its averages were verified and then submitted to the correlation test.

Handling Time Experiment

The handling time of predation was measured by placing 1 adult predator with 1 prey into separate containers and placing them in an 80 liters tank (total of 10 boxes and 10 predators) with seawater from the study area, constant aeration, temperature of 28°C and 35 of salinity. Observations were made every 2 hours during 24 hours over 30 days period. This experiment was replicated 10 times for each prey species. The time interval from the first successful attack to the separation of the predator and empty prey shell was recorded.

RESULTS

Observations made in the study area have shown the presence of *Aurantilaria aurantiaca* only on beach rocks. Three gastropod species were seen being preyed upon by it: *Pisania pusio* (Linnaeus, 1758) (Figure 3A and 3B), *Tegula viridula* (Gmelin, 1791) (Figure 3C and 3D) and *Stramonita brasiliensis* (Linnaeus, 1767) (Figure 3E and 3F).

Pisania pusio was found in cracks or under rocks, most of it being solitary individuals (Figure 3A). *Tegula viridula* and *Stramonita brasiliensis* were observed inhabiting the same area and these populations were always aggregated in large groups (Figure 3C and 3E).

The sampled specimens of *Aurantilaria aurantiaca* measured 66.48 ± 4.9 mm ($n = 18$), *Pisania pusio* measured 24.51 ± 1.23 mm ($n = 160$) and *Stramonita brasiliensis* 33.42 ± 2.19 mm ($n = 300$) in length. *Tegula viridula* measured 16.08 ± 0.89 mm ($n = 300$), considering the shell length the distance from the apex to the farthest point of the outer lip.

The stomach content of *Aurantilaria aurantiaca* showed no identifiable material.

Prey Preference

Aurantilaria aurantiaca showed preference for *Stramonita brasiliensis* that consumed in 60 days the total of 97 individuals, in a rate of 1.6 preys per day. The statistical test showed that the average number of individuals of *Stramonita brasiliensis* consumed per week had a normal distribution, with significant increase during the experiment ($p = 0.0008$; $r = 0.9050$), mainly from the fifth week, varying from 1.14 preys in the first week to 3.14 preys in the eighth week (Figure 4 and 5A).

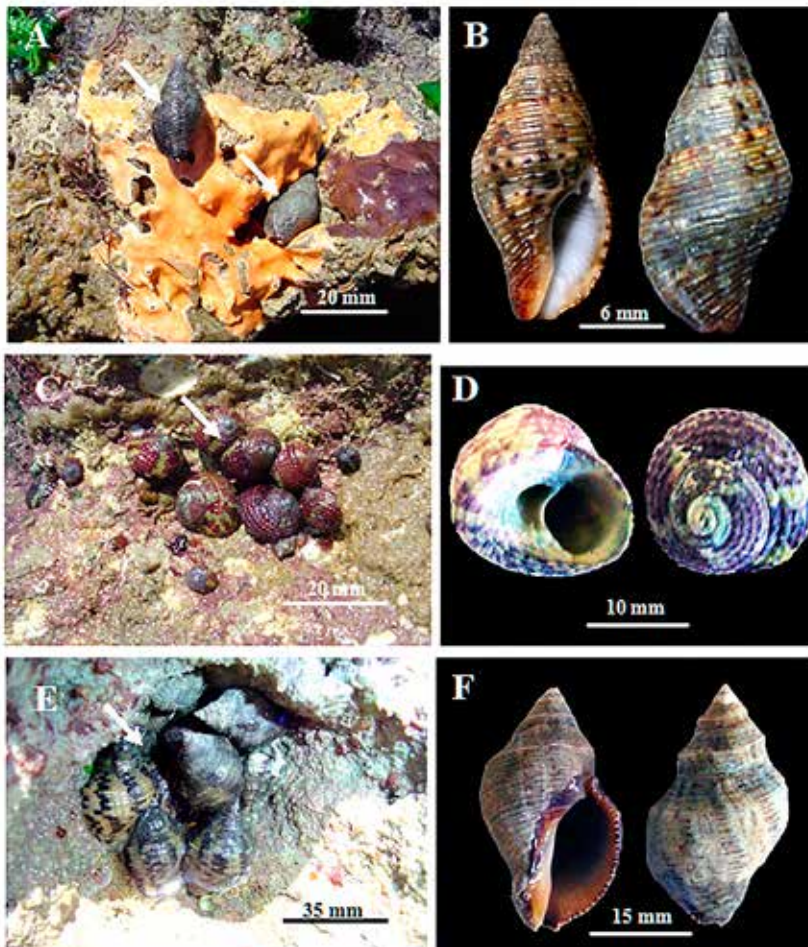


Figure 3 - Gastropods preyed by *Aurantilaria aurantiaca* at Pacheco Beach, Ceará State, Northeast Brazil. A. Individuals of *Pisania pusio*. B. Ventral and dorsal view of *P. pusio* shell. C. Individuals of *Tegula viridula*. D. Ventral and dorsal view of *T. viridula* shell. E. Individuals of *Stramonita brasiliensis*. F. Ventral and dorsal view of *S. brasiliensis* shell.

The second most consumed prey was *Pisania pusio*, in a total of 53 individuals. The weekly average of animals eaten did not have significant variation (normal distribution) ($p = 0.7235$; $r = 0.1379$) and the consumption rate was 0.88 prey per day. It was observed that in the second week the average number of consumed animals was higher than *S. brasiliensis*, occurring a high decreasing of these values until the fourth week, when no specimen of *Pisania pusio* was eaten (Figure 4 and 5B).

Tegula viridula was the prey that reached the lower number of animals eaten during the experiment, in a total of 25 individuals. The consumption rate was 0.41 individuals per day and the weekly average of animals eaten was not statistically significant (normal distribution) ($p = 0.2499$; $r = 0.4284$), reaching the same value that *Pisania pusio* did in the end of the eighth week (0.57 prey eaten/week) (Figure 4 and 5C).

The percentage of individuals of *Aurantilaria aurantiaca* that recognized *Stramonita brasiliensis* as a prey during the 8 weeks had a significant increase during the experiment ($p = 0.0007$), varying 50% in the first week to 100% in the eighth week (Figure 6).

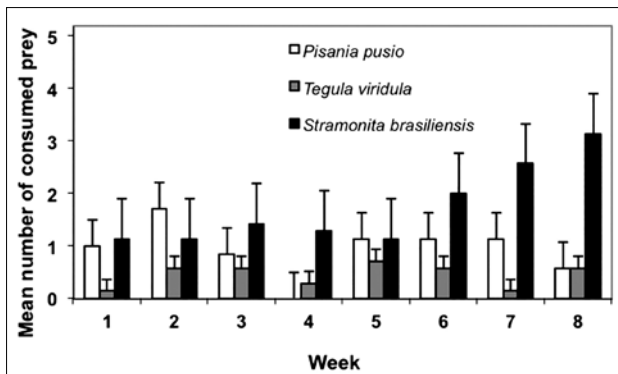


Figure 4 - Mean number of prey eaten by *Aurantilaria aurantiaca* during a 60 day period experiment (Error Bar = SD).

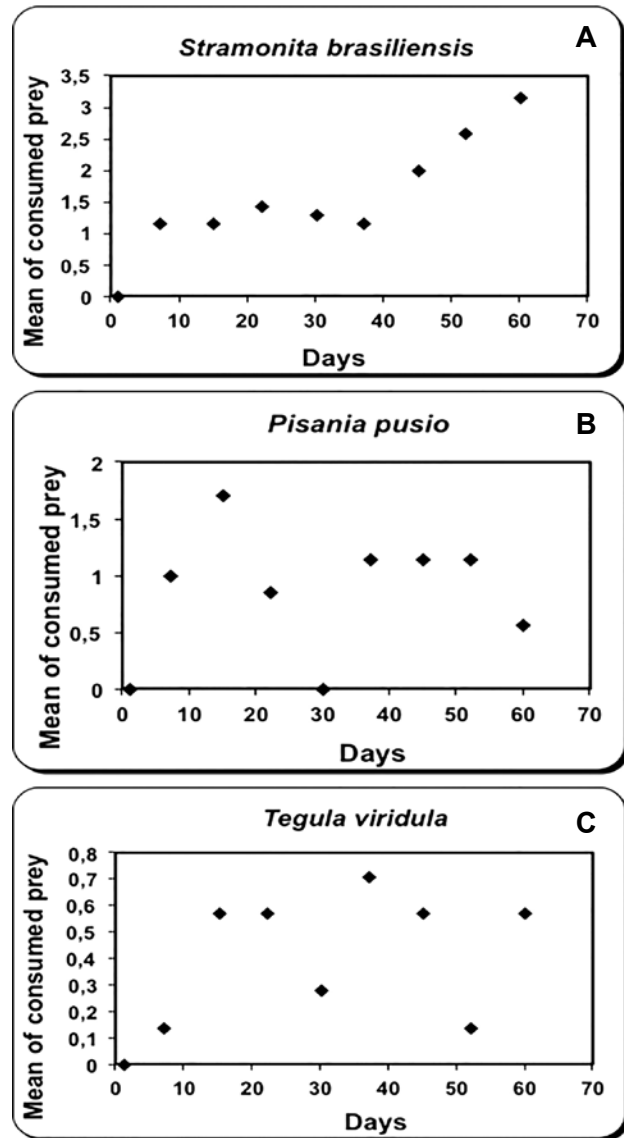
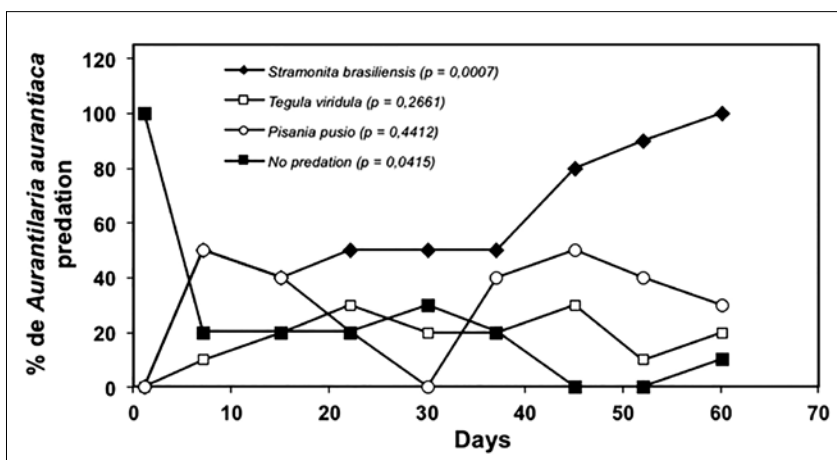


Figure 5- Variation of the mean number of prey eaten by *Aurantilaria aurantiaca* during a 60 day period experiment. A. *Stramonita brasiliensis* ($p=0,0008$; $r = 0,9050$). B. *Pisania pusio* ($p = 0,7235$; $r = 0,1379$). C. *Tegula viridula* ($p = 0,2499$; $r = 0,4284$).

Figure 6 - Percentage of individuals ($n = 10$) of *Aurantilaria aurantiaca* that recognized each prey during a 60 days period.



Although *Pisania pusio* was recognized with the same percentage that *Stramonita brasiliensis* during the two first weeks, it did not have significant weekly variation ($p = 0.4412$) during experiment (Figure 6). *Tegula viridula* was the least consumed species by *Aurantilaria aurantiaca*, reaching values between 10% and 30% of predators that recognized it as a prey. *Pisania pusio* also did not reach significant variation of predator recognition during the experiment ($p = 0.2661$) (Figure 6).

It was observed that during the 60 days of the experiment, the percentage of predators that did not feed in each week decreased significantly ($p = 0.0415$) (Figure 6).

Handling Time

The handling time was shorter when *Aurantilaria aurantiaca* preyed on *Stramonita brasiliensis* (2.5 ± 0.3 hrs, $n = 161$) (Table I) (Figure 7) than when it preyed on the two others species, *Pisania pusio* 4.83 ± 1.8 hrs ($n = 88$) (Table I) (Figure 7) and *Tegula viridula* 7.24 ± 3.1 hrs ($n = 46$) (Table I) (Figure 7).

All predators preyed on *S. brasiliensis*, sometimes more than one prey per day. The amount of individuals of *S. brasiliensis* consumed per predator during 30 days was 15.83 (Table I), *P. pusio* was 12.09 and *T. viridula* was 4.32 (Table I).

Predatory Behavior

Aurantilaria aurantiaca has the same predatory behavior when attacks the 3 preys used in this study. After the identification of the prey, the predator holds it firmly with the foot, trying to keep the

cephalic region in contact with the aperture of the prey shell.

After this first contact, *Aurantilaria aurantiaca* used two ways of predation: (1) immediately attacked the prey with its proboscis, placing it between the aperture of the prey shell and the operculum, preventing the prey to retract to the interior of the shell; (2) when the prey retracted before the introduction of predator proboscis, the predator tried to suffocate it with the foot, covering all the area of the prey shell aperture (Figure 8).

The aperture of the shells of the 3 prey species did not presented any type of breaking or damage after the predation ($n = 100$). Almost all soft parts of the prey were consumed, remaining only some parts of the muscle of the foot on the operculum. The examined opercula did not show any type of scraped made by the radula ($n = 100$).

Stramonita brasiliensis presented 3 types of anti-predatory behavior: (1) it was the only species of prey that reacted before the presence of the predator, adopting behavior of escape and search for

Table I - Handling time of predation by *Aurantilaria aurantiaca* on *Pisania pusio*, *Tegula viridula* and *Stramonita brasiliensis* in laboratory conditions.

Handling Time Exp.	<i>Pisania pusio</i>	<i>Tegula viridula</i>	<i>Stramonita brasiliensis</i>
N. of observations	360	360	360
N. of replications	10	10	10
Total observations	3600	3600	3600
Total prey consumed/predator	12,09	4,32	15,83
Mean handling time (hours)	$4,83 \pm 1,8$	$7,24 \pm 3,1$	$2,5 \pm 0,3$

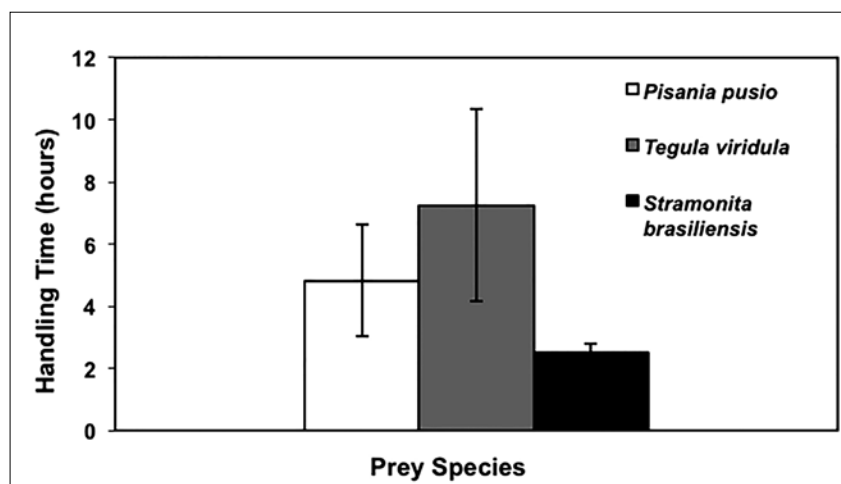


Figure 7 - Handling time of predation of *Aurantilaria aurantiaca* on *Pisania pusio*, *Tegula viridula* and *Stramonita brasiliensis* in laboratory conditions (Error bar = SD).

shelter. It crawled to the top of the predator shell in some observations, avoiding the predator searching; (2) in the moment of the predator attack, some individuals of *Stramonita brasiliensis* extruded the proboscis and counterattacking using the radula; (3) in the instant of the attack, it was possible to observe clearly the release of a liquid substance from the prey, of yellowish tone that in contact with the seawater became purple. This substance is very common in Thaididae (Nicol, 1964).

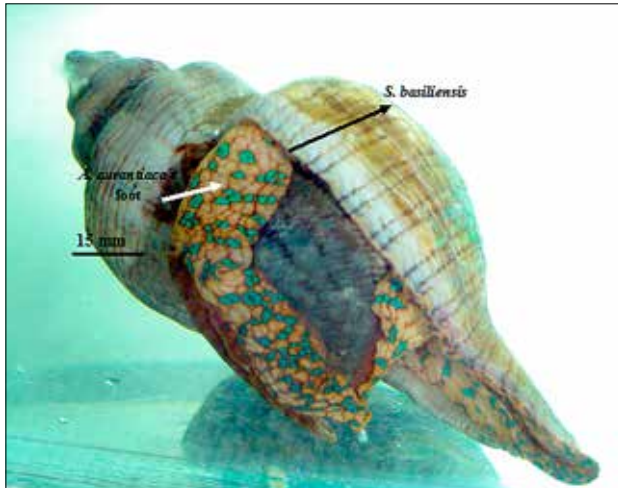


Figure 8 - *Aurantilaria aurantiaca* and its suffocating predatory behavior when it tries to prey an individual of *Stramonita brasiliensis*.

DISCUSSION

The preference for *Stramonita brasiliensis* over *Pisania pusio* and *Tegula viridula* demonstrated by *Aurantilaria aurantiaca* may be due to the fact that *S. brasiliensis* requires a shorter handling time and the aperture of its shell is wider than that from the other preys.

Although *S. brasiliensis* was the only prey that presented relatively aggressive anti-predatory behavior, it did not show much efficiency when tried to escape from the predator. *S. brasiliensis* is a moluscivore species as well as *A. aurantiaca* and did not prey any of the other species used in the experiment.

The vulnerability of the prey is higher when it is under stress energy, due to allocation of the available energy for the anti-predatory behavior (Caraco *et al.*, 1980; Fitzgibbon, 1989; Bachman, 1993; Lima, 1998). In the preference experiment, the presence of *A. aurantiaca* probably inhibited the predatory behavior and stimulating the anti-predatory behavior in *S. brasiliensis*, probably making it more vulnerable.

Induced defenses by the presence of the predator are a generalized phenomenon, especially in marine shallow waters (Vermeij, 1987; Harvell, 1990). An anti-predatory specific type in an only time and space can be a characteristic badly adaptative if applied to others, therefore, induced defenses would have to favor in cases where the predatory pressure varies in time and space, thus getting trustworthy strategies (Havel, 1987; Harvell, 1990; Yamada *et al.*, 1998).

Tegula viridula was the less consumed prey, probably due to the long handling time associated with the small aperture of its shell.

Probably the optimal foraging theory can explain the preference of prey by *Aurantilaria aurantiaca*, since that the anti-predatory behavior of *Stramonita brasiliensis* did not interfere with the prey choice and that, although the predation on *Pisania pusio* and *Tegula viridula* were not statistically significant, the predator showed a generalist predatory behavior, consuming all 3 prey species.

The preference experiment showed that the specimen number of *Stramonita brasiliensis* preyed in each week increased significantly, including the percentage of predators that recognized them as a prey. Probably, *Aurantilaria aurantiaca* showed a process of ingestive conditioning (Wood, 1968).

According to Wood (1968), ingestive conditioning is a modification and/or reinforcement of prey preferences in response to chemicals from prey that had been consumed recently. Ingestive conditioning may involve a training process (Hall *et al.*, 1982). For example, in birds this training involves the formation of a search image (Royama, 1970; Dawkins, 1971). In gastropods the process was shown after the predator had many encounters with the prey (Murdoch, 1969) but it must be chemical and not visual as in birds.

The handling time presented for *Stramonita brasiliensis* demonstrated that the predator probably already has been in contact with the prey. The results indicate that until the second week of experiment of alimentary preference, attacks from *A. aurantiaca* over *S. brasiliensis* and *Pisania pusio* were the same, but later, the preference for *S. brasiliensis* increased significantly. It decreased for *P. pusio*, reaching zero attack in the fourth week.

The learning process in *Aurantilaria aurantiaca* can clearly be seen when we observe its predation on *Tegula viridula*, which presented in the first week of experiment the handling time of 12 hours. In the end of the experiment this time decreased to 4 hours i.e. the predator tends to increase its efficiency at the moment

when it has a repetitive contact with the same type of prey (West, 1988) because it reduces the time of the identification, attack and consumption of prey.

West (1988) studied a population of *Vasula melones* (Duclos, 1832) and found, in a same population, some individuals were specialists and others were generalists. According to West (1988) this difference between individuals were maintained by the fact that each individual increased its efficiency by handling the same type of prey, because this reduced the time taken to identify, attack and consume the prey.

This probably explains how individuals eventually get their particular feeding preferences and how and why predators start to switch to relatively more abundant prey (Murdoch, 1969).

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REFERENCES

- Abe, N. Prey value to the carnivorous gastropods *Morula musiva* (Kiener) and the two forms of *Stramonita clavigera* (Kuster): effect of foraging duration and abandonment of prey. *Malacologia*, v.30, p. 373-395, 1989.
- Alford, R.A. Variation in predator phenology affects predator performance and prey community composition. *Ecology*, v.70, p.206-219, 1989.
- Ankel, W.E. Erwerb und aufnahme der nahrung bei den gastropoden. *Verh. Dtsch. Zool. Ges.*, v. 0, p. 223-295, 1938.
- Bachman, G. The effect of body condition on the trade-off between vigilance and foraging in Beldings ground squirrels. *Anim. Behav.*, v. 46, p. 233-244, 1993.
- Brown, K.M. Size-specific aspects of the foraging ecology of the southern oyster drill *Stramonita brasiliensis* (Kool, 1987). *J. Exp. Mar. Biol. Ecol.*, v.214, p. 249-262, 1997.
- Burrows, M.T. & Hughes, R.N. Natural foraging of the dogwhelk, *Nucella lapillus* (Linnaeus): the weather and wheter to feed. *J. Mollus. Stud.*, v.55, p. 285-295, 1989.
- Caraco, T.; Martindale, S. & Pulliam, H.R. Avian time budgets and distance to cover. *The Auk*, v.97, p. 872-875, 1980.
- Curio, E. *The Ethology of predation*. Springer-Verlag, 250 p., New York, 1976.
- Dawkins, M. Perceptual changes in chicks: another look at the "search image" concept. *Anim. Behav.*, v.17, p. 134-141, 1971.
- Duarte, L.F.L. Seleção de presas e distribuição do gastrópode *Stramonita brasiliensis* (L.) no costão da Praia do Rio Verde, Estação Ecológica de Juréia - Itatins, Estado de São Paulo. Tese de Doutorado, Universidade Estadual de Campinas, São Paulo, Brasil, 1990.
- Eisenberg, J.N.S., Washburn, J.O. & Schreiber, S.J. Generalist feeding behaviors of *Aedes sierrensis* larvae and their effects on protozoan populations. *Ecology*, v. 81, p. 921-935, 2000.
- Etter, R.J. The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L.). *J. Exp. Mar. Biol. Ecol.*, v.196, p. 341-356, 1996.
- Fairweather, P.G. & Underwood, A. J. The apparent diet of predators and biases due to different handling times of their prey. *Oecologia*, v. 56, p. 169-179, 1983.
- Fitzgibbon, C.D. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim. Behav.*, v.37, p. 508-510, 1989.
- Fretter, V. & Graham, A. *British prosobranch molluscs*. Ray Society, 755 p., London, 1962.
- Graham, A. Mollusca diets. *Proc. Malacol. Soc. Lond.*, v. 31, p. 144-59, 1955.
- Hall, S.J.; Todd, C.D. & Gordon, A. D. The influence of ingestive conditioning on the prey species selection in *Aeolidia papilosa* (Mollusca: Nudibranchia). *J. Anim. Ecol.*, v.51, p. 907-921, 1982.
- Havel, J.E. Predator-induced defenses: a review, p.263-278, in Kerfoot, W.C. (ed), *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover/London, 1987.
- Harvell, C.D. The ecology and evolution of inducible defenses. *Q. Rev. Biol.*, v. 65, p. 323-340, 1990.
- Hughes, R.N. Optimal foraging theory in the marine context. *Oceanog. Mar. Biol.*, v. 18, p. 423-481, 1980.
- Hughes, R.N. *A functional biology of marine gastropods*. Croom Helm Ltd., 245 p., London, 1986.
- Hughes, R.N. & Burrows, M.T. Predation behaviour of the intertidal snail, *Nucella lapillus*, and its effect

- on community structure, p.63-83, in Kawanabe, H.; Cohen, J.E. & Iwasaki, K. (eds) Mutualism and community organization. Oxford Science Publications, Oxford, 1993.
- Hughes, R.N. & Burrows, M.T. An interdisciplinary approach to the study of foraging behaviour in the predatory gastropod, *Nucella lapillus* (L.). *Ethol. Ecol. Evol.*, v. 6, p. 75-85, 1994.
- Hughes, R.N. & Drewett, D. A comparison of the foraging behaviour of dogwhelks, *Nucella lapillus* (L.), feeding on barnacles or mussels on the shore. *J. Mollus. Stud.*, v. 51, p. 73-77, 1985.
- Hughes, R.N. & Dunkin, S.B. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on barnacles or mussels, *Mytilus edulis* L., in the laboratory. *J. Exp. Mar. Biol. Ecol.*, v. 77, p. 45-68, 1984a.
- Hughes, R.N. & Dunkin, S.B. Effect of dietary history on selection of prey, and foraging behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). *J. Exp. Mar. Biol. Ecol.*, v. 79, p. 159-172, 1984b.
- Hughes, R.N.; Burrows, M.T. & Rogers S.E.B. Ontogenetic changes in foraging behaviour of the dogwhelk *Nucella lapillus* (L.). *J. Exp. Mar. Biol. Ecol.*, v. 155, p. 199-212, 1992.
- Krebs, J. Optimal foraging: theory and experiment. *Nature*, v. 268, p. 583-584, 1977.
- Kurzava, L.M. & Morin, P.J. Tests of functional equivalence: complementary roles of salamanders and fish in community organization. *Ecology*, v. 79, p. 477-489, 1998.
- Lambin, X.; Petty, S.J. & MacKinnon, J.L. Cyclic dynamics in field vole populations and generalist predation. *J. Anim. Ecol.*, v. 69, p. 106-118, 2000.
- Lima, S.L. Stress and decision making under the risk of predation: recent developments from behavioural, reproductive and ecological perspectives. *Adv. Study. Behav.*, v.27, p. 215-290, 1998.
- Matthews-Cascon, H., 1997. Predation by *Nucella lapillus* (Linnaeus, 1758) on *Littorina obtusata* (Linnaeus, 1758) and *Mytilus edulis* (Linnaeus, 1758). Tese de Doutorado, University New Hampshire, New Hampshire, EUA, 1997.
- Matthews-Cascon, H. Comparison of the predatory behavior of two populations of *Nucella lapillus* (Linnaeus, 1758) in the presence of the green crab *Carcinus maenas* (Linnaeus, 1758). *Thalassas*, v. 19, p. 9-15, 2003.
- Matthews-Cascon, H.; Matthews, H.R. & Kotzian, C.B. Os Gêneros *Fasciolaria* Lamarck, 1799 e *Leucozonia* Gray, 1847 no Nordeste Brasileiro (Mollusca: Gastropoda: Fascioliariidae). *Mem. Inst. Oswald Cruz*, v. 84, p. 357 - 364, 1989.
- McQuaid, C.D. Differential effects of predation by the intertidal whelk *Nucella dubia* (Kr.) on *Littorina africana knysnaensis* (Phillipi) and the barnacle *Tetraclita serrata* Darwin. *J. Exp. Mar. Biol. Ecol.*, v. 89, p. 97-107, 1985.
- Meirelles, C.A.O. & Matthews-Cascon, H. Relations between shell size and radula size in marine prosobranchs (Mollusca: Gastropoda). *Thalassas*, v. 19, p. 45-53, 2003.
- Menge, B.A. Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia*, v. 34, p. 1-16, 1978.
- Menge, B.A. & Sutherland, J.P. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.*, v. 110, p. 351-369, 1976.
- Moran, M.J. The timing and significance of sheltering and foraging behaviour of the predatory intertidal *Morula marginalba* Blainville (Muricidae). *J. Exp. Mar. Biol. Ecol.*, v. 93, p. 103-114, 1985.
- Murdoch, W.W. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.*, v. 39, p. 335-354, 1969.
- Nicol, J.A.C. Special effectors: luminous organs, chromatophores, pigments, and poison glands, p.353-381, in Wilbur, K.M. & Yonge, C.M. (eds), *Physiology of Mollusca 1*. Academic Press, New York and London, 1964.
- Owen, G. Feeding, p.1-51, in Wilbur, K.M. & Yonge, C.M. (eds), *Physiology of Mollusca 2*. Academic Press, New York and London, 1966.
- Paine, R.T. Feeding rate of a predaceous gastropod *Pleuroploca gigantea*. *Ecology*, v. 44, p. 402-403, 1963.
- Palmer, A.R. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology*, v. 71, p. 759-775, 1990.
- Peterson, C.H. & Bradley, B.P. Estimating the diet of a sluggish predator from field observations. *J. Fish. Res. Board Can.*, v. 35, p. 136 - 140, 1978.
- Richardson, T.D. & Brown, K.N. Wave exposure and prey size selection in an intertidal predator. *J. Exp. Mar. Biol. Ecol.*, v. 142, p. 105-120, 1990.
- Richardson, T.D. & Brown, K.N. Predation risk and

- feeding in an intertidal predatory snail. *J. Exp. Mar. Biol. Ecol.*, v. 163, p. 169-182, 1992.
- Royama, T. Factors governing the hunting behavior and selection of food by the great tit *Parus major*. *J. Anim. Ecol.*, v. 39, p. 619-668, 1970.
- Schmitt, G.S., 1994. Estudo da Predação e Polimorfia em *Fasciolaria aurantiaca* (Lamarck, 1816) (Mollusca: Gastropoda: Fascioliidae). Monografia de Graduação, Universidade Federal do Ceará, Ceará, Brasil, 1994.
- Sih, A. & Christensen, B. Optimal diet theory: when does it work, and when and why does it fail? *Anim. Behav.*, v. 61, p. 379-390, 2001.
- Spiller, D.A. & Schoener, T.W. A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. *Nature*, v. 347, p. 469-472, 1990.
- Vermeij, G.J. *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, 1987.
- West, L. Prey selection by the tropical snail *Stramonita melons*: a study of interindividual variation. *Ecology*, v. 69, p. 1839-1854, 1988.
- Wood, L. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). *Malacologia*, v. 6, p. 267-320, 1968.
- Wootton, J.T. (1997) Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecol. Monogr.*, v. 67, p. 45-64.
- Yamada, S.B.; Navarrete, S.A. & Needham, C. Predation induced changes in behavior and growth rate in three populations of the intertidal snail, *Littorina sitkana* (Philippi). *J. Exp. Mar. Biol. Ecol.*, v. 220, p. 213-226, 1998.
- Yamamoto, T. Prey composition and prey selectivity of an intertidal generalist predator, *Muricodrupa fusca* (Kuster) (Muricidae). *Mar. Ecol.*, v. 25, p. 35-49, 2004.