UNIVERSIDADE ESTADUAL DE CAMPINAS

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"COMPORTAMENTO ALIMENTAR DO ESQUILO *SCIURUS INGRAMI* (RODENTIA: SCIURIDAE)"

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Orientador: Prof. Dr. João Vasconcellos Neto

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Resumo. O objetivo deste estudo foi investigar padrões de forrageamento do esquilo *Sciurus ingrami* em frutos de palmeiras. No primeiro capítulo foi avaliada a eficiência e o aprendizado de diferentes estratégias de forrageio em frutos de *Syagrus romanzoffiana*. No segundo capítulo comparamos a ocorrência de diferentes estratégias de forrageio em frutos de *Syagrus oleracea* e *S. romanzoffiana*. Os resultados obtidos indicam que o esquilo *S. ingrami* pode utilizar diferentes estratégias de forrageio quando se alimenta de frutos de palmeiras. Algumas estratégias são evidentemente mais eficientes e possibilitam o melhor aproveitamento do endosperma gorduroso. Também foi registrado um caso de aprendizado de novas estratégias de forrageio. Essas características podem ter um papel importante na capacidade do esquilo *S. ingrami* de se adaptar a novos ambientes e contribuir para sua ampla ocorrência.

Abstract. The objective of this study was to investigate the squirrel's *Sciurus ingrami* foraging patterns in palm fruits. In the first chapter, efficiency and learning of different foraging strategies in *Syagrus romanzoffiana* fruits was assessed. In the second chapter, we compared the occurrence of distinct foraging strategies in *Syagrus oleracea* and *S. romanzoffiana* fruits. The results indicate that *S. ingrami* can use different foraging strategies when feeding in palm fruits. Some strategies are clearly more efficient in obtaining the fatty endosperm within the seeds. A case of learning of new foraging strategies was also recorded. These traits probably play an important role on the squirrel's ability to adapt to new environments and contribute to its widespread occurrence.

Introdução Geral

A teoria do forrageamento ótimo prediz que organismos realizam escolhas de modo a obter alimento com o menor custo e o maior benefício possíveis (Emlen 1966, MacArthur & Pianka 1966, Krebs & McCleery 1984, Stephens & Krebs 1986, Krebs & Kacelnik 1991, Bulmer 1994, entre outros). O estudo dessas escolhas envolve investigar quais são os custos de determinado comportamento de forrageio e quais os benefícios associados a essa estratégia. Diversos autores, através de modelos matemáticos, desenvolveram teorias para o estudo de padrões de forrageamento ótimo. MacArthur & Pianka (1966) definiram como dieta ótima aquela que minimiza o tempo de busca, obtenção e manuseio de um determinado alimento por um animal qualquer. Pulliam (1974) desenvolveu uma abordagem matemática para predadores móveis se alimentando de presas estacionárias, além de abranger conceitos como dietas especializadas ou generalistas. Neste modelo, o autor define como forrageamento ótimo uma seqüência de escolhas bem sucedidas pelo predador que maximizam a taxa de ganho calórico por unidade de tempo. Outros autores também enfatizam a maximização de obtenção de energia por tempo, como Emlen (1966, 1968), Rapport (1971), Schoener (1969a, 1969b, 1971) e Estabrook & Dunham (1976). Katz (1974) salienta que o surgimento de estratégias ótimas de forrageio está relacionado à previsibilidade de um ambiente e de adaptações em longo prazo.

Muitos autores utilizam os modelos teóricos para fundamentar descrições de comportamentos de forrageio em animais em habitats naturais ou em cativeiro. Benkman (1993) notou que as quatro subespécies da ave *Loxia curvirostra* têm morfologias de bico diferentes entre si. Avaliando a eficiência de forrageio, o autor verificou que cada variedade de tamanho de bico é adequada a uma das quatro espécies de coníferas

encontradas na região do estudo. Cada subespécie se adaptou a um tamanho distinto de semente, aumentando a eficiência na alimentação e diminuindo pressões de competição.

O estudo de Moller (1986) identificou diferentes estratégias que esquilos vermelhos europeus (*Sciurus vulgaris*) utilizam no manuseio de cones do pinheiro *Pinus sylvestris*. O autor percebeu que cada esquilo poderia ser categorizado em "cortador" ou "rasgador", de acordo com a maneira que o animal retirava as escamas dos cones. Moller também registrou esquilos jovens retirando sementes dos cones sem remover as escamas, indicando uma provável técnica rudimentar e pouco eficiente. Goheen *et al*. (2003) avaliaram a eficiência de alimentação do esquilo vermelho norte-americano *Tamiasciurus hudsonicus*. Os resultados mostraram que esquilos de diferentes regiões têm diferentes morfologias cranianas. Essas diferenças permitem uma obtenção de energia mais eficiente para o tipo de alimento predominante em cada região.

O estudo de estratégias e eficiência de forrageio está, muitas vezes, relacionado à compreensão de processos de aprendizado de técnicas pelos animais. Nos estudos pioneiros de Eibl-Eibesfeldt (1951, 1956, 1963), o autor ofereceu avelãs para esquilos vermelhos europeus (*Sciurus vulgaris*) que nunca tinham entrado em contato com esse tipo de alimento antes. Os resultados mostraram que, no início, os esquilos abriam as avelãs de forma imprevisível e pouco eficiente no aproveitamento da semente. Através de tentativa e erro, os animais aprimoraram a técnica de abertura, retirando a semente inteira para ingestão. Ades & Busch (1999) verificaram o mesmo processo de aprendizado através da experiência para camundongos (*Calomys callosus*) se alimentando de sementes de girassol. Aumento na eficiência de forrageio também foi observado em aves da espécie *Mimus polyglottos*, pelos autores Breitwisch *et al.* (1987). Neste trabalho, verificou-se que aves

jovens têm menos sucesso na captura de insetos, além de obterem presas geralmente menores que aquelas capturadas por aves adultas.

Weigl & Hanson (1980) demonstraram que o processo de aprendizado pode ser melhorado se os esquilos observarem indivíduos experientes manuseando alimento. Experimentos em cativeiro mostraram que aqueles animais que puderam observar um esquilo "modelo" reduziram pela metade o tempo de manuseio e o gasto energético, em relação aos indivíduos isolados. Observações similares foram realizadas com outros roedores, como o estudo de Zohar & Terkel (1996). Neste, os autores observaram que filhotes de ratos negros (*Rattus rattus*) aprendiam de suas mães a técnica para se alimentar de pinhas de forma eficiente. Drapier & Thierry (2002) observaram em macacos da espécie *Macaca tonkeana* o aprimoramento na obtenção e ingestão de frutos, bem como a transmissão cultural de algumas peculiaridades na técnica, passadas de mães para filhotes.

O estudo de Bordignon *et al*. (1996) avaliou as formas de abertura realizadas pelo esquilo *Sciurus ingrami* em frutos da palmeira *Syagrus romanzoffiana*, registrados anteriormente por Maia *et al.* (1987). Bordignon *et al*. (1996) constataram que a estratégia na qual o esquilo fixa os incisivos no poro germinativo e abre o endocarpo de forma triangular é a mais freqüente, além de demandar um menor tempo de manuseio. Os autores sugerem que a forma triangular é a mais eficiente e também citam a possibilidade da existência de um processo de aprendizagem das formas de abertura.

Muitos dos trabalhos citados acima foram realizados com roedores da família Sciuridae como objetos de estudo. Esta família possui 50 gêneros e 260 espécies e se distribui amplamente em diversos habitats, não ocorrendo somente na Austrália, Madagascar, extremo sul das Américas e regiões desérticas (Nowak 1995). Existem 28 espécies do gênero de esquilos arborícolas *Sciurus* e apenas oito delas ocorrem no

Holoártico (Gurnell 1987, Nowak 1995). Nas Américas do Sul e Central ocorrem mais de 20 espécies descritas desse gênero (Heaney & Thorington 1978) e no Brasil são encontradas cinco dessas espécies (Nowak 1995). O esquilo *Sciurus ingrami* Thomas, 1901, também conhecido como caxinguelê ou serelepe, é encontrado em diversos ambientes, ocorrendo do sul da Bahia até o Rio Grande do Sul (Oliverio-Pinto 1931). Ainda escassos, valiosos estudos investigaram aspectos de dieta e comportamentos de forrageio (Maia *et al.* 1987, Galetti *et al*. 1992, Paschoal & Galetti 1995, Bordignon *et al.* 1996, Bordignon & Monteiro Filho 1999, Miranda 2005, Alvarenga & Talamoni 2006), atividade diária e padrões de acasalamento (Bordignon & Monteiro Filho 1997, 2000).

O objetivo deste estudo foi investigar padrões de forrageamento do esquilo *Sciurus ingrami* em frutos de palmeiras. No primeiro capítulo foi avaliada a eficiência e o aprendizado de diferentes estratégias de forrageio em frutos de *Syagrus romanzoffiana*. No segundo capítulo comparamos a ocorrência de diferentes estratégias de forrageio em frutos de *Syagrus oleracea* e *Syagrus romanzoffiana*.

Capítulo 1

Efficiency and learning of opening forms of *Syagrus romanzoffiana* (Palmae) fruits by *Sciurus ingrami* (Rodentia: Sciuridae).

Abstract

The objective of the present study was to investigate efficiency and learning of different techniques used by the Brazilian squirrel *Sciurus ingrami* to open *Syagrus romanzoffiana* seeds. The study was carried out in the Serra do Japi city reserve in Jundiaí, Brazil**.** Five hundred dry *S. romanzoffiana* seeds with clear evidence of *S. ingrami* predation were collected and categorized, according to the opening marks left on the endocarp, into triangular and irregular shape. For each category the opening size, handling time and weight of uneaten endosperm was measured. The later measure was also done with previously captured and marked squirrels, to verify the occurrence of learning of opening forms. The triangular opening form was the most frequent, with the larger opening, shorter handling time and with less uneaten endosperm. The switch from irregular to triangular opening form could be observed in one young marked female along with the decrease of uneaten endosperm weight. The results provide strong evidence that the triangular opening form is the most efficient feeding strategy and indicate the occurrence of learning of feeding techniques. These traits probably play an important role on the squirrel's ability to adapt to new environments and contribute to its widespread occurrence.

Introduction

The seek for the most efficient form of obtaining food agrees with the optimal foraging theory (Emlen 1966, MacArthur & Pianka 1966), in which natural selection molds the foraging behavior of animals to increase fitness. Many studies on feeding strategies were performed using captive and wild animals, in order to better understand these behaviors. Studies on tree squirrels have investigated feeding techniques on cones (Moller 1986), efficiency on energy extraction of different types of seeds (Goheen *et al*. 2003) and learning and optimization of feeding behavior (Eibl-Eibesfeldt 1951, 1956, 1963, Weigl & Hanson 1980).

In Bordignon *et al.* (1996) the authors studied the opening forms of *Syagrus romanzoffiana* (Palmae) seeds made by *S. ingrami*. The work suggests that the opening form with lower number of incisions, with a nearly triangular shape, is the most efficient, since it was the most frequent and had a shorter handling time. The authors also suggest that young squirrels learn the most efficient opening form as they grow up. Efficiency and learning of feeding techniques was also studied on mice (Ades & Busch 1999), rats (Zohar & Terkel 1996) and other vertebrates (e.g. Breitwisch *et al*. 1987 on mockingbirds, Drapier & Thierry 2002 on Tonkean Macaques).

In Central and South America occur more than 20 species of the tree-squirrel genus *Sciurus* (Heaney & Thorington 1978, Nowak 1995), however there is little information on neotropical squirrels ecology. Studies on the Brazilian squirrel *Sciurus ingrami* Thomas 1901 (Fig. 1a) demonstrate that palm tree fruits are an important food item in its diet (Galetti *et al*. 1992, Paschoal & Galetti 1995, Bordignon *et al.* 1996, Bordignon & Monteiro Filho 1999, 2000, Alvarenga & Talamoni 2006). The objective of the present

study is to investigate efficiency and learning of different opening forms of *S. romanzoffiana* (Fig. 1b) seeds by the Brazilian squirrel *S. ingrami*.

Methods

Study site. The study was carried out in the Serra do Japi city reserve (23º12`-20` S, 46º53`-47` W) in Jundiaí, Brazil, an approximately 10.000ha area in a mountain dominated terrain, with altitudes from 700m to 1.300m (Santoro & Machado-Junior 1992). The climate is characterized by a dry, cold season (May to August) and a wet, warm season (September to April) (Pinto 1992). The vegetation consists primarily of semideciduous forests and canopy is approximately 25m high (Leitão-Filho 1992). All trapping and observations were made near the reserve's office, where several palm trees can be found.

Trapping and marking squirrels. Squirrels were trapped in eight Tomahawk live-traps baited with *Syagrus romanzoffiana* fruits, placed on the ground or in low branches of trees. Captured squirrels were handled with a cloth handling bag according to Koprowsky (2002) and marked with a plastic collars according to Wood (1976) for individual identification with 8x21 binoculars.

Seed opening forms analysis. Five hundred dry *S. romanzoffiana* seeds with clear evidence of *S. ingrami* predation were collected from the study site and categorized into five groups according to Bordignon *et al.* (1996): group I, the endocarp is opened in a nearly triangular shape, with two conspicuous longitudinal incisions; group II, the seed is split in two uneven parts, along its transversal axis; group III, the endocarp is opened in a nearly square shape, with two approximately parallel incisions; group IV, the opening form is round or ovoid, with variable number and position of incisions; and group V which

(a)

(b)

Fig. 1 - (a) The Brazilian squirrel *Sciurus ingrami*. (b) Fruit buds of the palm tree *Syagrus romanzoffiana* (photo (a) by Eduardo Pereira and (b) by Gustavo Romero).

comprehends all opening forms too variable to be categorized. In this paper, group I will be referred as triangular opening form, and groups II, III, IV and V, when gathered, as irregular opening form (Fig. 2). The opening size (maximum longitudinal and transversal measures) was measured in 50 random seeds from each of both triangular and irregular opening forms categories.

Handling time. As an estimate of effort made by the squirrel to eat one palm fruit, 15 opening time measures of both triangular and irregular forms were taken. Each measure was divided in two parts: (1) gnawing, characterized by the distinct sound made by the squirrel's incisive on the endocarp, and (2) eating, from the moment the animal stops gnawing until the release of the fruit. The total time was considered the handling time of each fruit. All measures were made in non-captive animals.

Feeding techniques efficiency and learning. To evaluate the efficiency of a seed predation event, fruits were collected immediately after a squirrel had eaten and released it. The remaining content of endosperm was immediately removed from the seed and stored in

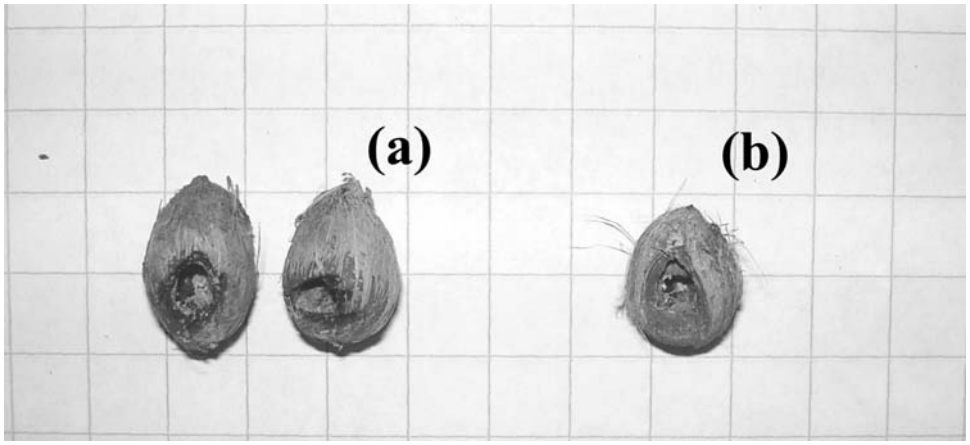

Fig. 2 - *Syagrus romanzoffiana* fruits predated by *Sciurus ingrami* opened in (a) irregular forms and (b) triangular form (scale = 1cm).

a 1.5ml sealed tube for further weighting with a 0.001g precision balance. The opening form was recorded according to the two categories previously described. The heavier the mass of endosperm not eaten by the squirrel, the less efficient the foraging event was considered. The same procedure was done with marked squirrels to verify if learning of opening form and improvement on foraging efficiency occurs. Seed size (maximum longitudinal and transversal measures) was measured for all collected fruits.

Data analyses. The frequencies of opening forms were compared using Chi-square test (Zar 1999). T-test (Zar 1999) was used to compare means of gnawing and total handling times. Mann-Whitney non-parametric test (Zar 1999) was used to compare means of opening forms and seed sizes, means of endosperm mass measured and means of eating time. All analyses were made using the BioEstat 3.0 Software (Ayres *et al.* 2003).

Table 1 – Handling time (gnawing time, eating time and total handling time) of *Syagrus romanzoffiana* fruits by *Sciurus ingrami* for different opening forms.

	Opening form	
	Irregular	Triangular
Gnawing**	4’29’’ ± 1’00’’	2’37’’ ± 0’34’’
Eating*	3’13’’ ± 1’03’’	2’16’’ ± 0’33’’
Total**	7’42’’ ± 1’44’’	4’53’’ ± 0’44’’

* t-test, $p<0.001$ **Mann-Whitney, $p<0.05$

Results

Trapping and marking squirrels. Eight individuals, five males and three females, were captured from November 2004 to December 2005 (mean weight = 150g, SD = 33.8g). Only two females (numbers 7 and 8) were still opening fruits in irregular forms during the study period, while the other squirrels were opening in triangular form.

Seed opening forms analysis. The triangular opening form (group I) was the most frequent, with 425 seeds, followed by 53 on group III, 12 on IV, six on II and four on V (χ^2 = 1336.3; D.F. = 4; $p<0.001$). Even after pooling all other forms into one category (irregular), the triangular form was still the most frequent technique (χ^2 = 245; D.F. = 1; $p<0.001$). The mean longitudinal measure was significantly wider in the triangular opening form (group I) (mean = 0.95cm; SD = 0.13cm) than in irregular opening forms (mean = 0.84cm; SD = 0.14cm) (Mann-Whitney; U = 723; $p<0.001$) (Fig. 3a). The mean transversal measures showed no statistical difference between the two groups (triangular: mean = 0.59cm; SD = 0.09cm; irregular: mean = 0.56cm; SD = 0.10cm) (Mann-Whitney; U = 984; $p = 0.0672$).

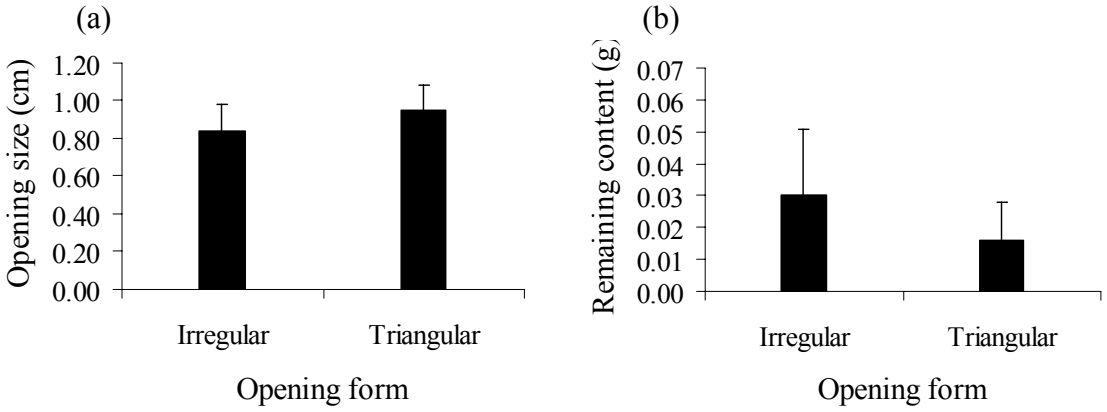

Fig. 3 - (a) Mean longitudinal size (b) remaining content of endosperm of triangular opening form and irregular opening form made by *Sciurus ingrami* in *Syagrus romanzoffiana* fruits.

Handling time. The mean time of irregular opening was greater than of triangular opening for gnawing (t-test: $t = 6.27$; $p<0.001$), eating (Mann-Whitney: $U = 43.50$; $p<0.05$) and total handling time (t-test: $t = 5.76$; $p<0.001$) (Table 1).

Feeding techniques efficiency and learning. The remaining content of endosperm of fruits opened in irregular forms (mean = 0.030g; SD = 0.021; n = 43) was significantly heavier than of fruits opened in triangular form (mean = 0.016g; SD = 0.012g; n = 36) (Mann-Whitney: $U = 368$; $p<0.001$) (Fig. 3b), confirming the later form as the most efficient. The switch from irregular to triangular opening form could be observed in one young marked female (individual 8). Figure 4 shows means of remaining endosperm of fruits eaten by individual 8 in both irregular, recorded in November and December 2005 (mean = 0.040g; SD = 0.023g; n = 22), and triangular opening form, recorded in January and February 2006 (mean = 0.013g; SD = 0.01g; n = 20) (Mann-Whitney: $U = 35$;

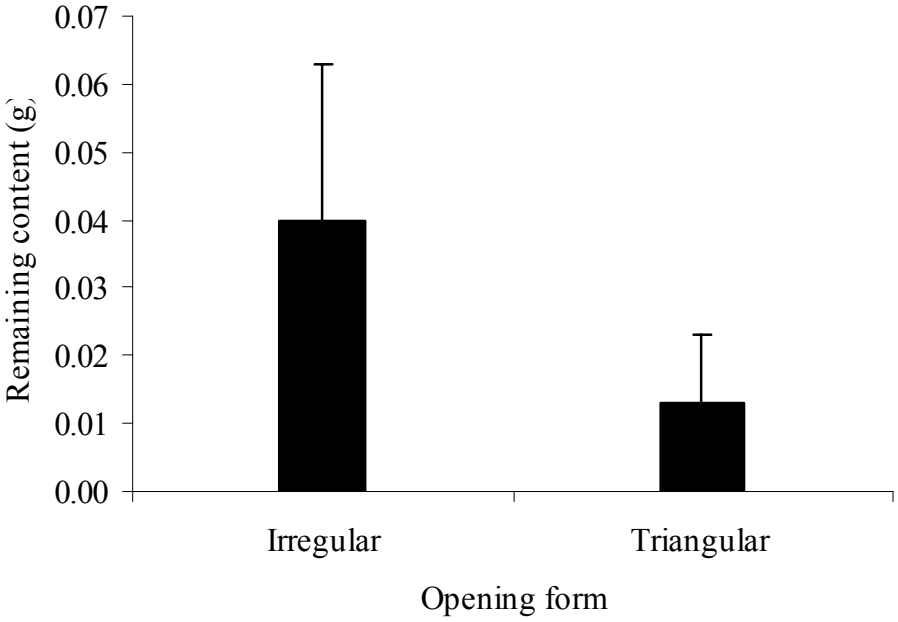

Figure 4 - Remaining content of endosperm of *Syagrus romanzoffiana* fruits opened in irregular forms (recorded in November and December 2005 of a marked female individual of *Sciurus ingrami*) and fruits opened in triangular form (recorded in January and February 2006 of the same individual).

$p<0.001$). Fruits opened in both triangular and irregular forms showed no statistical difference in size (longitudinal, Mann-Whitney: $U = 275$; $p>0.05$; transversal, Mann-Whitney: $U = 185$; $p>0.05$), indicating that a lighter mass of uneaten endosperm is due to a heavier mass of eaten endosperm and, thus, a greater caloric intake.

Discussion

The results provide strong evidence that the triangular opening form is the optimal feeding strategy, as suggested by Bordignon *et al.* (1996). The shorter handling time fits the optimal diet definition of MacArthur & Pianka (1966), in which the time for search, pursuit and handling is minimized. The shorter gnawing time can also be considered an honest estimate of less energy spent in opening the hard endocarp. Shorter eating time along with maximization of endosperm mass eaten, both recorded for the triangular opening form, also agrees with the definition of optimal diet as the one which maximizes intake of food value per unit of time (Emlen 1966, 1968, Rapport 1971, Schoener 1969a, 1969b, 1971, Pulliam 1974, Estabrook & Dunham 1976). Besides that, wider opening sizes for the triangular form indicate an easier access for squirrels to a larger part of the fat endosperm in these seeds. Apparently, this improvement in the squirrel's feeding strategy represents selective pressures strong enough to mold an optimal foraging behavior, since the triangular opening form was by far the most frequent.

The learning process recorded for the young female individual suggests that the occurrence of different, and less efficient, opening forms are due to young inexperienced individuals. Several studies show that young animals are less efficient foragers than adults (Norton-Griffiths 1969, Orians 1969, Recher & Recher 1969, Buckley & Buckley 1974, Davies & Green 1976, Burger 1980, Weigl & Hanson 1980, Gochfield & Burger, Breitwisch *et al.* 1987 among others.). The decrease of uneaten endosperm mass between the opening forms switch matches the previous evaluation of irregular and triangular form efficiency, and indicates an increase of feeding success through optimization of handling

techniques. Handling optimization through experience had been recorded for several rodents (Eibl-Eibesfeldt 1951, 1956, 1963, Weigl & Hanson 1980, Ades & Busch 1999) and this flexibility in behavioral traits plays an important role in a species' ability to adapt to new environments (Zohar & Terkel 1991, Goheen *et al.* 2003). Learning abilities in *Sciurus ingrami* may have contributed for its widespread occurrence (Oliveira Pinto 1931, Moojen 1952, Lange & Jablonsky 1981), including disturbed habitats (Bordignon & Monteiro-Filho 1999, Miranda 2005).

Quantitative records of improvement of feeding techniques in captive squirrels had been demonstrated by Weigl & Hanson (1980), and the present study demonstrates it to non-captive animals. In further studies, more information can be revealed by following the learning process of several non-captivity animals, and how different opening forms of palm fruits appear during trial-and-error behaviors. Experiments with squirrels in laboratory can also provide more details of this important topic squirrels ecology. Despite the large contribution of recent works on *Sciurus ingrami*, little is known on neotropical sciurids, although these rodents may play an important role in forest dynamics.

Capítulo 2

Opening forms of palm fruits *Syagrus romanzoffiana* and *Syagrus oleracea* (Palmae) by the Brazilian squirrel *Sciurus ingrami* (Rodentia:Sciuridae).

Abstract

The objective of the present study was to compare the opening forms of the hard endocarp of *Syagrus romanzoffiana* and *Syagrus oleracea* palm fruits to access the fat endosperm, made by the Brazilian squirrel *Sciurus ingrami*. The study was carried out in Núcleo Santa Virginia, in the Parque Estadual da Serra do Mar reserve, and in the Serra do Japi city reserve in Jundiaí, both southeastern Brazil. Five hundred dry *S. romanzoffiana* seeds and 280 of *S. oleracea* with clear evidence of *S. ingrami* predation were sampled and categorized into opening forms. The opening size was measured in 50 seeds of each category. For *S. romanzoffiana*, the triangular opening form was the most frequent and presented the widest opening size, when compared to irregular opening forms category. For *S. olearacea*, irregular opening forms were predominant over the regular form, even though the later presented a wider opening size. Wider opening sizes indicate an easier access for squirrels to a larger part of the fat endosperm within these seeds. This indicates a more efficient feeding strategy and explains why, in *S. romanzoffiana*, the triangular form was the most frequent. The predominance of irregular forms in *S. oleracea* may be due to an unlikely age structure in the population of squirrels in that area, with high proportions of young inexperienced individuals. Larger palm fruits, like *S. oleracea*, may provide a large nutritive reward for the squirrel even if opened in non-optimal forms. In that case, selective

pressures for learning of new and most efficient opening forms would not be as intense as in squirrels feeding on *S. romanzoffiana*, resulting in a more often occurrence of irregular opening forms.

Introduction

The Brazilian squirrel *Scirus ingrami* Thomas, 1901, can be found in a number of habitats, and occurs from southern Bahia state to Rio Grande do Sul (Oliverio-Pinto 1931). Recent studies investigated the squirrel's diet composition (Bordignon & Monteiro-Filho 1999, Paschoal & Galetti 1995, Miranda 2005,), foraging behavior (Bordignon *et al.* 1996, Galetti *et al.* 1992, Maia *et al.* 1987, Alvarenga & Talamoni 2006), daily activity and mating behavior (Bordignon & Monteiro-Filho 1997, 2000).

Rodents play a major role on dispersion and predation of hard nuts (Smythe 1989) and palm fruits are an important item in the diet of neotropical squirrels (Glanz 1981). Bordignon *et al.* (1996) study described opening strategies of hard *Syagrus romanzoffiana* seeds made by *S. ingrami*. The authors suggest the strategy in which the animal uses the germinative pore and opens in a nearly triangular shape is the most efficient, since it was the most frequently observed and demands a lower handling time. The paper also suggests that squirrels can learn and improve the opening form of the endocarp along their growth. In the first chapter, we demonstrate that the squirrels can learn new opening forms and that the triangular opening form provides a larger nutritional reward for less effort.

However, little is known on how squirrels handle larger palm fruits, which provides a much larger nutritional reward per fruit. In the present study, we compare the opening

forms made by squirrels in *Syagrus romanzoffiana* and in a larger palm fruit, *Syagrus oleracea*.

Methods

The study was carried out in Núcleo Santa Virginia (23°17'-24' S, 45°03'-11' W), in the Parque Estadual da Serra do Mar reserve, and in the Serra do Japi city reserve (23º12`-20` S, 46º53`-47` W) in Jundiaí, both southeastern Brazil. Núcleo Santa Virginia terrain, located at 740m of altitude, is characterized by mountains and accentuated slopes (Radambrasil 1983). The climate is humid throughout the year, with average annual of 20^{o}C and annual rainfall near 1340mm (MME 1983). Vegetation consists mainly in dense ombrofilous forests (Veloso *et al.* 1991), however with large areas of disturbed habitats (Tabarelli & Mantovani 1999). Serra do Japi is an approximately 10.000ha area in a mountain dominated terrain, with altitudes from 700m to 1.300m (Santoro & Machado-Junior 1992). The climate is characterized by a dry, cold season (May to August) and a wet, warm season (September to April) (Pinto 1992). The vegetation consists primarily of semideciduous forests and canopy is approximately 25m high (Leitão-Filho 1992).

Syagrus romanzoffiana is a palm tree with large solitary stems from 10 to 15m high and widespread distribution, ranging from eastern Brazil to Uruguay, Paraguay and Argentina. It produces numerous fruits with 1-3cm long and 1-2cm wide (Henderson *et al.* 1995). *Syagrus oleracea* has solitary stems from 5 to 25m high and occurs from eastern Brazil to Paraguay. The palm fruits are 4-5.5cm long and 2.5-3cm wide (Henderson *et al.* 1995).

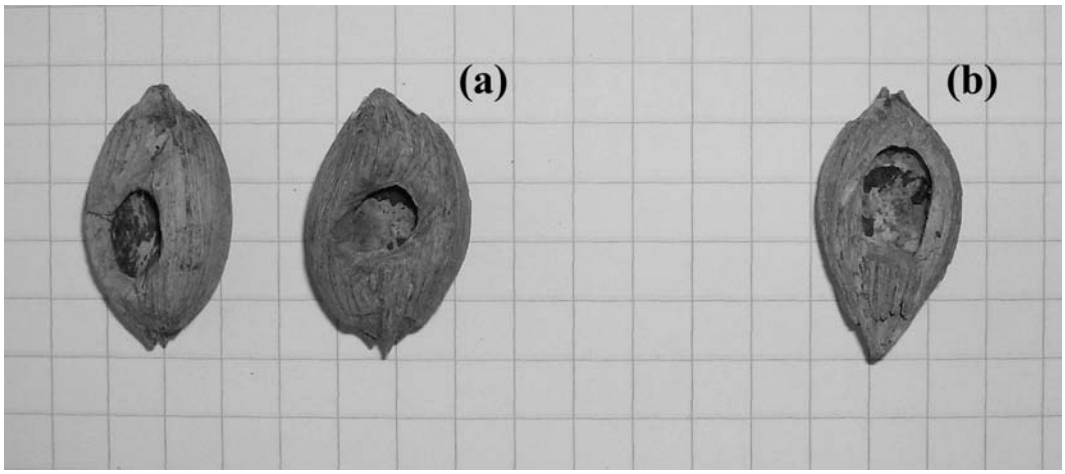

Fig. 5 - *Syagrus oleracea* fruits predated by *Sciurus ingrami* opened in (a) irregular forms and (b) regular form (scale = 1cm).

Five hundred dry *Syagrus romanzoffiana* seeds with clear evidence of *Sciurus ingrami* predation were collected from Serra do Japi and 280 of *Syagrus oleracea* from Santa Virgínia. *S. romanzoffiana* seeds were categorized into two groups, similar to Bordingon *et al.* (1996): group I, triangular opening form, in which the squirrel gnaws two longitudinal incisions, with upper incisive teeth into the germinative pore, and cracks the basis of the triangle formed by the incisions; group II, irregular opening forms, which comprehends four of the non-triangular shaped categories described by Bordingon *et al.* (1996) (see Fig. 2 in Chapter 1), gathered in this paper for comparison purposes with *Syagrus oleracea* categories. In preliminary observations, we could categorize *S. oleracea* also in two groups: group I, regular opening form, similar to the triangular opening form described for *S. romanzoffiana*, with a cracked, instead of gnawed, edge of the opening, however with a variable number of incisions, mostly two or three; group II, irregular opening forms, in which no pattern can be observed (Fig. 5). The opening size (maximum

longitudinal and transversal measures) was measured in 50 random seeds from each category of both species of palm fruits.

Student's t-test (Zar 1999) was used to compare means of longitudinal measures for *S. oleracea* opening size. Means of transversal measures for *S. oleracea* and longitudinal and transversal measures for *S. romanzoffiana* opening size was compared using Mann-Whitney non-parametric test (Zar 1999). All analyses were made using the BioEstat 3.0 Software (Ayres *et al.* 2003).

Results

For *Syagrus romanzoffiana*, the triangular opening form was the most frequent, with 425 seeds against 75 opened in irregular forms ($\chi^2 = 245$; G.L. = 1; $p<0.001$). The mean longitudinal measure was significantly wider in the triangular opening form (group I) (mean = 0.95cm; SD = 0.13cm) than in irregular opening forms (groups II) (mean = 0.84cm; SD = 0.14cm) (Mann-Whitney; U = 723; $p<0.001$) (see Fig. 3a in Chapter 1). The mean transversal measures showed no statistical difference between the two groups (triangular: mean = 0.59cm; SD = 0.09cm; irregular: mean = 0.56cm; SD = 0.10cm) (Mann-Whitney; U = 984; $p = 0.0672$).

For *Syagrus oleracea*, the irregular opening form was the most frequent, with 205 seeds, and 75 seeds presented the regular opening form ($\chi^2 = 60.36$; G.L. = 1; $p<0.001$). Both mean longitudinal and transversal measures were significantly wider in the regular opening form (group I) (longitudinal: mean = 1.77cm; SD = 0.21cm; transversal: mean = 1.18cm; SD = 0.10cm) than in irregular opening forms (group II) (longitudinal: mean =

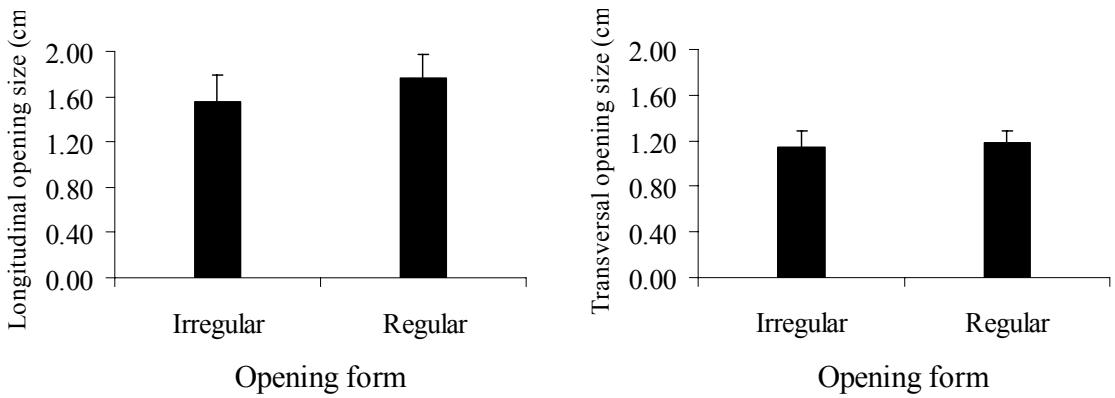

Figure 6 - Mean (a) longitudinal and (b) transversal size of irregular opening form and regular opening form made by *Sciurus ingrami* in *Syagrus oleracea* fruits.

1.57cm; SD = 0.23cm; transversal: mean = 1.14cm; SD = 0.15cm) (longitudinal: t-test; t = 4.47; $p<0.001$; transversal: Mann-Whitney; U = 848.5; $p<0.01$) (Fig. 6).

Discussion

Wider opening sizes for both triangular, in *Syagrus romanzoffiana*, and regular, in *Syagrus oleracea*, forms indicate an easier access for squirrels to a larger part of the fat endosperm within these seeds. The first chapter confirms that, in triangular opened *S. romanzoffiana* fruits, the remaining content of uneaten endosperm is lesser than in irregular opening forms. This fact, along with other triangular opening form advantages (Bordignon *et al.* 1996, see first chapter), explains why this is the far most frequent opening form in a random sample of dry seeds of this species. Apparently, this feeding strategy is the most efficient, and thus, positively selected (Stephens & Krebs 1986, Krebs & Kacelnik 1991, Bulmer 1994, among others).

Even though the larger opening size of the regular form in *S. oleracea* indicates that this is a more efficient strategy than irregular opening forms, the later predominated in the sample. This predominance may be due to an unlikely age structure in the population of squirrels in that area. If the same learning process observed in squirrels opening *S. romanzoffiana* seeds (see first chapter) happens in the case of *S. oleracea*, a large proportion of irregularly opened seeds reflects a large proportion of young inexperienced individuals in the population.

The size of *S. oleracea* fruits may also explains the high numbers of irregular opening forms. *S. oleracea* fruits are much larger than *S. romanzoffiana* fruits (Lorenzi 1992) and so, even if opened in a non-optimal form, it would provide a large nutritive reward for the squirrel. In that case, selective pressures for learning of new and most efficient opening forms would not be as intense as in squirrels feeding on *S. romanzoffiana*, resulting in a more often occurrence of irregular opening forms.

Learning processes, handling time and efficiency of feeding may vary in different fruit sizes and different squirrel populations. Further studies on foraging behavior of neotropical squirrels feeding on large palm fruits can bring more information on opening forms patterns and its role on this plant- predator/disperser relationship.

Conclusão Geral

Os resultados obtidos indicam que o esquilo *Sciurus ingrami* pode utilizar diferentes estratégias de forrageio quando se alimenta de frutos de palmeiras, e aquelas que possibilitam a maior eficiência na obtenção de energia são, aparentemente, selecionadas positivamente. Tais características condizem com a teoria do forrageamento ótimo (MacArthur & Pianka 1966, Krebs & McCleery 1984, Stephens & Krebs 1986, Krebs & Kacelnik 1991, Bulmer 1994, entre outros).

O primeiro capítulo confirma as expectativas sugeridas por Bordignon *et al.* (1996). A forma de abertura triangular mostrou-se a estratégia que demanda menos tempo de manuseio e que possui a maior abertura de acesso ao interior das sementes de *Syagrus romanzoffiana* permitindo, assim, o melhor aproveitamento do endosperma gorduroso. Além disso, a ocorrência predominante desta forma de abertura pode indicar que a estratégia é selecionada positivamente. O caso de aprendizado acompanhado indica que processos similares aos que ocorrem em esquilos do hemisfério norte (Eibl-Eibesfeldt 1951, 1956, 1963, Weigl & Hanson 1980) e em outros roedores (Zohar & Terkel 1996, Ades & Busch 1999) também podem ocorrer em esquilos neotropicais, como aprendizado por tentativa e erro. Essas características podem ter um papel importante na capacidade do esquilo *Sciurus ingrami* de se adaptar a novos ambientes e contribuir para sua ampla ocorrência.

As formas de abertura encontradas em frutos de *Syagrus oleracea*, no segundo capítulo, se assemelham aos padrões observados em sementes de *Syagrus romanzoffiana*. Em *S. oleracea*, a forma de abertura com o menor número de marcas de incisões realizadas pelos esquilos é também a maior, permitindo, provavelmente, um melhor acesso ao

endosperma gorduroso. Entretanto, a forma de abertura aparentemente mais eficiente, não é a mais freqüente, como em *S. romanzoffiana*. Se processos de aprendizado também ocorrem em esquilos se alimentando em *S. oleracea*, a maior proporção de formas irregulares pode ser devido a uma distribuição etária pouco usual da população da área amostrada, com um número muito grande de jovens inexperientes. Uma outra explicação pode estar no tamanho do fruto dessas palmeiras. Frutos grandes podem fornecer uma recompensa nutritiva grande, mesmo quando abertos de formas não ideais. Dessa forma, pressões seletivas para o aprendizado de novas formas não seriam tão intensas quanto em populações que se alimentam de *S. romanzoffiana*.

Estudos futuros podem elucidar estratégias de forrageio de esquilos tropicais em frutos de palmeiras. A análise de taxas metabólicas de cada estratégia de abertura de sementes duras pode trazer mais informações sobre o custo de cada tipo de comportamento. Avaliações do valor calórico e composição química do endosperma também permitem uma melhor compreensão dos benefícios obtidos pelos animais. Além disso, o estudo de estratégias de forrageio em sementes grandes, como *S. oleracea*, podem revelar padrões diferentes daqueles encontrados em esquilos que se alimentam de frutos pequenos. O entendimento dos processos de aprendizado de técnicas de forrageio também pode ser objeto de diversos estudos, como o acompanhamento de outros casos de aprendizado e experimentos em laboratório. Aspectos sociais do aprendizado, como observados por Weigl & Hanson (1980), também podem trazer mais informações sobre a história natural desses roedores.

Esquilos neotropicais são, ao mesmo tempo, predadores e dispersores de sementes e podem desempenhar um papel importante na dinâmica de florestas. Seus comportamentos de forrageio podem revelar padrões importantes em processos populacionais de palmeiras e

outras plantas. Além disso, pouco é conhecido hoje sobre esses animais e a compreensão de sua história natural pode ser vital para sua conservação.

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