Scatter-hoarding Behavior of Two

Amazonian Rodents: Theory and Application

in Forest Fragments

BY

MARIA LUISA S. P. JORGE
B.S. Universidade de São Paulo, 1996
M.Sc. Universidade de São Paulo, 2000

THESIS

Submitted as partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Biological Sciences
in the Graduate College of the
University of Illinois at Chicago, 2007

Chicago, Illinois

I dedicate this work to my parents,

Maria Eduarda and *Alberto*,

for teaching me

to be strong in difficult moments

and to never lose hope.

ACKNOWLEDGEMENTS

ACKNOWLEDGEMENTS (continued)

ACKNOWLEDGEMENTS (continued)

I thank my daughter, Marina, for being part of my life in the last nine months. She gave me a lot of strength and focus to finish my thesis. I certainly owe many thanks to my mother-in-law, Dulce, for helping with Marina in two crucial periods: when she was first born, and when I was finishing my dissertation.

Finally, I thank my husband, Guilherme. We came together, we started our PhDs together, we went through six years of PhD madness together, we had a baby together, we took care of her together, we finish our PhDs together... and we are still together! Much of it is because of his endless patience, motivation and love.

MLSPJ

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF TABLES

LIST OF FIGURES

SUMMARY

In the present work, I investigated what evolutionary and environmental factors motivate an animal to scatter-hoard. Scatter-hoarding occurs when animals cache food individually under the soil surface to harvest them later. In order to answer my question, I used two complementary approaches: a theoretical one and an empirical one. The theoretical approach was a two-time step model based on Holling's disc equation of harvest rate. It was intended to be simple and general, using general parameters to investigate caching dynamics: total foraging time, resource abundance, handling time, energetic content, and predation risk. The model depicted four general motives for an animal to cache when caching: 1) allows the animal to gain search time when search time is cheaper (*search-time reallocation*); 2) balances food intake over time (*consumption reallocation*); 3) decreases predation risk (*predator avoidance*); finally 4) when food quality increases while cached (*food aging*);

The empirical study was conducted in forest fragments (one, ten and hundred hectares) and continuous forest of the *Biological Dynamics of Forest Fragments*, Central Amazon, Brazil. The objects of the study were: agoutis (*Dasyprocta leporina*), acouchies (*Myoprocta acouchy*) and palm nuts (*Astrocaryum aculeatum*). Overall, the study showed that changes in scatter-hoarding behavior (levels of removal and caching, as well as caching distance) can be greatly explained by changes in resource abundance. Where there was more food, fewer seeds were removed. And when there was more food, more seeds were cached and they were cached farther away. But when looking specifically at effects of forest fragmentation, the relationship between resource abundance and removal

SUMMARY (continued)

or caching did not occur. More seeds were removed in smaller fragments; fewer seeds were cached in smaller fragments; and the ones cached were cached at shorter distances. Nevertheless, fragment size did not affect resource abundance. Factors such as a decrease in predation risk, decrease in pilferage, and the increase of the relative importance of agoutis as the agents of scatter-hoarding (which are the only scatter-hoarders capable of visiting the small fragments) may explain the changes observed in small forest fragments.

I. INTRODUCTION

In the present work, I studied the dynamics of scatter-hoarding behavior. Specifically, I was compelled to understand the set of evolutionary and ecological conditions that motivate an animal to hoard an item rather than immediately consume it. The inspiration for this research was to understand the consequences of an animal's choice to the seeds it hoards. A considerable proportion of seed species from Neotropical rainforests are heavier than one gram (approximately 5% on Barro Colorado Island, Panama – Foster 1982; approximately 25% in Manu, Peru – Foster and Janson 1985; and 40-50% in Mabura Hill, Guyana – Hammond and Brown 1995) and experience dispersal limitation. In some species, seeds fall or are dropped under parent trees (Smythe 1989) where they experience high rates of density-dependent mortality. In other cases, seeds are ingested by large frugivores (*e.g.* large birds, primates and tapirs – Forget and Milleron 1991). Primary or secondary dispersal by two genera of Neotropical rodents, *Dasyprocta* spp. (agoutis), and *Myoprocta* spp. (acouchy) enhance the probability of seed survival by scatter-hoarding seeds because many are not recovered later.

Scatter-hoarding is a conditional mutualism (*sensu* Bronstein 1994). The same animal that acts as a seed disperser in some conditions, may act as a seed predator in others (Theimer 2005). The decision to hoard or eat likely involves both evolutionary (*e.g.* seed traits) and ecological factors (*e.g.* resource abundance and predation risk). In the present research, I chose two approaches to investigate how those factors affect the animal's decision to hoard or to eat.

1

First, I developed a theoretical model of hoarding behavior (Chapter II). Other models of hoarding behavior exist, but their motives and approaches differ from what I present here. Most aim to describe detailed environmental and physiological conditions that compel an animal to cache, employing complex multi-step stochastic dynamic programming (Lucas and Walter 1991, Clark 1994) and state-dependent parameters to predict caching decisions in specific systems (*e.g.* chickadees) under specific conditions (e.g. starvation) (Brodin and Clark 1997, Pravosudov and Lucas 2001). In the model presented in Chapter II, I used a minimal number of general parameters (resource abundance, handling cost, and food energetic content) that are most likely to influence an animal's decision to hoard or eat. The model is a two-time step model based on Holling's equation of harvest rate (Holling 1965). The first period is the period of caching and the second is the period of retrieving the cached food. In both periods the animal may also eat food from the environment. The decision to cache or eat is investigated in three scenarios that reflect distinct motivations and environmental conditions (short-term caching; long-term caching, and caching under predation risk). The model predicts that an animal should cache if, by caching, the animal: 1) gains search time when search time is cheaper; 2) balances food intake over time; 3) decreases predation risk; 4) or increases food quality.

The model was an invitation to think about the caching behavior of two South-American scatter-hoarding rodents – agoutis (*Dasyprocta leporina*) and acouchies (*Myoprocta acouchy*) – in a scenario of forest fragmentation. In this empirical approach, I examined how hoarding patterns of agoutis and acouchies are affected by changes in

forest size (Chapter III) and how those patterns correlate with changes in the abundances of the animals (Chapter IV) and their food (Chapter V).

Schupp (1993) proposed that dispersal effectiveness should be separated into two categories: quantity and quality. Quantity refers to the number of visits made to a plant and the number of seeds dispersed per visit. Quality refers the treatment that each individual seed receives (*e.g.* how they are handled and where they are deposited). The decision to cache or eat upon encountering a seed can be categorized as a qualitative aspect of the scatter-hoarding dispersal system. Previous work has shown that fragmentation negatively affects the quantitative aspect of scatter-hoarding systems. In places where scatter-hoarders decrease in numbers, removal rates of large seeds from the ground also decrease, more seeds suffer from density-dependent mortality, and ultimately, plant recruitment is lowered (Asquith et al. 1997, 1999, Wright et al. 2000, Wright and Duber 2001, Guariguata et al. 2002). But until now, no one has tested if the qualitative aspect of the scatter-hoarding system is also affected by forest fragmentation.

Fruit abundance naturally oscillates over a year in Neotropical rainforests (Foster 1982, Gentry and Emmons 1987). Agoutis and acouchies hoard most of the seeds when fruit abundance is high (Hallwachs 1986, Smythe 1989, Forget 1990, 1996) and harvest buried seeds (and others found in the environment) when fruit abundance is low. Forest fragmentation could negatively affect proportion of seeds cached if resource and animal abundance changed independently of each other and overall resource abundance per scatter-hoarder decreased when compared to levels present in intact forest.

In the simplest scenario, resource density changes in forest fragments due to sampling effects. Most tree populations are not distributed uniformly in a forest and forest fragments may have tree composition and abundance distributions radically different from one another and from intact forests in the same region. This aspect is intensified in tropical rainforests where tree diversity is very high and most tree species are present in very low densities (lower than one individual per species per hectare – Pitman et al. 2001). Tree densities in fragments may also change over time. Trees near the edges are negatively affected by desiccation, wind shear (Laurance et al. 1998), and liana infestations (Laurance et al. 2001b). There is also higher mortality of larger trees in smaller fragments (Laurance et al. 2000). This should negatively affect the availability of fruits because these larger individuals are usually the ones that contribute the most to fruit production. Furthermore, large trees that die at fragment edges are substituted by pioneer trees (Tabarelli et al. 1999) which produce smaller fruits and seeds that represent lower quality resources for the rodents.

Forest fragmentation may also affect animal abundances. Some changes are directly related to changes in resource abundances (bottom-up effect). Those should not qualitatively affect scatter-hoarding dynamics because they do not change the ratio between fruit and animal abundances. Factors independent of resource abundance may also affect animal abundances. Migration is one of them. Animals are highly mobile, and their abundances within a patch depend on movements of individuals between patches. Forest fragmentation makes the landscape structurally more heterogeneous. Some animals change their movement patterns in a more heterogeneous landscape and that affects animal abundance within a fragment independent of resource abundance. Invasion

of non-forest species into the forest fragments or increase or decrease of predator abundances are other factors that may change rodent abundances without necessarily affecting resource abundance.

In Chapter III, I empirically test whether fragmentation qualitatively affects the scatter-hoarding system. I set up artificial experimental stations with palm seeds (*Astrocaryum aculeatum*, Arecaceae) in fragments of one and ten hectares and in continuous forest, quantifying removal numbers and caching proportions. Chapter III shows that indeed forest fragmentation affects scatter-hoarding patterns, but not in a linear manner. In Chapter IV, I quantify the abundance of agoutis and acouchies in the same fragments and tracts of continuous forest using line-transect census technique. Chapter IV illustrates that two morphologically similar and evolutionarily related genera can respond in contrasting ways to forest fragmentation. In Chapter V, I quantify fruit availability on the forest floor. Chapter V shows that changes in resource abundance varies spatially and seasonally, but are not affected by fragmentation of the forest. Together, the last three chapters bring a comprehensive picture of how the animals and their resources are affected by forest fragmentation and how they correlate to changes of scatter-hoarding dynamics.

II. ANALYTICAL MODEL OF CACHING BEHAVIOR

II.1. <u>Introduction</u>

Food caching is a widespread behavior. It occurs in taxa as far related as spiders and mammals, in regions as divergent as tropical rainforests and temperate deserts, and in dietary groups as different as herbivores and carnivores (Vander Wall 1990 and references therein). Yet, caching may be explained by few general motives. Some species cache food for short periods, to meet daily shortage of supply (*e.g.* marsh tits – Stevens and Krebs 1986). Others cache food to harvest it in safer places (*e.g.* red tree voles – Howell 1926). Others use cached food to supply resource shortage over the long run (*e.g.* honey bees – Seeley 1985; jays, nutcrackers and squirrels – Vander Wall 1988, Thompson and Thompson 1980). In summary, some animals that deal with temporal variability of food supply, cache food to better control this variability over time; either to decrease foraging costs and predation risk, or to guarantee balanced energy intake over time.

Previous models of caching behavior used stochastic dynamic programming to explore state-dependent caching decisions in a daily temporal sequence of days and months (Lucas and Walter 1991, Clark 1994, Brodin and Clark 1997, Pravosudov and Lucas 2001). They are successful in predicting caching decisions of chickadees and tits, based on levels of body-fat and environmental temperature change over time. Yet, they do not fulfill the scope of predicting the motives for caching in a more general way.

6

In this chapter, I present a two-time step model in which an animal needs to survive in an environment that offers benefits (energy from food items) and costs (search time, handling time and predation risk). It builds on Gerber *et al.* (2004) model of caching behavior in the sense that it is based on Pulliam's prey selection model (Pulliam 1974). Nevertheless, the model presented in this chapter incorporates fundamental variations in the basic fitness function and expands the Gerber *et al.* model to include three scenarios with distinct fitness objectives. In the first scenario, or short-term caching, the animal's goal is to maximize energy intake. In the second scenario, or long-term caching, the animal's goal is to balance food intake. In the last scenario, the animal deals with two contrasting objectives: maximize energy intake while minimizing predation risk.

II.2. <u>The general model: describing the basic functions</u>

I envision an animal that gains energy (G) from searching and handling food over two periods, each of them consisting of T time units. I assume that there is no resource depletion and that resource harvest corresponds to Holling's disc equation (Holling 1965):

$$G = \frac{a\,Re}{1+aRh} * T,$$ (1)

Where a is encounter probability, e is the energy value of a resource item, R is resource abundance, and h is handling time.

The animal forages over two time periods and resource abundance in period one (R_1) may differ from that of period two (R_2). Moreover, in order to evaluate the importance of handling time and energy as conditions that favor caching, each of those parameters is

presented in two distinct forms. Time taken to consume an item (h_e) may differ from the time taken to cache it (h_c). And energy obtained from a fresh item (e_e) may differ from the energy gained from a cached item (e_c). Definitions and units for each parameter are presented in Table I.

While foraging during the first period, upon encountering a food item, the animal has the option of consuming or caching it. The total energy gained from food consumed during period 1 (forager's fitness) is given by:

$$G_1 = \frac{aR_1 e_e (1-\mu)}{1 + aR_1 [(1-\mu)h_e + \mu h_c]} * T , \tag{2}$$

Where μ is the proportion of encountered items that the forager caches. Notice that the more items the animal caches, the less energy it gains in the period.

During time period 2, the animal gains energy from two sources: (a) the food cached earlier:

$$G_{2a} = \frac{aR_1 e_c \mu}{1 + aR_1 [(1-\mu)h_e + \mu h_c]} * T ; \tag{3}$$

b) and food from the environment:

$$G_{2b} = \frac{aR_2 e_e}{1 + aR_2 h_e} * \left[T - \left(\frac{aR_1 \mu h_e}{1 + aR_1 [(1-\mu)h_e + \mu h_c]} * T \right) \right] . \tag{4}$$

Notice that in expression (4) foraging time is total foraging time T minus the time spent handling the cached food, in order for total time foraging to be a fixed parameter, as it is in time period one.

II.3. <u>Scenarios for the evolution of caching behavior</u>

I consider three scenarios for the evolution of caching which differ in the forager's fitness objectives. **Scenario I** represents short-term caching. The forager aims to maximize resource consumption over the two periods, and I use an additive function to represent this objective:

$$G_T(I) = G_1 + G_{2a} + G_{2b}. \tag{5}$$

Scenario II represents long-term caching, in which the forager aims to balance food consumption over the two periods. In this case, I use a multiplicative Cobb-Douglas function to represent the animal's goal:

$$G_T(II) = G_1^{\alpha} * \left(G_{2a} + G_{2b}\right)^{\beta}, \tag{6}$$

Where the product represents the complementary nature of food consumption between the two time periods and $\alpha + \beta = 1$.

With this objective function, there are diminishing returns to increasing food consumption within a time period, and consumption of food in a period increases the value of food consumption during the other period.

Scenario III represents short-term caching under predation risk in which the forager aims to balance food and safety. The forager must survive both periods to enjoy any fitness benefits from food harvest. There are risks of predation in both periods (γ_1 and γ_2) and I assume that predation risk is incurred only while searching for food and the forager is safe while handling food items. Handling may be safer either because the forager can

carry the food item to a safe place for handling (Lima and Valone 1986) or because the forager is able to be more vigilant and attentive to potential threats while handling food. The forager's objective is to maximize food consumption across the two time periods subject to predation, and the objective function is represented by the energy gained (sum of energy gained during the two periods) multiplied by the probability of surviving to enjoy these gains:

$$G_T(III) = e^{-T(q_1\gamma_1 + q_2\gamma_2)} * [G_1 + G_{2a} + G_{2b}], \tag{7}$$

Where γ_1 and γ_2 are the instantaneous risks of predation while searching for food during periods one and two; and q_1 and q_2 are the proportions of time spent searching during periods one and two, defined as:

$$q_1 = \frac{1}{1 + aR_1[h_e(1-\mu) + h_c\mu]}, \tag{8}$$

$$q_2 = \left[\frac{1}{1 + aR_2h_e}\right] * \left[\frac{1 + aR_1[h_e(1-2\mu) + h_c\mu]}{1 + aR_1[h_e(1-\mu) + h_c\mu]}\right]. \tag{9}$$

II.4. Analyses

To determine the importance of caching on the forager's fitness (G_T), I evaluate the influence of caching on the forager's objective function: $\partial G_T/\partial\mu$ (hereafter called *derivative function*).

TABLE I: DESCRIPTION OF THE PARAMETERS USED IN ALL EXPRESSIONS OF THE ANALYTICAL MODEL OF CACHING BEHAVIOR

Parameter	Description of the parameter	Units
G_1	Total energy gained in period one	Calories
G_{2a}	Total energy gained from caches in period two	Calories
G_{2b}	Total energy gained from environment in period two	Calories
a	Encounter probability	minutes / time
R_1	Resource abundance in time period one	number of items
R_2	Resource abundance in time period two	number of items
h_e	Handling time eating	minutes / item
h_c	Handling time caching	minutes / item
e_e	Energy from items from environment	calories / item
e_c	Energy from cached items	calories / item
μ	Proportion of items cached	dimensionless $(0 < \mu < 1)$
T	Time spent foraging	minutes
α	Diminishing returns in time period one	dimensionless $(0 < \alpha < 1)$
β	Diminishing returns in time period two	dimensionless $(0 < \beta < 1)$
γ_1	Predation risk in time period one	dimensionless $(0 < \gamma_1 < \infty)$
γ_2	Predation risk in time period two	dimensionless $(0 < \gamma_2 < \infty)$
q_1	Search time in time period one	Minutes
q_2	Search time in time period two	Minutes

The *derivative function* when no food is cached ($\partial G_T/\partial \mu \mid_{\mu=0}$) sets the threshold between "no caching" and "some caching." At this threshold, if the derivative function is negative ($\partial G_T/\partial \mu \mid_{\mu=0} < 0$), the forager prefers "no caching", and if it is positive ($\partial G_T/\partial \mu \mid_{\mu=0} > 0$), the forager prefers "some caching". If it is zero ($\partial G_T/\partial \mu \mid_{\mu=0} = 0$), the forager is indifferent to "no caching" and "some caching" and this will be called the **some-caching isoleg**. Using the same reasoning, the *derivative function* when all food is cached ($\partial G_T/\partial \mu \mid_{\mu=1}$) sets the threshold between "some caching" and "caching all" and $\partial G_T/\partial \mu \mid_{\mu=1} = 0$ defines the **all-caching isoleg**.

Both isolegs will be investigated in the state space of R_1 and R_2 ($R_2 = f(R_1)$) so that R_1 and R_2 will be the anchor parameters to explore the conditions that favor caching. In that state space, the **some-caching isoleg** defines all combinations of R_1 and R_2 such that the forager is indifferent between "no caching" and "some caching". The **all-caching isoleg** defines all combinations of R_1 and R_2 such that the forager is indifferent between "some caching" and "caching all". My objective is to investigate how the isolegs in the state space of R_2 *versus* R_1 are influenced by differences in handling time (h_e and h_c), energy reward (e_e and e_c), and predation risk (γ_1 and γ_2).

II.5. Results

II.5.a. Scenario I: short-term caching

When the goal of the animal is to maximize food consumed over the two periods, the **some-caching** and **all-caching isolegs** merge together to become the same expression (refer to *Appendix A* for the analytical development):

$$R_2 = \frac{e_e\left(1+aR_1 h_c\right)-e_c\left(1+aR_1 h_e\right)}{ah_e\left[e_c\left(1+aR_1 h_e\right)-e_e\left(2+aR_1\left(h_c+h_e\right)\right)\right]}. \tag{10}$$

This means that if the animal's motive is to maximize food consumption, the optimal levels of caching are either "no caching" or "caching all", and intermediate levels of caching do not occur.

When there are no differences in handling times and energy per item ($h_c = h_e$ and $e_c = e_e$ in expression 10) caching is never optimal ($R_2 = 0$). All combinations of R_1 and R_2 that promote caching are negative, or not biologically feasible. Therefore, in *Scenario I*, for caching to be promoted, the animal must either take less time to cache an item then to consume it ($h_c < h_e$), or cached foods must yield a higher energy reward than "fresh" food ($e_c > e_e$).

To explore how handling time affects caching, I set $e_c = e_e$ in expression 10, so that:

$$R_2 = \frac{\left(h_e - h_c\right) R_1}{h_e \left(1+aR_1 h_c\right)}. \tag{11}$$

Now, caching may be optimal as long as handling time caching is smaller than handling time eating ($h_c < h_e$) and there is more food in period 1 than 2 ($R_1 > R_2$), which may be defined as search-time reallocation. Moreover, handling time interacts with resource abundance in a way that as h_c becomes relatively smaller, caching is optimal at smaller differences between R_1 and R_2 (Figure 1).

The isoleg levels off for large values of R_1 as search time in period one becomes

negligible in comparison to handling time. At this point, the only factors that influence

the decision to cache are handling time and food abundance in period two.

To explore how energy affects caching, I set $h_c = h_e$ in expression 10, so that:

$$R_2 = \frac{e_c - e_e}{ah(2e_e - e_c)}.$$ (12)

In this case, caching is optimal as long as energy from caching is greater than energy

from the environment ($e_c > e_e$). Note that the effects of energy are independent of R_1.

This happens because energy from caches only affects total energetic gain of period two

(expressions 2 to 4).

On the other hand, energy interacts with R_2 because, by caching, the forager loses

time available to search (it is obligated to handle the cached food, therefore spends less

time searching for new food) but gains if there is an enhancement in energy value from

caching ($e_c - e_e$). In summary, when caching makes food more valuable ($e_c > e_e$), it may

be optimal even when food abundances are lower in period one than period two as long

as energetic gain surpasses all time costs (Figure 2)
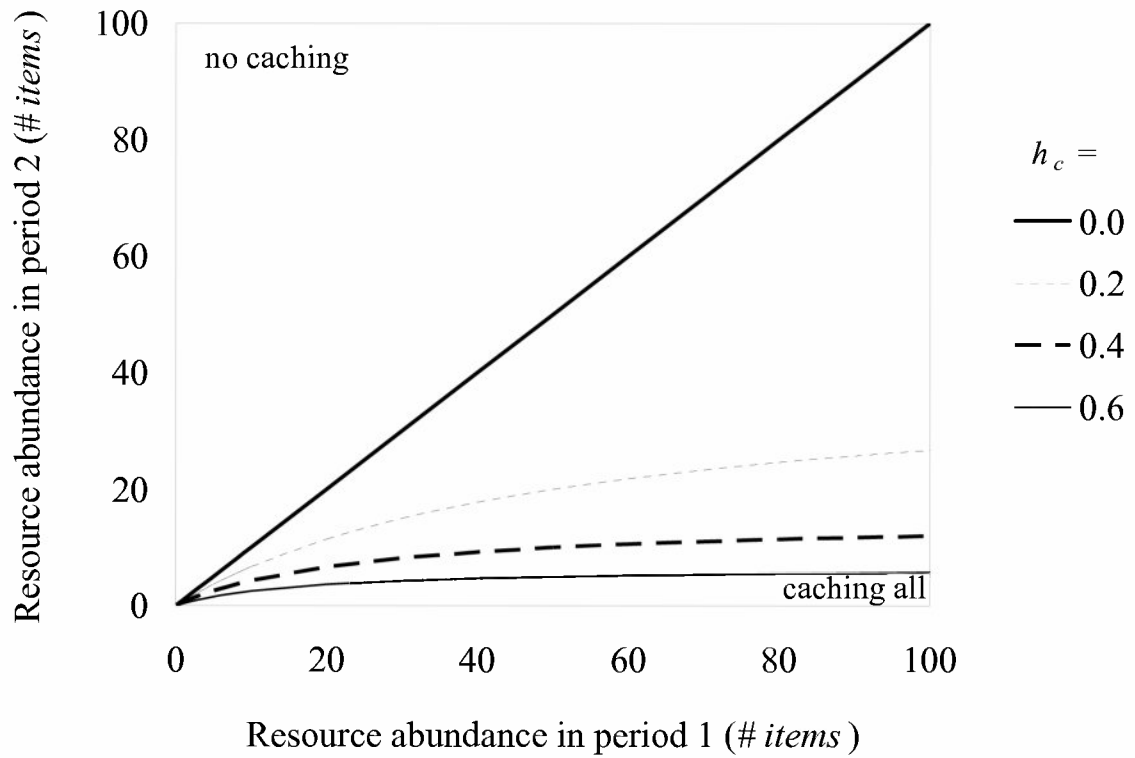
Figure 1: In short-term caching, the **some-caching** and the **all-caching isolegs** collapse into a single isoleg that determines when it is best not to cache at all (above the isoleg) or cache everything (below the isoleg). Caching becomes less and less likely as handling time caching increases. Other parameters equal: $h_e = 1.0$; $e_e = e_c = 1.0$; $a = 0.1$. When $h_c = 1$, $R_2 = 0$, and when $h_c = 0$, $R_2 = R_1$.
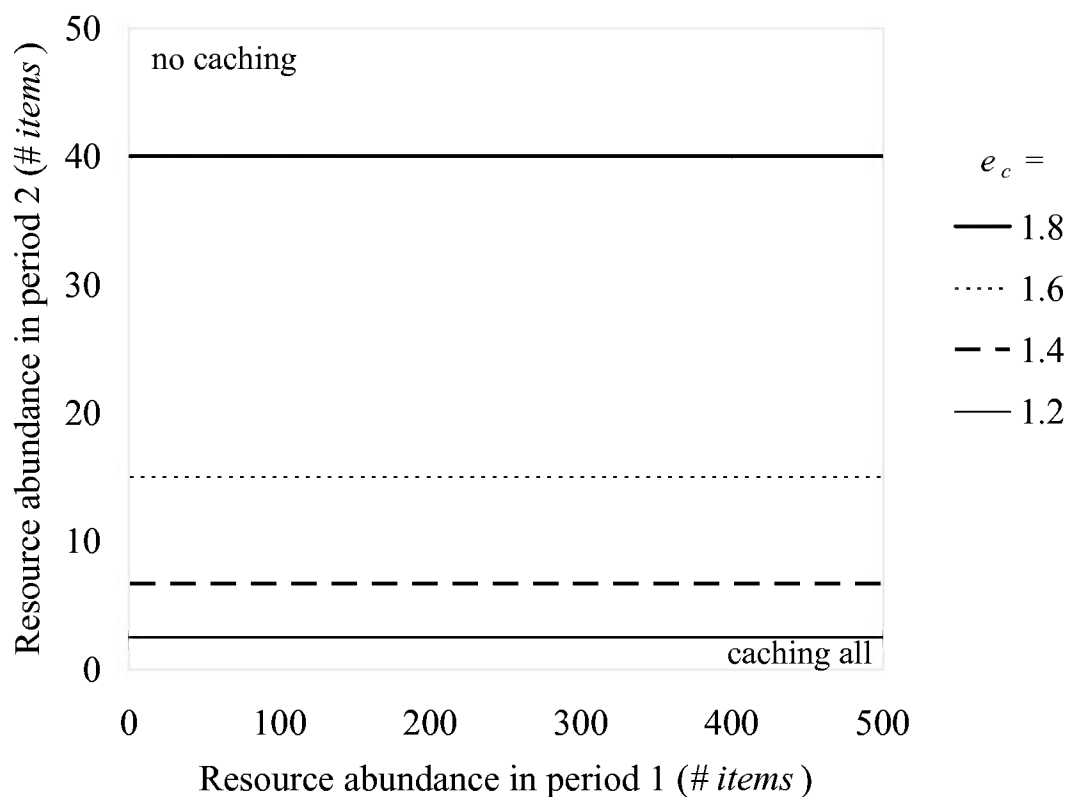
Figure 2: In short-term caching, the **some-caching** and the **all-caching isolegs** collapse into a single isoleg that determines when it is best not to cache at all (above the isoleg) or cache everything (below the isoleg). The horizontal isolegs indicate that caching is solely determined by a threshold abundance of food in period two. Caching becomes increasingly likely as the value of cached food increases relative to the value of fresh food. Other parameters equal: $e_e = 1.0$; $h_e = h_c = 1.0$; $a = 0.1$.

II.5.b. Scenario II: long-term caching

When food consumption in period one and two are complementary, intermediate levels of caching may occur ($0 < \mu < 1$), and complete caching is never possible (at $\mu = 1$, $R_2 < 0$, which is not biologically meaningful). This is an expected result. By definition complementarity means that the organism must consume some food in each period in order to survive, and caching everything forbids any energetic intake in the first period. The **some-caching isoleg** is given by (refer to *Appendix B* for analytical development):

$$R_2 = \frac{\beta\, e_c R_1}{\beta\, aR_1 h_e (e_e - e_c) + \alpha\, e_e (1 + aR_1 h_c)}. \tag{13}$$

In *Scenario I*, the simplest conditions for caching to evolve were either handling time caching smaller than eating or energy from caching greater than from the environment. In *Scenario II*, at sufficiently large differences between R_1 and R_2, caching is promoted, , even if handling times and energies are equal, as a means of balancing food consumption between the periods (Figure 3).

When $e_c = e_e$ and $\alpha = \beta$, the effects of handling time are similar to what was seen in *Scenario I* (expression 11):

$$R_2 = \frac{R_1}{1 + aR_1 h_c}, \tag{14}$$

Such that R_1 must be greater than R_2 for caching to be optimal, and the interaction between handling time and R_1 becomes negligible at large values of R_1 (Figure 3).
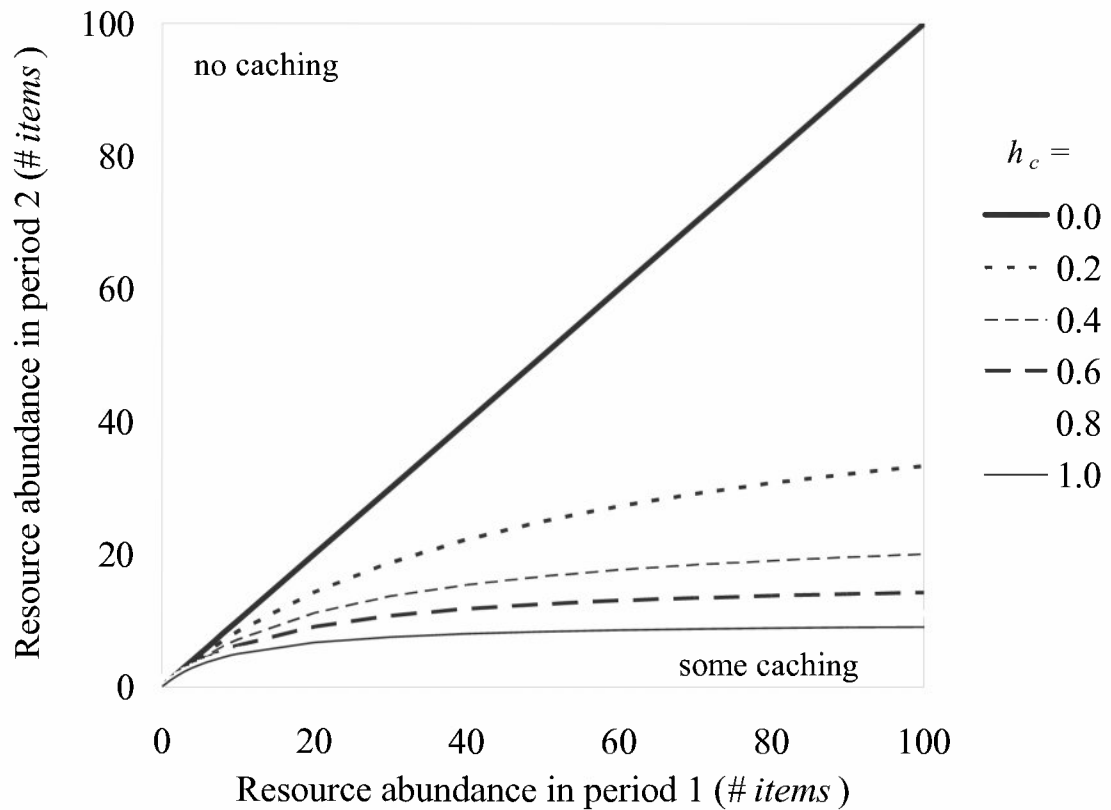
Figure 3: In long-term caching, the only biologically meaningful isoleg is the **some-caching isoleg** (the **all-caching isoleg** is always negative). The **some-caching isoleg** separates caching nothing (above the line) from intermediate levels of caching (below the curve). Similar to short-term caching, caching is more likely to occur as handling time caching decreases. In contrast to short-term caching, caching is possible even when handling time caching and eating are the same, at sufficiently large differences between resource abundance in periods one and two. Other parameters are: $h_e = 1.0$; $e_e = e_c = 1.0$; $\alpha = \beta = 0.5$; $a = 0.1$.

On the other hand, the effects of energy are no longer independent of resource

abundance in period one (as they were in *Scenario I*): When $h_c = h_e$ and $\alpha = \beta$:

$$R_2 = \frac{e_c R_1}{a R_1 h \left(2e_e - e_c \right) + e_e}.$$

(15)

The dynamics is similar to that of handling time in which R_1 must be greater than R_2 and

e_c must be greater than e_e for caching to be optimal, and the interaction between energy

and R_1 becomes negligible at large values of R_1 (Figure 4).

II.5.c. Scenario III: caching under predation risk

Predation risk can produce intermediate levels of optimal caching, like in *Scenario*

II, and complete caching, like in *Scenario I*. The two isolegs are complex; therefore they

will be only presented in *Appendix C*, with the analytical development that permitted

their derivation. The two isolegs divide the state space of resource abundances into the

three regions: "no caching", "some caching", and "caching all".

The isolegs are no longer independent of foraging time, T, and as T increases, so

does the likelihood of caching. This is probably due to the fact that increasing foraging

time increases search time, which directly increases predation risk. By caching, the

animal decreases search time in period two because it has to eat all the cached food

before looking for new food. Caching becomes a safety refuge, a finding made more

apparent when looking at the other parameters.
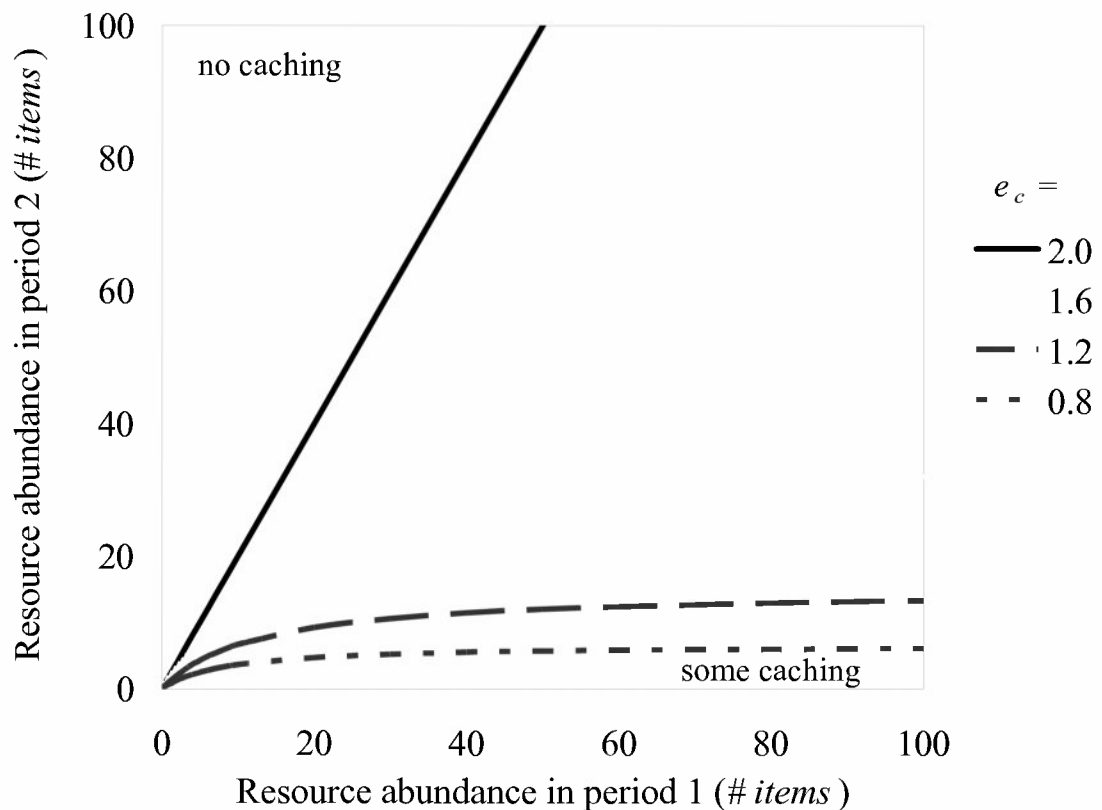
Figure 4: In long-term caching, the only biologically meaningful isoleg is the **some-caching isoleg** (the **all-caching isoleg** is always negative). The **some-caching isoleg** separates caching nothing (above the line) from intermediate levels of caching (below the curve). Similar to short-term caching, caching is more likely to occur as energy from caches increases. Different to short-term caching, caching is affected by resource abundance in period one. Other parameters are: $e_e = 1.0$; $h_e = h_c = 1.0$; $\alpha = \beta = 0.5$; $a = 0.1$.

When predation risk is included in the model, some caching and caching all are possible scenarios , even when caching is as time consuming as eating ($h_c = h_e$), and food values are the same ($e_c = e_e$), as long as there are sufficient differences in resource abundance between periods one and two (Figure 5a). This parallels *Scenario II*, in which sufficiently large differences of resource abundance between the two periods allowed caching to evolve, with no need of differences in any other parameters.

The importance of caching as a safety refuge becomes more evident by setting $h_c = 0$ while keeping $e_c = e_e$ and $\gamma_1 = \gamma_2$. When $h_c = 0$ and the animal caches everything, it spends all of its time searching during period one, which decreases its probability of surviving. However the negative effect is completely balanced by the safety brought by decreasing search time during time period two. Therefore, the decision to cache all or eat all depends solely on the period when there is more food and search time is cheaper (Figure 5b).

As h_c increases, differences between R_1 and R_2 need to be greater for the animal to cache (Figures 5c and 5d). When $h_c > h_e$, caching is more favored at small R_1 than at large R_1 (Figures 5e and 5f). This apparently odd effect emerges from the interplay between caching as a time-cost on searching for food and as a refuge from predation. When $h_c < h_e$, caching makes more time available for searching in period one, but increases exposure to predation (benefit and cost). On the other hand, it decreases search time in period two and enhances safety (double benefit).

a)   b)
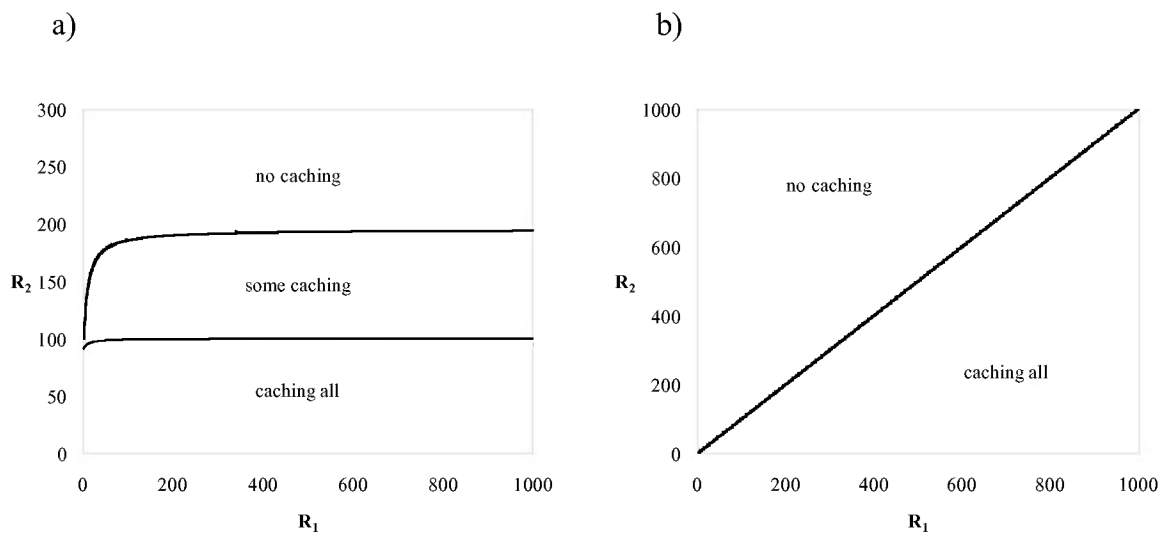
Figure 5: Under predation risk, there are distinct **no-caching** and **all-caching isolegs** that divide the state space into regions of "caching all", "some caching", and "no caching" (a) when handling times are the same; (b): with no handling time caching the two isolegs almost coincide; (c) and (d): increasing handling time caching increases probability of intermediate levels of caching; and (e) and (f): once handling time caching exceeds that of consuming a food item both isolegs take on negative rather than positive slopes. Handling time caching values are: a) $h_c = 1.0$; b) $h_c = 0.0$; c) $h_c = 0.3$; d) $h_c = 0.7$; e) $h_c = 1.3$; f) $h_c = 1.7$. Other parameters are: $h_e = 1.0$; $e_e = e_c = 1.0$; $\gamma_1 = \gamma_2 = 0.1$; $a = 0.1$; $T = 100$.
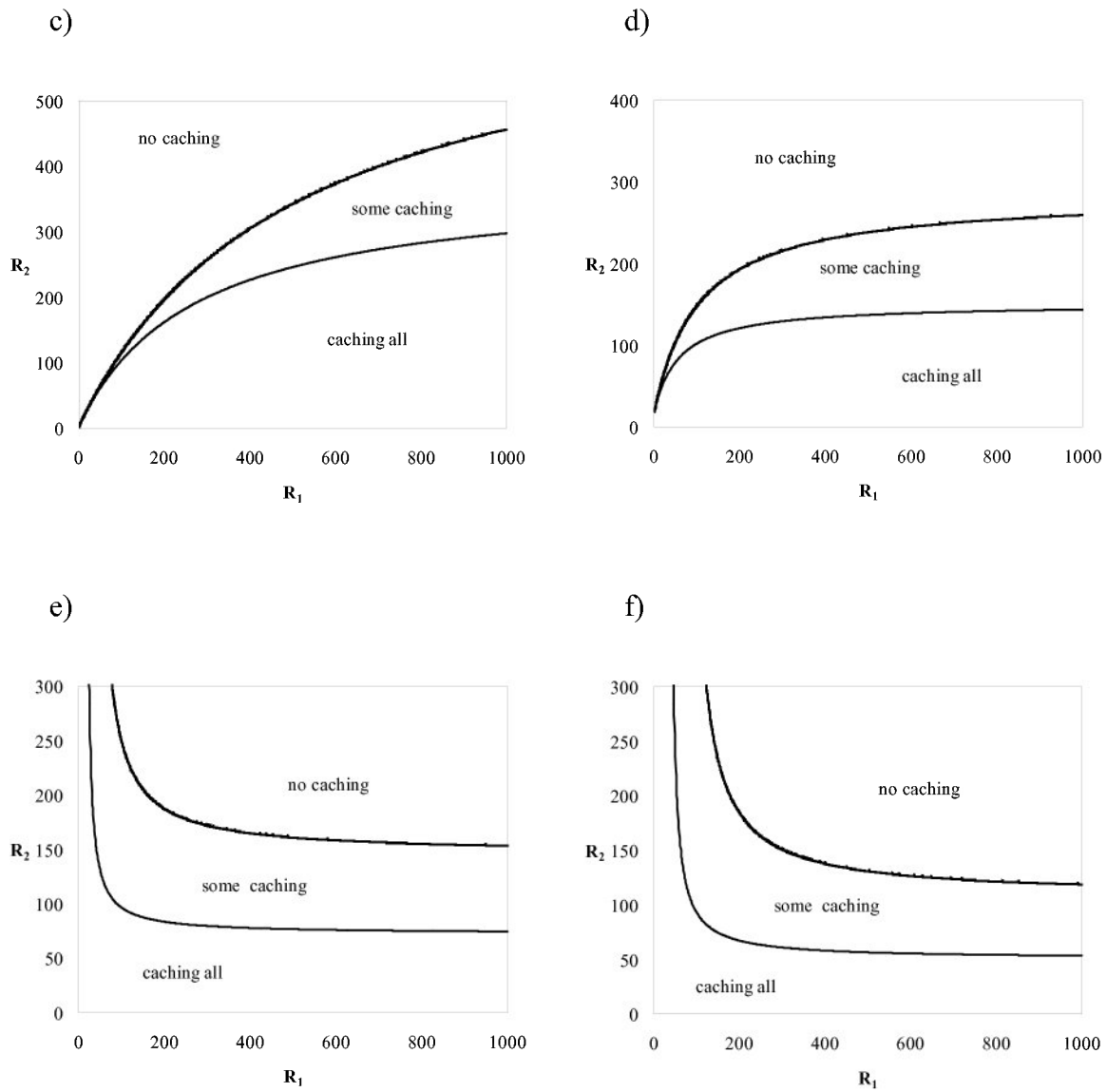
Figure 5: (*Continued*)

When $h_c > h_e$, caching decreases search time in periods one and two. This safety effect becomes intensified when R_1 is low and a high fraction of time in period one is spent searching. The value of safety from caching declines when resource abundances in period one is high, and relatively little time is spent searching.

Because of the importance of handling time as a safety resource, an interaction between predation risks and handling times is expected. When $h_c < h_e$, caching is less likely to evolve if $\gamma_1 > \gamma_2$ (Figure 6a). This happens because $h_c < h_e$ increases the amount of time spent seeking food during the riskier period ($\gamma_1 > \gamma_2$). But when $h_c > h_e$, caching is more likely to be promoted if $\gamma_1 > \gamma_2$, because it provides a safety refuge (Figure 6b). By caching the forager reduces search time in both periods.

When $\gamma_1 < \gamma_2$, caching becomes increasingly likely under practically all situations because it always provides a means of reducing search time during the riskier period (period two), whether $h_c < h_e$ or $h_c > h_e$. As before, if $h_c > h_e$, the likelihood is intensified at small R_1 (Figures 6c and 6d). Increasing predation risk simultaneously in both periods does not change the likelihood of caching when $h_c < h_e$ (Figure 6e), but greatly amplifies it when $h_c > h_e$ (Figure 6f). Once again, this illustrates the importance of caching as a safety time in both periods, especially when resources are low in period one.

a)

b)
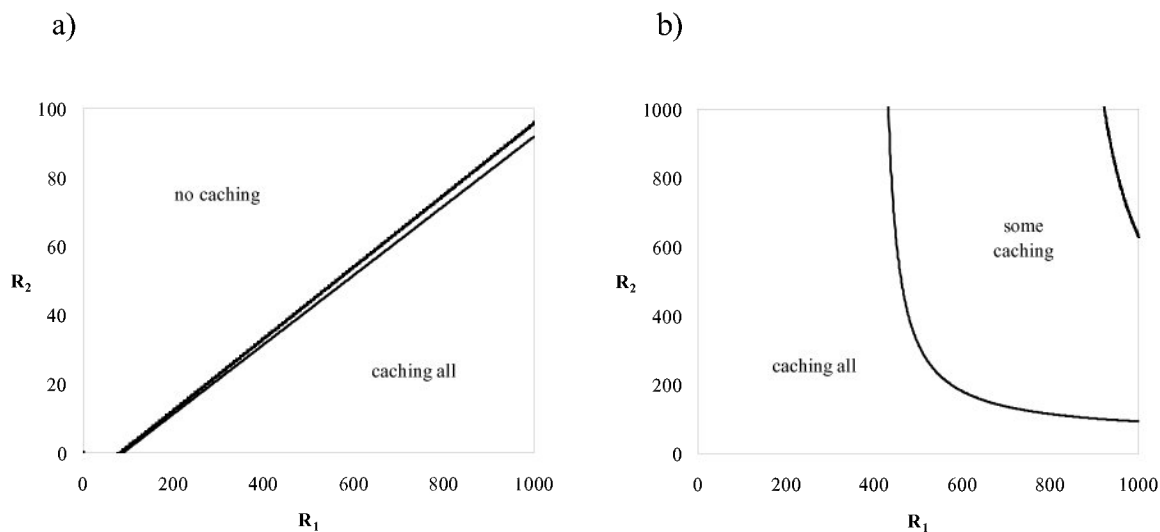
Figure 6: Under predation risk, when there is no cost of caching (a, c, and e), only predation risk in period two (γ_2) affects likelihood of caching (a): $\gamma_1 > \gamma_2$ and likelihood of caching increases; (c): $\gamma_1 < \gamma_2$ and likelihood of caching decreases; (e) $\gamma_1 = \gamma_2$ and likelihood of caching does not change. When handling time caching is greater than eating, caching is favored in all situations of increased predation risk: (b): when $\gamma_1 > \gamma_2$; (d): when $\gamma_1 < \gamma_2$; and (f): γ_1 and γ_2 both higher. Handling time caching and predation risks are: a) $h_c = 0.0$; $\gamma_1 = 1.0$ and $\gamma_2 = 0.1$; b) $h_c = 1.7$; $\gamma_1 = 1.0$ and $\gamma_2 = 0.1$; c) $h_c = 0.0$; $\gamma_1 = 0.1$ and $\gamma_2 = 1.0$; d) $h_c = 1.7$; $\gamma_1 = \gamma_2 = 1.0$; e) $h_c = 0.0$; $\gamma_1 = \gamma_2 = 1.0$; f) $h_c = 1.7$; $\gamma_1 = \gamma_2 = 1.0$. Other parameters are: $h_e = 1.0$; $e_e = e_c = 1.0$; $a = 0.1$; $T = 100$.

c)

d)

e)

f)
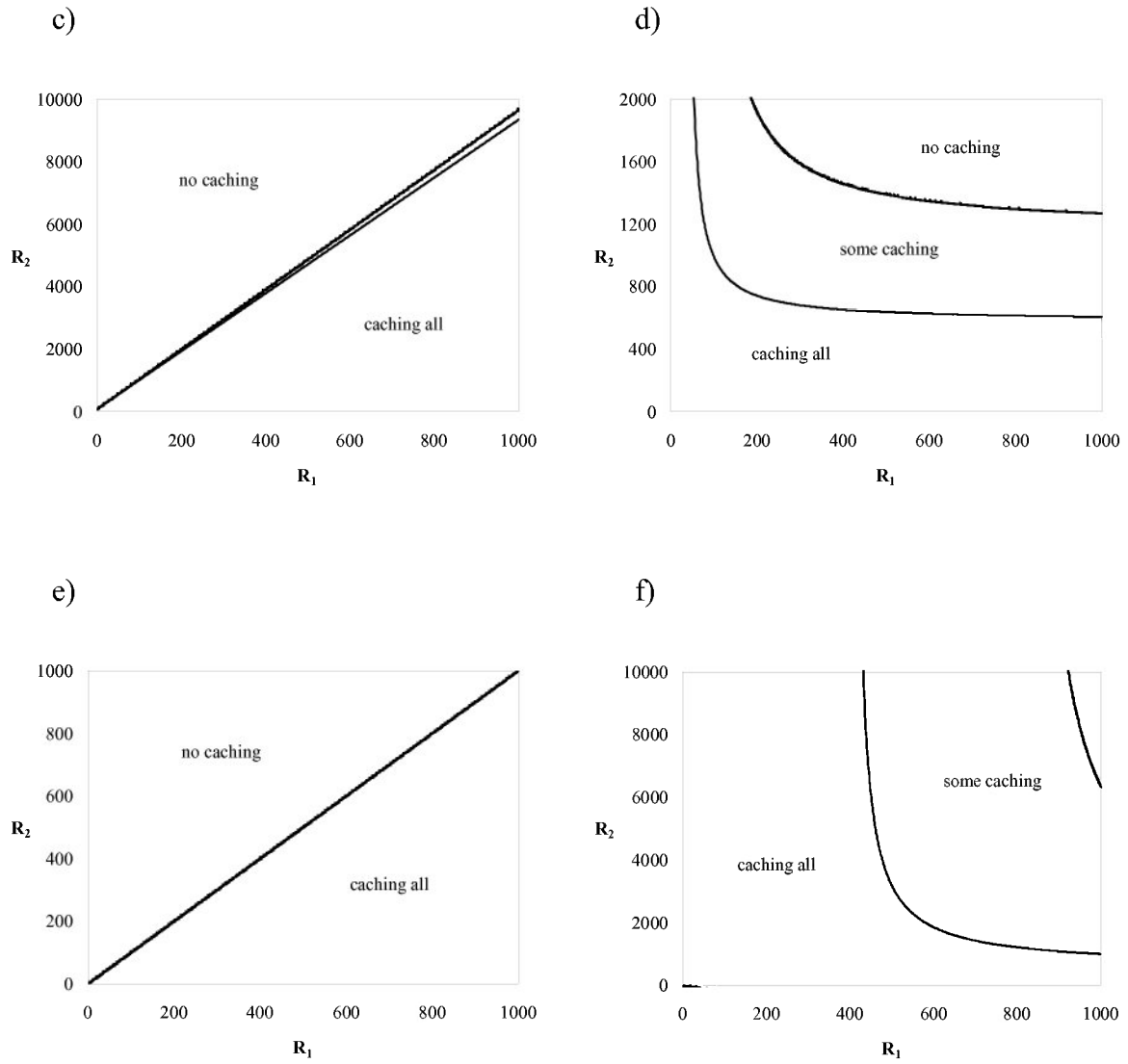
Figure 6: (*Continued*)

II.6. <u>Discussion</u>

I have modeled an animal that forages over two time periods. The time periods may vary in their resource abundance and predation risk. In the first time period to the forager has the option of either consuming or caching each encountered food item. In the second time period the forager consumes the food that has been cached and uses any remaining time to search for and handle newly encountered food items.

In one way this model is quite simplistic. Previous models have evaluated the evolution of caching with state-dependent parameters (*e.g.* body-fat) and dynamic stochastic programming (Lucas and Walter 1991, Brodin and Clark 1997, Pravosudov and Lucas 2001). These models consider specific environments, with specific choices being made at each time step. Such models have often been developed for particular caching phenomena (minimize starvation risk) or organisms (chickadees and tits).

What my model lacks in specificity and complexity, it gains in generality. It integrates four selective forces that can promote or inhibit caching: 1) search-time reallocation, 2) food aging, 3) consumption reallocation, and 4) predator avoidance. In the next sections, I will evaluate the predictions that emerge from integrating these forces.

II.6.a. Search-time reallocation

Caching may permit the forager to emphasize searching for food during periods when food is abundant and emphasize consumption during periods when food is scarce.

This aspect emerged most clearly under the assumption of short-term caching where the forager's objective is to maximize the sum of food consumed over the time periods.

In a two-time step model, two conditions must be met for caching to evolve. Resource abundance must be higher in the first period than the second, and the time required to cache a food item must be less the time required to consume a food item. With these two conditions met, when caching in the first period, the forager decreases time searching in the second period by increasing time spent consuming cached food. Short-term caching results in an all-or-nothing rule. It is either optimal for the forager to cache all or none of the items harvested during the first time period.

My model for short-term caching was inspired by that of Gerber and colleagues (2004). They too consider a two-time period horizon with short-term caching. They also predict a zero-one rule for the optimal level of caching during the first period. However, their model has the peculiarity of being time vague. Rather than fixing the amount of time available for searching and handling during the two periods, the forager's decision to cache in the first period changes the total time available during the second one. As a consequence, in Gerber and colleagues (2004), handling time does not influence the optimal level of caching.

Caching as a means for search-time reallocation supports the general conclusion that caching is promoted in response to temporal food scarcity (Vander Wall 1990). Previous models (Lucas and Walter 1991) and examples from nature also support this conclusion (Toates 1978, Wolff and Bateman 1978, Jaeger 1982, James and Verbeek 1984).

The likelihood of caching in the first period increases with food abundance in period one and the handling time required to consume a food item. The likelihood of caching declines with food abundance in period two and the time required to cache an item. Eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*) consuming black walnut (*Juglans nigra*), and red-rumped agoutis (*Dasyprocta leporina*) consuming Brazil nuts (*Bertholletia excelsa*) provide examples of systems where caching may have evolved because it takes less time to cache a food item then to consume it.

II.6.b. Food aging

Caching may be favored if food cached becomes more nutritious as it ages. Pikas (*Ochotona princeps*) are known to cache vegetation by drying it first (Dearing 1997). Yellow-pine chipmunks (*Tamias amoenus*) may harvest unripe fruit and then cache it securely to permit it to ripen prior to consumption or longer-term caching. Steele and colleagues (2006) showed that tree squirrels (*Sciurus* spp.) perform embryo-excision in hoarded white-oak acorns (*Quercus alba*) to preclude them from germinating while hoarded and the same behavior was shown in red acouchies (*Myoprocta exilis*) handling Crabwood seeds (*Carapa procera* – Jansen et al. 2006). These are not exactly examples of food aging, but of retarding energy loss from cached food, which could be included in a broader definition of food aging. The likelihood of caching in the first period increases with the nutritional value of cached food and decreases with initial nutritional value of the food.

With the short-term caching model (maximize the sum of food consumed over the two time periods), food aging can promote caching even when the first time period has

lower food abundance and when time to cache takes longer than time to consume. Hence the benefits of food aging may amplify or over-rule the effect of search-time reallocation on caching.

II.6.c. Consumption reallocation

Caching may be favored if fitness is enhanced by balancing consumption over the two periods. This concept represents long-term caching where starvation results if some food is not consumed during each time period. I modeled this using a Cobb-Douglas function typical of economic models where the objective is to maximize consumption of complementary resources. This scenario can never result in complete caching as this would obviate any food consumption during the first period. However, a wide range of conditions can favor an intermediate level of caching.

No other models evaluate the conditions for long-term caching in the way our model does. Brodin and Clark (1997) presented a dynamic model for long-term hoarding in Paridae, but they were mainly interested in the effects of short-term and long-term caching on survival, not on influences of external factors on the probability of caching.

The present model assumes that the main motive for long-term caching is to balance food intake between time periods as opposed to simply maximizing cumulative intake summed over both periods (which defines short-term caching). Yet, the conditions for that favor long-term caching to evolve are similar to those that favor short-term caching, just broader.

As for short-term caching, in long-term caching the likelihood of caching increases with the abundance of food in the first period, handling time required to consume a food item, and food aging, and it declines with the time required to cache an item, the abundance of food in period two, and food decay. The value of consuming food in period two relative to period one also increases the likelihood of caching.

In nature, examples of long-term caching are much more abundant than those of short-term caching (Vander Wall 1990) and one could argue that this reflects the broader range of conditions that favor long-term caching.

II.6.d. Predator avoidance

Predation risk creates many more conditions that favor caching even if predation risks are the same in both periods. Moreover, if time periods present distinct predation risks, caching allows the forager to gather food during safe conditions and avoid searching under risky periods. If the first period is riskier than the second, caching may be favored if the time taken to cache the food item is lengthy and itself a safer activity than searching. If foraging during the second time period is riskier than during the first, caching becomes optimal as a means of focusing on searching during the safe period while deferring handling (which is safer than searching) to the second period.

Previous models have incorporated predation risk as a factor influencing short-term caching (Lucas and Walter 1991, Pravosudov and Lucas 2001). They require a mass-dependent predation risk where increased body mass results in an increased risk of predation. Under these circumstances a forager would rather cache a food item than put on extra-weight. The present model introduces a state-dependency in which the forager's

risk avoidance increases with its cumulative harvest. A forager in a better energetic condition has more to lose from predation than a forager in a lower energetic condition (Asset Protection Principal – Clark 1994). In the state space of resource abundances in the two time periods, predation risk can result in two isolegs. The first represents all of those environmental conditions where the forager is indifferent between caching all and caching some food items. The second describes conditions where the forager is indifferent between caching some and caching no items.

Hence, with predation risk it is possible to have optimal levels of caching that span the entire continuum between no caching and caching all items. This contrasts with short-term caching or search-time reallocation where optimal caching behavior is all or none. And, it contrasts with long-term caching or consumption reallocation where the optimal level of caching can lie on a continuum that is always less than complete caching.

In this model, predation risk is fixed within a period and varies between the two periods. The model predicts that increased predation risk favors the evolution of caching if time spent caching is shorter than time spent consuming a food item. More interesting, and somewhat counter-intuitive, predation risk favors caching even if time spent caching one item is greater than time spent eating. This unexpected outcome occurs because searching is riskier than handling food items. Handling may be safer either because the forager can carry the food item to a safe place for handling (Lima and Valone 1986) or because the forager is able to be more vigilant and attentive to potential threats while handling food. Therefore, caching removes search time from total foraging time (caching time in period one plus consumption time in period two) than simply consuming the food item (no-caching only removes consumption time from period one).

If predation risk is higher in period one, likelihood of caching increases as time required to cache increases. If predation risk is higher in period two, likelihood of caching increases as time spent consuming increases; and it decreases as time spent caching increases. Furthermore, caching increases with an overall increase in predation risk in both time periods and with an overall increase in food abundance in both time periods (Asset Protection Principal – Clark 1994).

II.6.e. Summary

Vander Wall (1990) provides perhaps the most detailed description yet of caching behaviors found in nature as it describes the intuition behind why animals may want to cache. Yet general models and general suites of predictions have been somewhat lacking.

A simple, two-time-period model integrates and describes the general conditions that favor caching. With short-term caching, temporal variation in resource availabilities and nutritional enhancement of aged food promotes caching as a means of *search-time reallocation* and *food aging*. Furthermore, long-term caching becomes additionally favored as a means of balancing food consumption among time periods (starvation avoidance being an extreme example). *Consumption reallocation* strongly favors intermediate levels of caching. Predation risk offers the most diverse means for producing the full spectrum of caching strategies as varying risk between time periods, overall risk, varying resource abundances, overall resource abundances, and varying levels of risk between searching for and handling food items conspire to produce the optimal level of caching. The present model invites students of caching behavior to

increase their focus on the evolutionary motives for caching, realizing that these motives

may be integrated rather than mutually exclusive.

III. Forest fragmentation and the scatter-hoarding behavior of two Amazonian rodents

III.1. Introduction

Widespread deforestation is rapidly removing large tracts of tropical forest around the world. Net world deforestation rates from 1990 to 2000 were estimated to be between 4.9 and 12 million hectares per year (Achard et al. 2002, Hansen and DeFries 2004) with no significant decrease by 2005 (FAO 2005). Forest fragmentation, one consequence of deforestation, has negative effects on many species. Organisms that are naturally rare, or have patchy distributions, become randomly absent from forest patches (Terborgh and Winter 1980). Organisms with poor dispersal abilities also rapidly decline in numbers in forest fragments (Laurance 1991). Ecological meltdown from disruption of inter-specific relationships further indirectly affects species that are not directly or immediately affected by forest fragmentation (Terborgh et al. 2001). Tropical forests have many inter-specific relationships and high levels of ecological complexity (Gilbert 1980). Yet, changes in biotic interactions are still among the most poorly understood consequences of forest fragmentation.

Throughout tropical forests, rodents scatter-hoard seeds for future use (Vander Wall 1990, Forget and Wall 2001). Seeds that are scatter-hoarded escape from negative density-dependent effects such as predation, attack from pathogens and competition under the parent tree. Furthermore, burials present better conditions for future germination than exposure on the forest floor (such as higher humidity), and seeds that are not retrieved later have better chances to survive. Nevertheless, scatter-hoarding is a

conditional mutualism (Bronstein 1994). Benefits for the plant depend on the animal's decision to cache or eat. Among other things, the decision to cache or eat depends on the relative abundance of seeds to the scatter-hoarder and the mutualism may be disrupted if the abundance changes. Forest fragmentation may negatively affect the number of seeds that a rodent decides to cache if resource abundance per rodent declines.

Agoutis (*Dasyprocta* spp.) and acouchies (*Myoprocta* spp.), mid-sized rodents restricted to the Neotropical rainforests, are scatter-hoarders (Morris 1962, Smythe 1978) responsible for dispersal of seeds of a large number of large-seeded trees in these forests (Table II). Acouchies are negatively affected by forest fragmentation even in mild conditions (Chapter IV). On the other hand, effects of forest fragmentation on populations of agoutis are context-dependent. Agouti populations decline in number in fragments surrounded by an inhospitable matrix (*e.g.* water) or fragments that experience hunting (Asquith et al. 1997, Chiarello 1999, Wright and Duber 2001). But they may be positively affected in fragments surrounded by a matrix of secondary vegetation at several stages of regeneration and close to large tracts of primary forest (Chapter IV).

In the present chapter, I present results on the effects of forest fragmentation on the scatter-hoarding behavior of red-rumped agoutis (*Dasyprocta leporina*) and red acouchies (*Myoprocta acouchy*), in a fragmentation scenario where acouchies decline in number as fragment size declines, but agoutis' numbers increase. I expect that such a scenario – where overall scatter-hoarder abundance is not changing, but the overall structure of the forest is – may reveal that a dispersal system is disrupted even though the abundances of the dispersal agents do not change.

TABLE II: NEOTROPICAL TREE SPECIES THAT DEPEND ON SCATTER-HOARDING BEHAVIOR OF AGOUTIS (*DASYPROCTA* SPP.) AND ACOUCHIES (*MYOPROCTA* SPP.) FOR RECRUITMENT

Country	Site	Species	Reference
Mexico	Chiapas	*Bursera simabura* *Erythrina goldmani* *Swietenia humilis* *Spondias mombin*	(Hammond and Brown 1995)
Belize	Bladen Nature Reserve	*Astrocaryum mexicanum* *Ampelocera hottlei* *Pouteria sapota*	(Brewer and Rejmanek 1999) (Brewer and Webb 2001)
Costa Rica	Santa Rosa	*Hymenaea courbaril*	(Hallwachs 1986)
	La Selva	*Welfia regia* *Minquartia guianensis* *Virola koschnyi* *Otoba novogranatensis* *Lecythis ampla* *Carapa nicaraguensis*	(Guariguata et al. 2000)
	Monte Verde	*Guarea glabra* *Guarea kunthiana* *Ocotea endresiana*	(Wenny 1999) (Wenny 2000)
Panama	Barro Colorado Island	*Astrocaryum standlenyanum* *Dipteryx panamensis* *Attalea butyracea* *Virola nobilis* *Gustavia superba* *Brosimum alicastrum* *Cupania latifolia* *Doliocarpus olivaceus* *Eugenia coloradensis* *Licania platypus*	(Smythe 1989) (Forget 1993) (Forget et al. 1994) (Asquith et al. 1997) (Forget 1992) (Forget et al. 1998)

TABLE II: (*CONTINUED*)

Country	Site	Species	Reference
Guyana	Mabura Hill	*Chlorocardium rodiei*	(Hammond et al. 1999)
French Guyana	Nouragues Paracou	*Vouacapoua americana* *Astrocaryum paramaca* *Carapa procera* *Virola michelii*	(Forget 1990) (Forget 1991) (Forget 1996) (Forget et al. 2001)
Brazil	Pinkaiti	*Bertholletia excelsa* *Attalea maripa*	(Peres and Baider 1997) (Salm 2006)
Peru	Cocha Cashu	*Astrocaryum macrocalyx* *Bertholletia excelsa* *Dipteryx micrantha* *Hymenaea courbaril*	(Terborgh et al. 1993)

III.2. <u>Study site</u>

The study was conducted at the *Biological Dynamics of Forest Fragments Project* (hereafter *BDFFP*) located 80 km north of Manaus, in Central Amazon, Brazil. The forest of the region is upland mature forest, not subjected to flooding (Floresta de Terra Firme) with annual precipitation of approximately 2600 mm (Bierregaard et al. 2001). Fragments were 20 to 25 years old during data collection (2004). They are surrounded by matrices composed by pasture and secondary vegetation (Table III) and spread among three cattle ranches (*Colosso, Porto Alegre* and *Dimona* – Figure 7). The ranches are five to ten kilometers apart from each other, and each of them is surrounded by large tracts of primary forest (hereafter called continuous forest), where control sites were established (*Km 41, Cabo Frio* and *Dimona*). In the present study, a total of six fragments (three of one hectare, and three of ten) and three sites within the continuous forest were surveyed.

III.3. <u>Study species</u>

Agoutis (*Dasyprocta* spp.) and acouchies (*Myoprocta* spp.), of the family Dasyproctidae, are restricted to the Neotropical region. The genus *Dasyprocta* has five to ten allopatric species, depending on the authority (Ximenes 1999, Voss et al. 2001), and ranges from Southern Mexico to Northern Argentina, east of the Andes. The species present near Manaus is the red-rumped agouti, *D. leporina* (Voss and Emmons 1996). It occurs from Central Amazon to Southeast Brazil. The genus *Myoprocta* is restricted to the core area of the Amazon, with two allopatric species, the red acouchy, *M. acouchy*, in Central and Central-East Amazon (the one present near Manaus – Voss and Emmons 1996), and the green acouchy, *M. pratti*, in Southwest Amazon.

Both genera are terrestrial and diurnal. They eat mainly fruits and seeds that fall on the forest floor (Dubost and Henry 2006) and scatter hoard seeds for future use (Morris 1962, Smythe 1978). They are similar morphologically, but acouchies are, on average, one third to half of the size of agoutis (0.5-1 kg vs. 3-6 kg). Ecologically, they exhibit few differences. Agoutis have larger home ranges: 5 to 10 ha (Silvius and Fragoso 2003, Jorge and Peres 2005) *versus* 1 to 2 ha for acouchies (Dubost 1988). During periods of fruit scarcity, agoutis switch their diet to mostly seeds whereas acouchies still include fruit pulp in their diet (Dubost and Henry 2006). Finally, agoutis appear to be more habitat generalists, while acouchies are restricted to mature forest (Dubost 1988, Voss et al. 2001). Therefore, although morphologically similar, they may respond differently to changes in habitat and resource conditions.

Astrocaryum aculeatum (Arecaceae) is a tall (10 to 25m height), monoecious palm (Uhl and Dransfield 1987). It is restricted to the Amazonian region (Uhl and Dransfield 1987, Kawn and Granville 1992) and can become common in the dense forests of Central Amazon where it occasionally dominates secondary forests (Kawn and Granville 1992, Henderson et al. 1995). The upper part of its stem has long black spines arranged in regularly spaced rings. As the tree grows, the oldest spines drop off, and the lower parts of the trunk typically become bare. The yellowish-green fruit of *A. aculeatum* consists of farinaceous mesocarp that involves a black, hard woody shell. The single kernel is white, oily, hard, and covered with an adherent brown testa (Pesce 1985, Almeida and Dantas da Silva 1997).

TABLE III: PHYSICAL CHARACTERISTICS OF THE FRAGMENTS OF *BIOLOGICAL DYNAMICS OF FOREST FRAGMENTS PROJECT*, MANAUS, BRAZIL (BIERREGAARD ET AL. 2001)

Ranch Name	*BDFFP* Reserve Code	Size (ha)	Topography and other remarks	Shortest distance to 2^{ary} forest with closed canopy or 1^{ary} forest (m)	Composition and age of 100-m band around fragment
Dimona	2107	1	Deep valley cuts the reserve towards the west; no stream.	150	*Vismia* 2-7 years
	2206	10	Strong topography with presence of two streams.	225	*Vismia* 2-7 years
	2303	100 [a]	Rugged landscape with small streams. Soil with more sand than the other reserves	150	*Vismia* 2-7 years
Porto Alegre	3114	1	Gentle slope; no streams.	200	Pasture
	3209	10	Gentle slope; no streams; indication of coal in the soil.	100	*Cecropia* 2-7 years
	3304	100 [a]	Undulated terrain. Three small streams cut the reserve.	< 100	*Cecropia* > 14 years
Colosso	1104	1	Completely flat; no streams.	< 100	*Vismia* > 14 years
	1202	10	Gentle slope; no streams.	700	Pasture

a: one-hundred hectare fragments were used only for data collection on the abundances of the animals (Chapter IV).
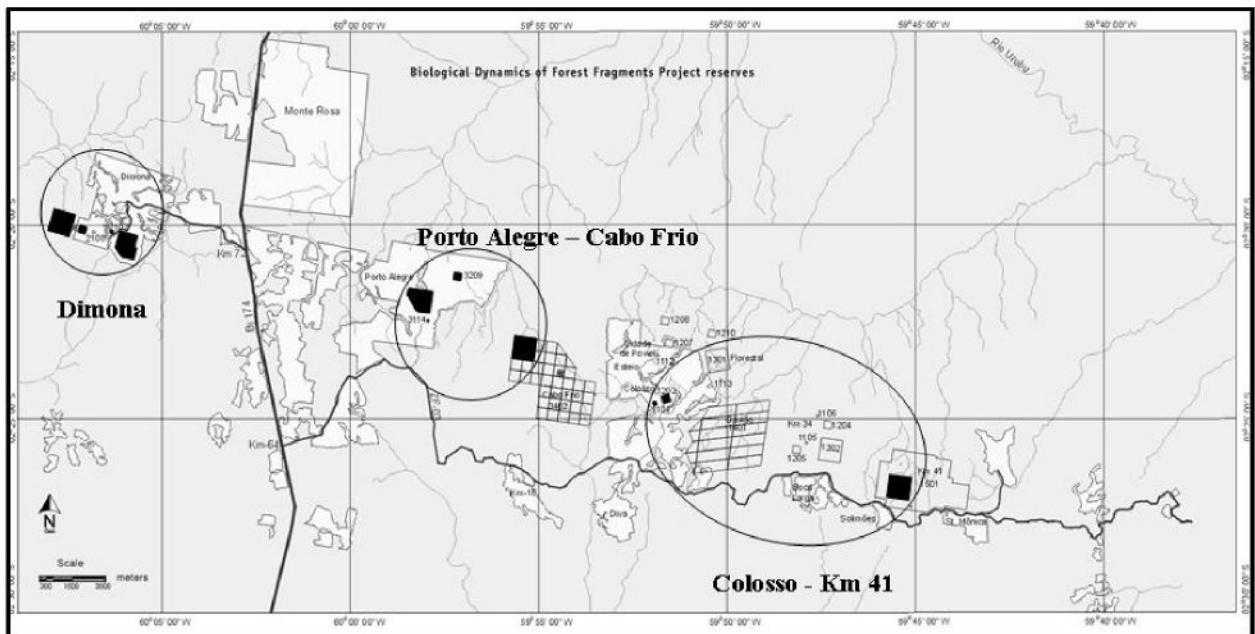
Figure 7: *Biological Dynamics of Forest Fragments Project*, Manaus, Amazonas, Brazil.

Fragments are distributed among three cattle ranches (*Dimona*, *Porto Alegre*, and

Colosso) and reserves of continuous forest used in this study were: *Km 41, Cabo Frio* and

Dimona. In each site, I sampled one fragment of one hectare (black dots), one of ten

(small black squares), and an area within the continuous forest (large black squares).

Secondary forest and pasture are represented by the light grey area and the primary forest

is represented by the darker grey area. One-hundred-hectare fragments (large black

polygons within light grey area) were used only for the survey of the animal abundances

(Chapter IV).

Astrocaryum fruits are consumed by arboreal mammals (Terborgh et al. 1993) which drop their seeds on the ground. Scatter-hoarding rodents recover the seeds from the ground for consumption and hoarding (Smythe 1989). The fruits are also collected by local people for pulp consumption and peeled seeds are easily found in open markets of Manaus. Scatter-hoarders' preference for *A. aculeatum* seeds and the facility to find large quantities in the market makes them excellent candidates for experiments of scatter-hoarding dynamics.

III.4. <u>Experimental design and data collection</u>

I placed ten palm seeds on the forest floor at random places in the fragments and control areas (hereafter *seed stations*). Seeds without pulp were acquired at several local markets of the nearest city (Manaus), where people consume the pulp and discard hundreds of peeled seeds every day. I used peeled seeds to eliminate the possibility of frugivores removing the fruits to eat the pulp and discarding the seeds, a behavior that was recorded in a pilot study. I attached a 15-centimeter long nylon thread to each seed with a screw. The nylon thread had a pink plastic flag at its other end, with an individual code for further identification.

I placed two seed stations in each one-hectare fragment; six in each ten-hectare fragment; and six to nine in the control sites (continuous forest of *Dimona* had fewer stations then the other sites of continuous forest because there were fewer trails to assess the forest in that site – Table IV). Experiments were set up in March, May and August of 2004, and checked in April, June and September, respectively. These months correspond to the peak of the rainy season (March-April), the transition between rainy and dry

seasons (May-June), and the peak of dry season (August-September – Bierregaard et al. 2001). The peak of the rainy season corresponds to the period of fruit abundance, and the dry season corresponds to the period of fruit scarcity (Chapter V).

Stations were checked only 20 to 30 later. I first set up the stations in all fragments of all three ranches, and then checked all of them using the same order, in order to minimize temporal variation between sites. At each check, I counted the number of seeds removed and searched for the removed seeds within a radius of approximately 30 meters with the help of assistants. I classified the seeds found in four categories: 1) cached: if the seed was buried in the soil; 2) eaten by a rodent: if the seed shell was gnawed, with no embryo left inside; 3) displaced: if the seed was removed from the station, but not cached or eaten; and 4) eaten by other animals: if seed shell without embryo was found, but there were no signs of gnawing. The majority of the seeds removed were cached, eaten by a rodent, or not found. Therefore, they were the only conditions considered for the analyses. In addition to the condition of the seed, the distance between the removed seed and the seed station was also measured.

III.5. <u>Statistical analyses</u>

I used a two-way analysis of variance with repeated measures to evaluate the effects of fragment size, site and month on: 1) number of seeds removed in each station; 2) proportion of seeds found among the ones removed; and 3) proportion of seeds cached among the ones found. To achieve assumptions of normality and homoscedasticity (Zar 1999), I square root transformed the number of seeds removed, and arcsine-square root transformed the proportion of seeds found and cached.

TABLE IV: NUMBER OF *SEED STATIONS* OF *ASTROCARYUM ACULEATUM* (ARECACEAE) PLACED ON THE FOREST FLOOR OF NINE SITES OF THE *BIOLOGICAL DYNAMICS OF FOREST FRAGMENTS PROJECT*, MANAUS, BRAZIL.

Site	Fragment Size	Month			Total
		April	June	Sept	
Colosso Km 41	1 hectare	2	2	2	6
	10 hectare	6	6	6	18
	Continuous Forest	8	8	8	24
Porto Alegre Cabo Frio	1 hectare	2	2	2	6
	10 hectare	6	6	6	18
	Continuous Forest	7	7	7	21
Dimona	1 hectare	2	2	2	6
	10 hectare	6	6	6	18
	Continuous Forest	6	6	6	18
Total		45	45	45	135

For the analysis of variance with repeated measures, only 81 cases were considered for the proportion of seeds found, due to lack of complete temporal replication for the three months in 25 cases. The same was true for the proportion of seeds cached. Only 66 cases were used for the analysis due to lack of temporal replication in 30 cases.

To test for the effects of fragment size, site and month on the distance that the seeds were cached, I used a log linear model because of the natural skewed distribution of data (Agresti 1996). I separated the dispersal distance into two categories: closer and greater than seven meters. I chose seven meters because in scatter-hoarding dispersal, animals do not take seeds very far, most being taken within five meters (Forget 1992, Peres and Baider 1997). I used a model with all two-way interactions because it was the most parsimonious one.

For the analysis on dispersal distance differences, I pooled together the data from all the seed stations and did not include the one-hectare fragments because there were very few seeds cached in those (9 *versus* 146 in ten-hectare fragments and 76 at continuous forest).

III.6. <u>Results</u>

Overall, there was a lot of activity from the scatter-hoarding rodents in the seeds stations. Out of the 135 seed stations*month that were put out (Table IV), 104 (77%) had at least one seed removed, and 96 (71%) had at least one seed found. Out of 1350 seeds, 875 (65%) were removed, 425 (31%) were found, and 219 (16%) were cached. On average, 6.5 ± 0.4 ($\pm$ SE) seeds were removed from each station, 4.1 ± 0.2 (or 0.5 ± 0.03 of the removed seeds) were found, and 2.3 ± 0.2 (or 0.5 ± 0.04 of the seeds found) were

cached. The maximum dispersal distance was 40 meters (N = 219 seeds), but more than 50% of the seeds (N = 115) were cached within 5 meters, with mean dispersal distance of 6.4 ± 0.3 meters.

III.6.a. Effects of fragment size, site and month on the number of seeds removed, found and cached

Fragment size and site had significant effects on the number of seeds removed, with a significant interaction between them. On the other hand, similar numbers of seeds were removed during each of the three months. On average, 9.4 ± 0.5 seeds (± SE; N = 18 stations) were removed from one-hectare fragments, 7.0 ± 0.6 (N = 54 stations) were removed from ten-hectare fragments, and 5.2 ± 0.6 (N = 63 stations) were removed from the continuous forest ($F_{2, 36}$ = 9.707; p < 0.001 – Figure 8a). As for site comparisons, more seeds were removed from *Colosso-Km 41* (8.8 ± 0.4; N = 48 stations) than the other two sites (*Porto Alegre-Cabo Frio*, 5.4 ± 0.7, N = 45 stations; and *Dimona*, 5.0 ± 0.8, N = 42 stations, Figure 8b, $F_{2, 36}$ = 4.916; p = 0.013). Nevertheless, number of seeds removed did not differ significantly among the three months ($F_{2, 72}$ = 2.139; p = 0.064; Figure 8c). Interaction between fragment size and site was the result of *Colosso-Km 41* having high removal numbers at all fragment sizes, whereas in the other two sites, there was a decline with an increase of fragment size ($F_{4, 36}$ = 3.865; p = 0.010 – Figure 9).

The proportion of seeds found did not differ significantly by fragment size, site or month (fragment sizes: $F_{2,24}$ = 2.330; p = 0.119; sites: $F_{2,24}$ = 1.720; p = 0.200: months: $F_{2, 48}$ = 0.325; p = 0.725). But the proportion of seeds cached differed significantly by fragment size and month. Only 0.16 ± 0.07 of the seeds found in one-hectare fragments

(N = 12 stations) were cached, whereas 0.63 ± 0.06 (N = 27 stations) were cached in ten-hectare fragments, and 0.50 ± 0.08 (N = 27 stations) in the continuous forest ($F_{2, 19}$ = 11.824; $p < 0.001$ – Figure 10a). Proportion of seeds cached was similar between the three sites ($F_{2, 19}$ = 1.789; $p = 0.194$; Figure 10b). But more seeds were cached in April (0.69 ± 0.08; N = 22 stations) than in June (0.48 ± 0.07; N = 22 stations) than in September (0.31 ± 0.08; N = 22 stations; $F_{2, 38}$ = 4.240; $p = 0.022$ – Figure 10c).

There was also a significant interaction between fragment size and month on the proportion of seeds cached ($F_{4, 38}$ = 3.368; $p = 0.019$). In April a high percent of seeds were cached in ten-hectare fragments (0.90 ± 0.04; N = 9 stations) and continuous forest (0.78 ± 0.11; N = 9 stations), whereas significantly fewer (0.03 ± 0.03; N = 4 stations) in the one-hectare fragments (Figure 11a). In June, the percentage of seeds cached were similar between fragment sizes (one-hectare: 0.38 ± 0.18; N = 4 stations; ten-hectare: 0.44 ± 0.10; N = 9 stations; continuous forest: 0.57 ± 0.11; N = 9 stations – Figure 11b). And in September, differences increased again, especially in 10-ha fragments, where caching was higher compared to the other two sizes (one-hectare: 0.06 ± 0.06; N = 4 stations; ten-hectare: 0.56 ± 0.11; N = 9 stations; continuous forest: 0.17 ± 0.11; N = 9 stations– Figure 11c). Overall, seed caching was low in one-hectare fragments, independent of month, high in ten-hectare fragments in April and September, and had a decreasing trend in continuous forest, as time went by.

III.6.b. Effects of fragment size, site and month on dispersal distance

Finally, proportionally more seeds were cached at longer distances in the continuous forest than in ten-hectare fragments, and the same was true for September when

compared to June and April. In the Continuous Forest, 45% of the seeds were cached at distances longer than seven meters (N = 76 seeds). In ten-hectare fragments, 29% of the seeds were cached at distances longer than seven meters (N = 134 seeds). (log linear model – fragment size*distance interaction: $\chi^2_{df=1}$ = 7.62; p = 0.006 – Figure 12a). The same log linear model depicted a marginal interaction between month and dispersal distance ($\chi^2_{df=2}$ = 5.00; p = 0.08 – Figure 12b) with more seeds cached at distances longer than seven meters in September (43% - N = 53 seeds) than June (35% - N = 49 seeds) than April (31% - N = 108 seeds).

Overall, there was significant site variation on the number of seeds removed, but not on proportion of seeds cached or dispersal distance. There was also significant temporal variation on the proportion of seeds cached and dispersal distance, but not on the number of seeds removed. Finally, fragment size had a negative effect on the number of seeds removed, a non-linear effect on the proportion of seeds cached (more seeds cached at fragments of intermediate size) and a negative effect on dispersal distance. Apparently, the factors that influence the number of seeds removed (site variation) are not the same that influence the number of seeds cached or the distance that they are cached (temporal variation). Moreover, forest fragmentation disrupts scatter-hoarding dynamics in all stages investigated in this study (removal, caching and dispersal distance), but for one of them (caching) not in a trivial manner.

a) Fragment Size Effect

b) Site Effect
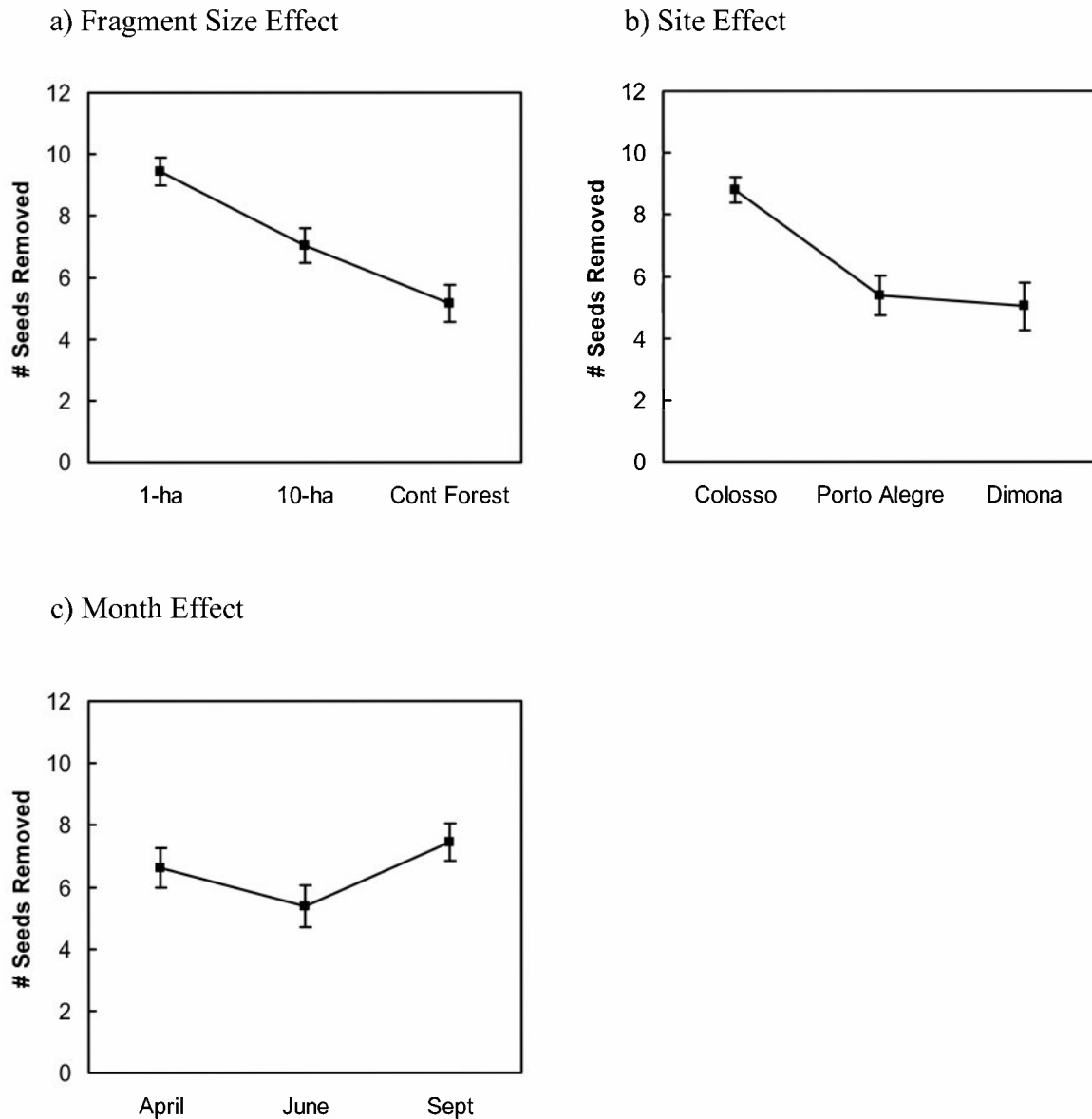
c) Month Effect

Figure 8: Effects of fragment size, site, and month, on the number of seeds removed per station (average ± standard error): (a) significant effect of fragment size ($F_{2,36} = 9.707$; p = 0.000; $N_{1\text{-ha}} = 18$; $N_{10\text{-ha}} = 54$; $N_{ContFor} = 63$); (b) significant effect of site ($F_{2,36} = 4.916$; p = 0.013; $N_{Colosso} = 48$; $N_{Porto\ Alegre} = 45$; $N_{Dimona} = 42$); (c) but no significant effect of month ($F_{2,72} = 2.139$; p = 0.064; $N_{April} = 45$; $N_{June} = 45$; $N_{September} = 45$).

a) Colosso-Km 41

b) Porto Alegre-Cabo Frio

c) Dimona
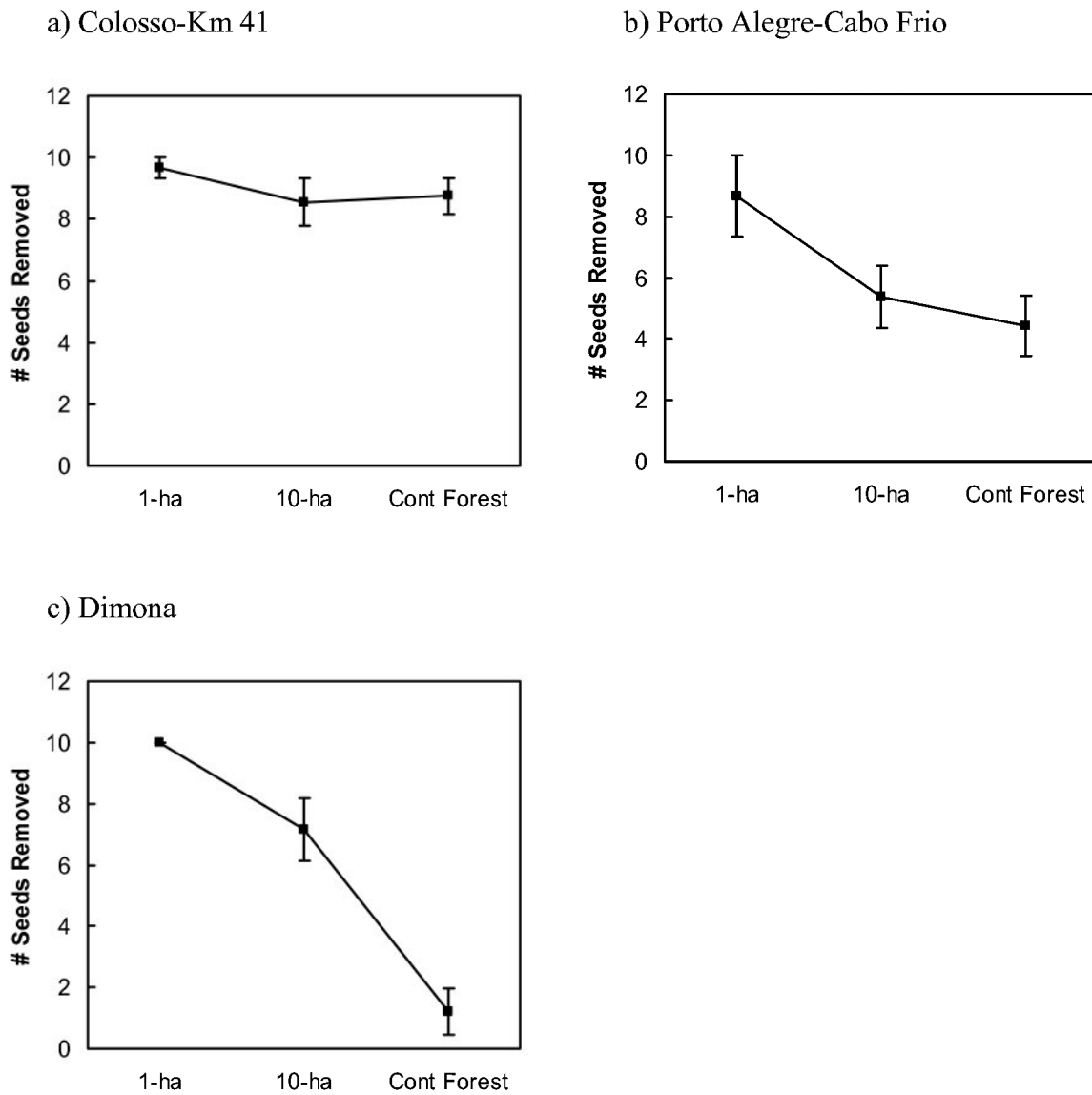
Figure 9: Effects of fragment size on the number of seeds removed per station (average ± standard error) in each site: (a) No significant effect of fragment size at *Colosso-Km 41* ($F_{2, 45}$ = 0.365; p = 0.696; N_{1-ha} = 6; N_{10-ha} = 18; $N_{ContFor}$ = 24); (b) no significant effect at *Porto Alegre-Cabo Frio* ($F_{2, 42}$ = 2.336; p = 0.109; N_{1-ha} = 6; N_{10-ha} = 18; $N_{ContFor}$ = 21); (c) but significant effect at *Dimona* ($F_{2, 39}$ = 19.509; p = 0.000; N_{1-ha} = 6; N_{10-ha} = 18; $N_{ContFor}$ = 18).

a) Fragment Size Effect

b) Site Effect
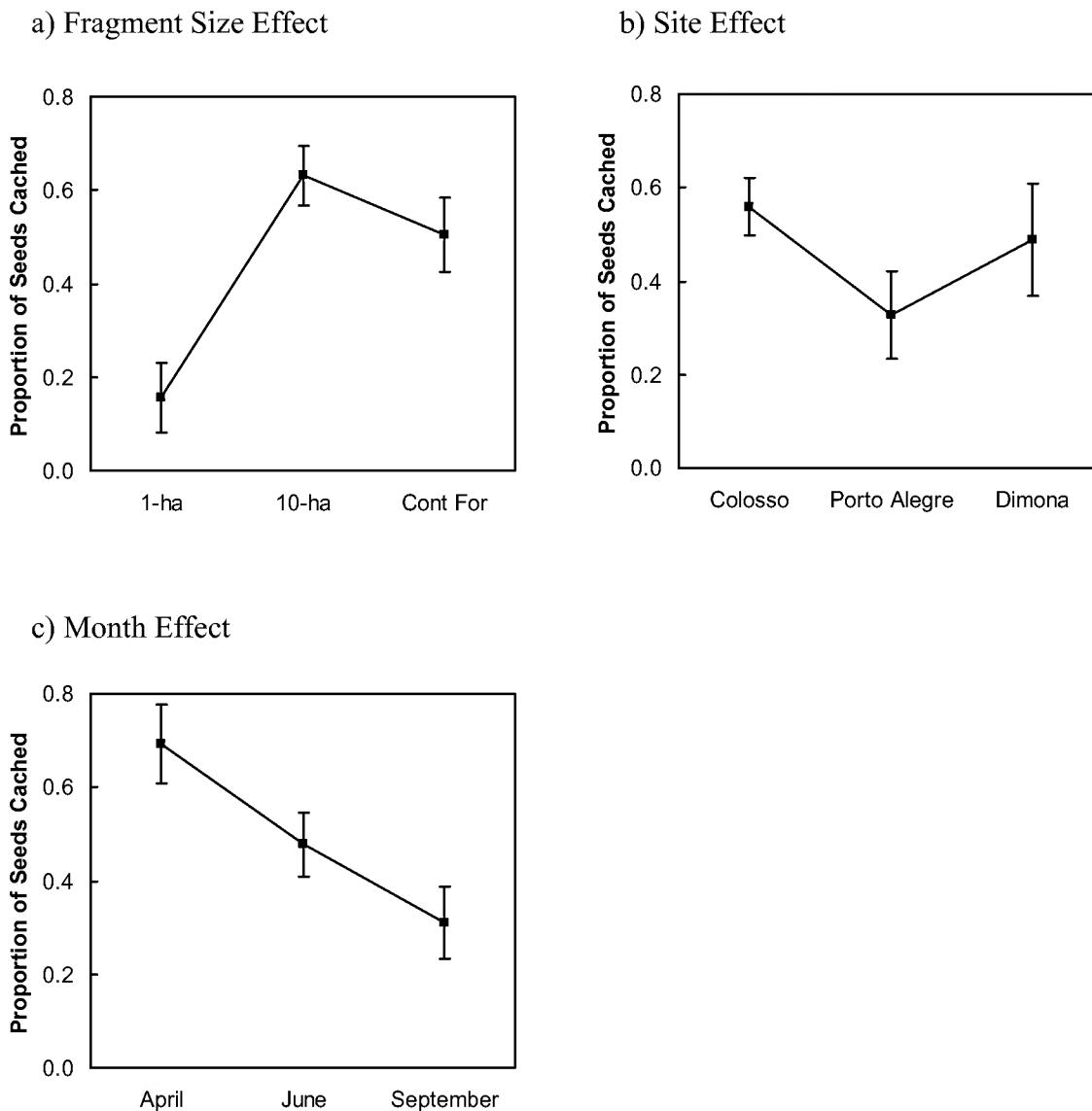
c) Month Effect

Figure 10: Effects of fragment size, site, and month, on the proportion of seeds cached per station (average ± standard error). (a) Significant effect of fragment size ($F_{2, 19}$ = 11.824; p = 0.000; $N_{1\text{-ha}}$ = 12; $N_{10\text{-ha}}$ = 27; $N_{ContFor}$ = 27); (b) no significant effect of site ($F_{2, 19}$ = 1.789; p = 0.194; $N_{Colosso}$ = 39; $N_{Porto\ Alegre}$ = 15; N_{Dimona} = 12); (c) significant effect of month ($F_{2, 38}$ = 4.240; p = 0.022; N_{April} = 22; N_{June}= 22; $N_{September}$ = 22).

a) April

b) June

c) September
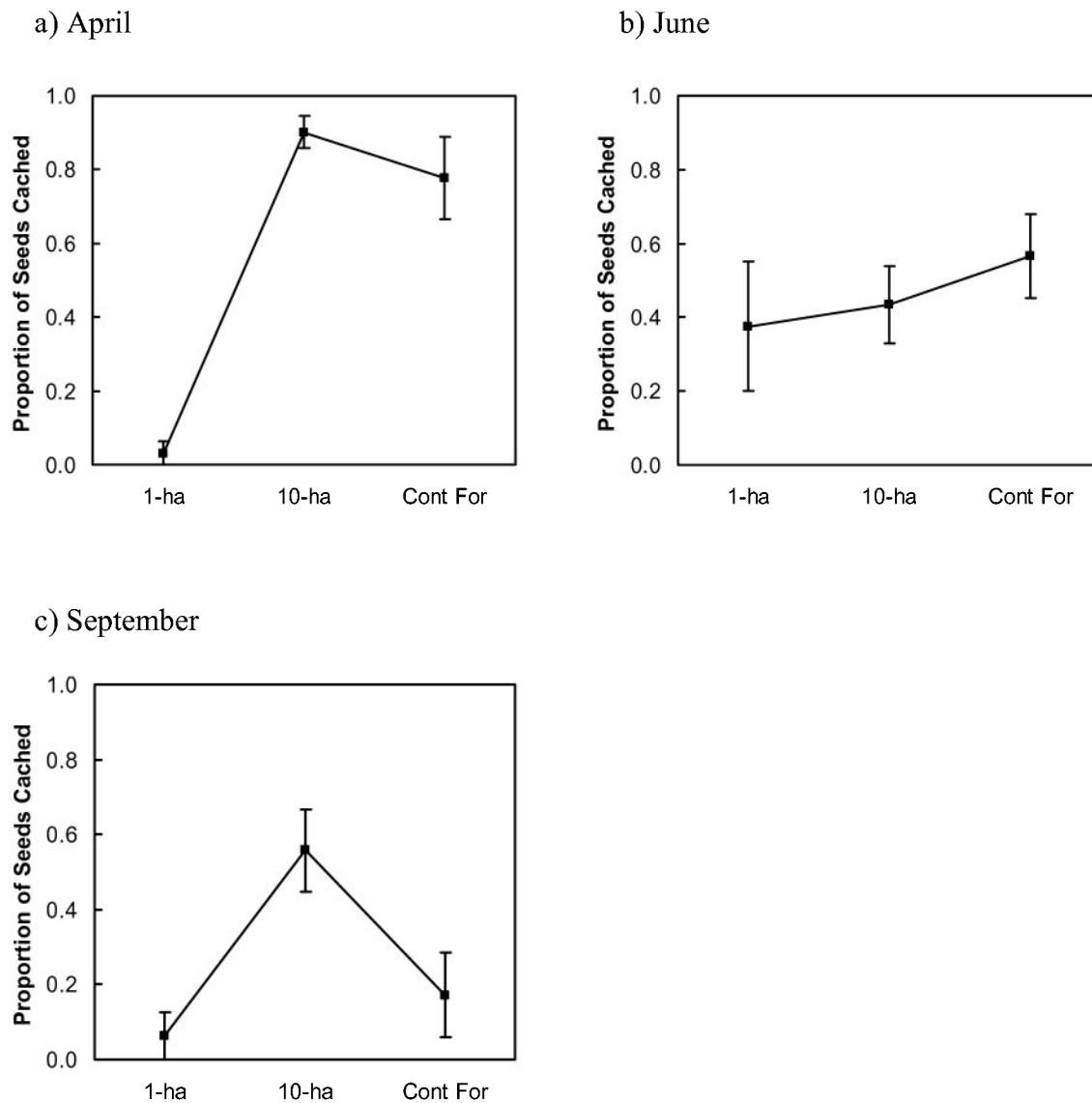
Figure 11: Effects of fragment size on the proportion of seeds cached per station (average ± standard error) in each month: (a) Significant effect of fragment size on April ($F_{2, 19}$ = 15.576; p = 0.000; $N_{1\text{-ha}}$ = 4); (b) no significant effect on June ($F_{2, 19}$ = 0.627; p = 0.545); (c) but significant effect on September again ($F_{2, 19}$ = 4.622; p = 0.023). Sample sizes for each month are: $N_{1\text{-ha}}$ = 4; $N_{10\text{-ha}}$ = 9; N_{ContFor} = 9.

III.7. <u>Discussion</u>

Throughout tropical and temperate regions, rodents scatter-hoard seeds for future use (Vander Wall 1990, Forget and Wall 2001). Scatter-hoarded seeds that are forgotten or never retrieved have greater probability of survival. But scatter-hoarding is a conditional mutualism (Theimer 2005). Upon encountering a seed, the animal may decide to either cache it or immediately consume it. That decision depends on evolutionary factors (*e.g.* seed size – Jansen et al. 2002) and environmental ones. Among the environmental factors, resource abundance seems to play a fundamental role in determining if the animal will cache or eat a seed as has been shown previously in the analytical model of caching behavior (Chapter II).

Resource abundance naturally varies in space and time (Foster 1982). Scatter-hoarding levels are shown to vary with spatial (Forget and Milleron 1991, Forget 1992) and temporal variation of resource abundance (Forget et al. 2002). At *BDFFP*, Central Amazon, I found that scatter-hoarding dynamics were affected by season and site. The number of seeds removed of *A. aculeatum* (Arecaceae) was affected by site, whereas proportion of seeds cached and dispersal distance were affected by season of the year.

a)
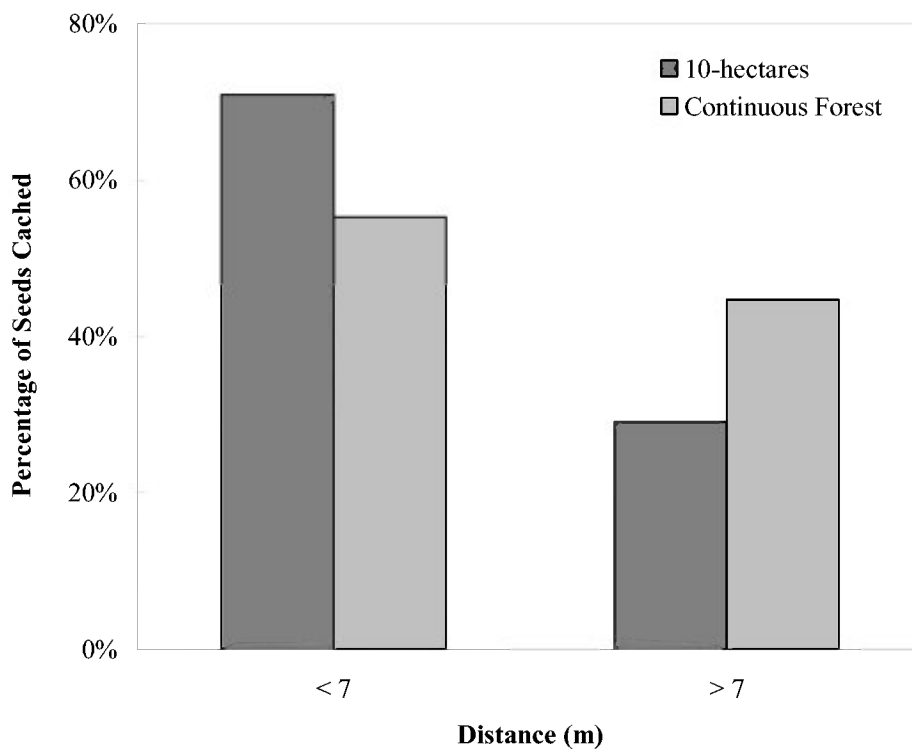
Figure 12: Effects of (a) fragment size and (b) month on the distance that seeds were cached. One-hectare fragments were not considered for this analysis due to the small sample size (N = 9); (a) in the Continuous Forest, 45% of the seeds were cached at distances longer than seven meters (N = 76); in 10-ha fragments, 29% of the seeds were cached at distances longer than seven meters (N = 134). (log linear model – fragment size*distance interaction: $\chi^2_{df=1}$ = 7.62; p = 0.006); (b) in September, 43% of the seeds were cached further than seven meters (N = 53), whereas in June, only 35% (N = 49), and in April, only 31% (N = 108) (log linear model – month*distance interaction: $\chi^2_{df=2}$ = 5.00; p = 0.08).

b)
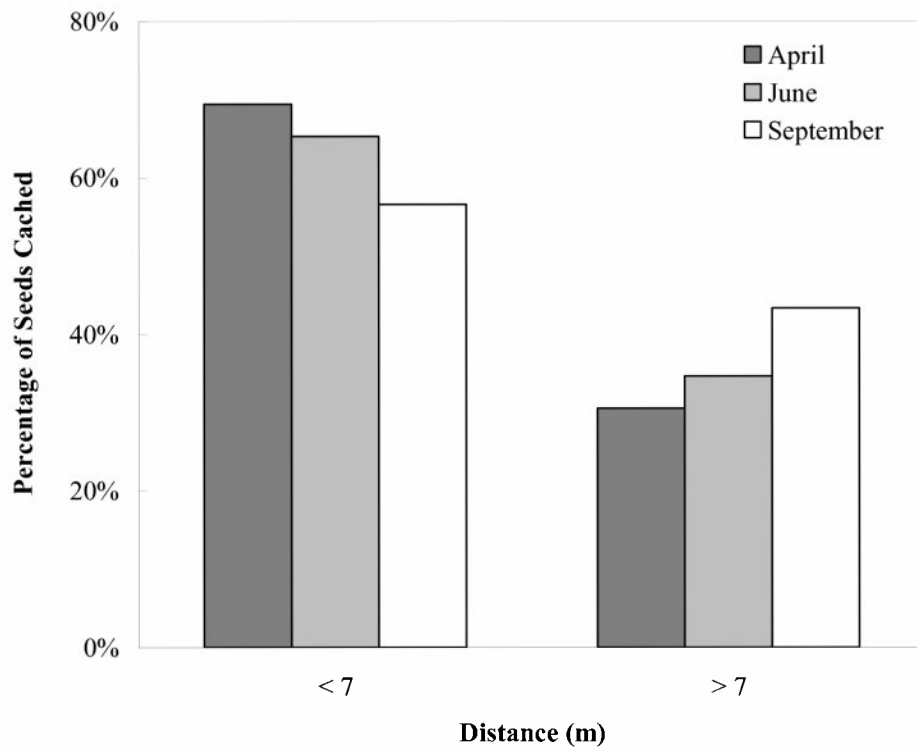
Figure 12: (*Continued*)

Fragmentation of the forest may disrupt scatter-hoarding dynamics as well (Theimer 2005). But that had not been tested until now. At *BDFFP*, I found that all three aspects of the scatter-hoarding dynamics investigated in this study (removal, caching and dispersal distance) were affected by fragment size. But one of them (caching) was affected in an unexpected way (more caching in intermediate size fragments). Therefore, my study demonstrates that effects of forest fragmentation on scatter-hoarding dynamics exist, nevertheless, do not linearly correlate to fragment size.

III.7.a. Site and temporal effects on removal and caching proportions of Astrocaryum aculeatum *(Arecaceae)*

There was significant site variation in the number of *A. aculeatum* seeds removed at *BDFFP*. Removal was greater in *Colosso-Km 41*, than at two other sites (*Porto Alegre-Cabo Frio* and *Dimona*). That difference was driven mainly by the results from the three areas of continuous forest. At *Km 41* removal numbers were much higher than at the two other sites of continuous forest. Other studies have found similar patterns. Forget and Milleron (1991) and Forget (1992, 1993) found that removal rates of three large-seeded species (*Virola nobilis*, Myristicaceae; *Gustavia superba*, Lecythidaceae; and *Dipteryx panamensis*, Fabaceae) depended upon the spatial variation in density of con-specific trees, on Barro Colorado Island (Panama). Feer and Forget (2001) found a site effect on removal of *Chrysophyllum lucentifolium* seeds (Sapotaceae) in French Guyana. Therefore, spatial variation of removal of large seeds by scatter-hoarding rodents in Neotropical rainforests seems to be a common phenomenon.

On the other hand, seasonal variation at *BDFFP* did not affect removal, but affected scatter-hoarding levels. Scatter-hoarding levels are expected to correlate with temporal variation in resource abundance. Animals hoard food in periods of surplus to survive through periods of scarcity (Vander Wall 1990). Forget and colleagues (2002) presented a compilation of results from Barro Colorado Island (Panama) that supports those expectations. But their comparison was made with three different species, one species in each season. Therefore, species-specific effects cannot be excluded. In the present study, scatter-hoarding levels of the same species (*A. aculeatum*) peaked in the peak of the rainy season (February-March) and decreased monotonically until the peak of the dry season (August-September). These results support expectations much more strongly.

III.7.b. Effects of fragment size on the removal, scatter-hoarding levels and dispersal distance of <u>Astrocaryum aculeatum</u> *(Arecaceae)*

More seeds should be removed in places where there is less food. Smaller fragments are expected to have less food. Therefore, more seeds should be removed in smaller fragments. That was exactly what happened with *A. aculeatum* in the *BDFFP* reserves. More seeds were removed from one-hectare fragments, intermediate levels from ten-hectare hectare fragments, and fewest from the continuous forest. Increased removal numbers of large seeds had been previously shown to negatively correlate with forest size (Guariguata et al. 2002) and positively with distance from the edges (Kollmann and Buschor 2003). Interestingly, both studies attribute the increases in removal rates to increases in abundance of smaller rodents that are strictly seed predators. That was not the case in the present study. Camera surveying of some seed stations and handling patterns of removed seeds revealed that most of the removal activity was conducted by

the two scatter-hoarding rodents present in the area. The natural question then becomes: what are they doing with the seeds that they remove?

As expected for seed removal, more seeds should be eaten when and where there is less food. Because smaller fragments are expected to have less food, more seeds should be eaten in smaller fragments. That was partially true. The present study shows that in one-hectare fragments, agoutis and acouchies are removing more seeds than anywhere else, and eating most of them. On the other hand, in ten-hectare fragments, they are removing more seeds than in the continuous forest, but scatter-hoarding most of them.

The final aspect to be looked at within the scenario of forest fragmentation is dispersal distance. Seeds that are taken to longer distances have a better chance of survival because they escape density-dependent mortality (Howe and Smallwood 1982). In the case of large seeds, at longer distances they also experience lower levels of pilferage (Daly et al. 1992, Leaver and Daly 1998, Jansen et al. 2002, Leaver 2004). In ten-hectare fragments, only 30% of the seeds were cached at distances longer than seven meters, whereas in the continuous forest, 45% of the cached seeds were taken to distances greater than seven meters. Previous studies showed the same positive correlation between fragment size and dispersal distance, or, a negative effect of forest fragmentation on dispersal distance (Wright and Duber 2001, Cordeiro and Howe 2003). At the end, the positive effect of more seeds being cached in ten-hectare fragments may be counter-balanced by the negative effect of seeds being cached at closer distances.

In conclusion, in the present study I was able to separately analyze three aspects of the scatter-hoarding dynamics: removal, caching and distance. Each of them responded

differently to spatial variation at site level, temporal variation, and forest fragmentation.

The complete picture confirms that scatter-hoarding is a multi-facet multi-step dynamics,

and needs to be looked at through all its stages in order to be fully understood.

IV. Effects of forest fragmentation on two close related species of Amazonian rodents (*Myoprocta acouchy* and *Dasyprocta leporina*)

IV.1. Introduction

The Amazon Basin, which holds the largest tract of continuous tropical forest in the world (FAO 2005), now experiences the greatest rate of deforestation (INPE 2002). At current rates, Amazonian forests will be completely fragmented in few decades (Laurance et al. 2001a). Many ground-dwelling mammals play key roles in Amazonian forest dynamics as seed dispersers, and seed and seedling predators (Smythe 1986). In particular, acouchies (*Myoprocta* spp., Dasyproctidae, Rodentia) and agoutis (*Dasyprocta* spp., Dasyproctidae, Rodentia) constitute the most important dispersal agents of several large-seeded Amazonian trees (Table II). Knowing their responses to forest fragmentation is essential both for predicting their own fates, and for understanding the fate of trees that depend on them for seed dissemination.

In the present chapter, I present the results of a two-year survey of the abundances of the red-rumped agouti (*Dasyprocta leporina*) and the red acouchy (*Myoprocta acouchy*) in fragments of one, ten and one-hundred hectares in Central Amazon, and compare with abundances in continuous forest of the same region (refer to Chapter III for site and species descriptions and Figure 7 for a detailed map of the site). Previous studies have shown that agoutis decline when forest is fragmented by inundation (Asquith et al. 1997 – Panama; Terborgh et al. 1997 – Venezuela), and in old (more than 80 years old) land fragments of the Atlantic forest (Chiarello 1999). But to date, there has been no study

examining fragmentation effects on acouchies, or on systems of co-occurring acouchies and agoutis.

Since the first studies of forest fragmentation, it has been recognized that species loss is not random (Terborgh 1974, Shaffer 1981, Diamond 1984, Gilpin and Soulé 1986, Pimm et al. 1988) and that body size is thought to contribute to this non-random loss (Pimm et al. 1988). Acouchies and agoutis are two sister genera, very similar morphologically and behaviorally. Their major morphological difference is their size (on average, agoutis weigh 3 to 6 times more than acouchies, 3-6 kg. vs. 0.5-1 kg.).

Larger animals are naturally found at lower densities and tend to have longer generation times and lower growth and reproductive rates than smaller ones (Damuth 1981). Those characteristics may increase their sensitivity to forest fragmentation. In support that idea, a negative correlation between abundance and fragment area related to body size has been shown in fragments surrounded by water (Asquith et al. 1997). In contrast, in land patches, body size has either no effect on abundance (Laurance 1991, de Castro and Fernandez 2004) or a positive one (Gehring and Swihart 2003). On land, dispersal ability through the surrounding matrix determines species persistence in fragments. Larger animals appear less sensitive to the surrounding matrix because they have greater mobility, greater perceptual range, and less susceptibility to predation (Zollner 2000). For agoutis and acouchies, if larger body size entails requiring larger tracts of continuous forest, agoutis should be more sensitive to forest fragmentation. In contrast, if by having larger bodies, agoutis become better dispersers through the matrix surrounding fragments, the opposite should be true and acouchies should be more sensitive.

IV.2. <u>Data collection</u>

Standard and sweep line-transect censuses were used to gather density data, following the protocol by Peres (1999). Particularly for this study, transects were walked at early morning (0600h – 0700h) and late afternoon (1700h – 1800h), peak activity periods for the two genera (Smythe 1978, Dubost 1988). Detections were visual and/or acoustic. Acoustic detections are possible because each species has a distinctive and loud flee bark. Upon detection, the observer identified the species, determined the number of individuals present, and estimated the perpendicular distance (hereafter *PD*) between the transect and the animal(s).

At all eleven sites, three parallel straight transects were sampled independently every month. In the continuous forest and one-hundred hectare fragments, transects were 1000-meter long and 200 meters apart from one another. In ten-hectare fragments, they were 350-meter long and 75 meters apart from one another. In one-hectare fragments, they were 100-meters long and 30 meters apart from one another. In one-hectare fragments, each survey was conducted by two to three observers at the same time to increase the probability of detection. If one or more animals were present in the fragment, they were usually detected by more than one observer and those double sightings were corrected later for the analyses (only one animal was counted). In 2003, I sampled two months in the rainy season (February and March) and two in the dry season (July and August). In 2004, sites were monthly sampled from February to August. The one-hundred hectare fragments could not be sampled in 2004 and were sampled in the same period, in 2005. Raining days and mornings after an evening rain were not sampled, due to background noise and impaired detection.

IV.3. <u>Statistical analyses</u>

Densities were chosen over encounter rates to determine fragment size effects because they are more informative, especially in the ten and one-hundred-hectare fragments and in the continuous forest. In one-hectare fragments, encounter rates would probably be more appropriate (at least agoutis have home ranges larger than one hectare – (Silvius and Fragoso 2003, Jorge and Peres 2005). Nevertheless, densities were used for all fragment sizes (including the smallest one) to make fragment-size comparisons possible.

The effective strip width (*ESW*) used to compute the area for density calculations (number of individuals per area) was estimated using the probability of detection as a function of the observed *PD*. This approach generates an *ESW* that takes into account possible decays in detection with increased *PD* and fits a model to a function, allowing for more robust *ESW* estimates (Buckland et al. 1993). The model choice is based on the smallest Akaike information criterium (*AIC*). Ideally, one *ESW* should be generated for each genus in each site. Nevertheless, samples sizes smaller than 30 make difficult to fit a smooth distribution and weaken the estimate (Buckland et al. 1993). Whenever necessary, data from different sites were pooled together within a species, using fragment size as the pooling criterion. *ESW*s were estimated using DISTANCE 4.1 (Thomas et al. 2003). One-way analysis of variance was then run to determine whether fragment size and year had an effect on densities, and *ad hoc* Tukey test of multiple comparisons was used to interpret differences. Statistical tests were conducted with SYSTAT 11.

IV.4. <u>Results</u>

Over the course of the study, we walked approximately 100 kilometers, encountering 138 acouchies and 40 agoutis (Tables V and VI). For density estimates, detections were lumped in three groups for acouchies – small fragments (N = 30 individuals), one-hundred hectare (N = 46 individuals), and continuous forest (N = 62 individuals) – and pooled all together for agoutis (N = 40 individuals). *ESW* ranged from 12.2 meters (acouchies in the continuous forest) to 15.7 meters (acouchies in the small fragments – Table VII).

Densities were significantly affected by fragment size for both genera (one-way analysis of variance with repeated measures, *Myo*procta: $F_{3,6}$ = 6.46, p = 0.026; *Dasyprocta*: $F_{3,6}$ = 5.44, p = 0.038). Densities of the smaller acouchies significantly increased with fragment size (Figure 13a), whereas densities of the larger agouti decreased (Figure 13b). For acouchies, densities in one-hectare fragments were significantly smaller than in any other fragment size (Tukey pairwise comparison with ten-hectare = 0.05; with one-hundred-hectare = 0.008; and with continuous forest = 0.001). For agoutis, densities in one-hectare fragments were only significantly larger than that of ten-hectare fragments (Tukey pairwise comparison with ten-hectare = 0.03), but did not differ from one-hundred hectare and continuous forest.

TABLE V: SAMPLING EFFORT, NUMBER OF DETECTIONS, ENCOUNTER RATES AND DENSITIES OF *MYOPROCTA ACOUCHY* (2003 AND 2004); *BIOLOGICAL DYNAMICS OF FOREST FRAGMENTS PROJECT*, MANAUS, BRAZIL.

	Fragment Area (ha)	Site	Sampling effort (m)	Number of Detections [a]	Enc Rate (inds/km)	Density (inds/ha) [b]
2003	1	Colosso	1,650	1	0.6	0.19
	1	Dimona	2,500	0	0	0
	1	Porto Alegre	1,400	0	0	0
	10	Colosso	3,240	3	0.9	0.29
	10	Dimona	5,200	2	0.4	0.12
	10	Porto Alegre	3,240	4	1.2	0.39
	100	Dimona	9,700	15	1.5	0.5
	100	Porto Alegre	7,080	11	1.6	0.5
	Continuous	Km 41	14,700	19	1.3	0.52
	Continuous	Dimona	3,300	8	2.4	0.99
	Total		**52,010**	**63**	-	-
2004	1	Colosso	3,900	2	0.5	0.19
	1	Dimona	2,900	0	0	0
	1	Porto Alegre	4,500	0	0	0
	10	Colosso	3,240	4	1.2	0.29
	10	Dimona	1,750	1	0.6	0.12
	10	Porto Alegre	5,040	13	2.6	0.39
	100	Dimona [c]	7,200	8	1.1	0.5
	100	Porto Alegre [c]	5,600	12	2.1	0.5
	Continuous	Km 41	13,000	21	1.6	0.62
	Continuous	Dimona	3,700	5	1.4	0.55
	Continuous	Cabo Frio	7,950	9	1.1	0.41
	Total		**58,780**	**75**	-	-

a: One detection is defined as one sight or hearing event. There were two events (*Colosso* and *Porto Alegre*) with two individuals and one (*Colosso*) with three; all events corresponded to a single individual.

b: Densities were estimated with *Distance Software* v. 4.1. See detailed explanation in the text.

c: Data for one-hundred hectare fragments were collected in 2005 instead of 2004.

TABLE VI: SAMPLING EFFORT, NUMBER OF DETECTIONS, ENCOUNTER RATES AND DENSITIES OF *DASYPROCTA LEPORINA* (2003 AND 2004); *BIOLOGICAL DYNAMICS OF FOREST FRAGMENTS PROJECT*, MANAUS, BRAZIL.

| | Fragment Area (ha) | Site | *Dasyprocta leporina* | | | |
			Sampling effort (m)	Number of Detections [a]	Enc Rate (inds/km)	Density (inds/ha) [b]
2003	1	Colosso	1,650	6	3.6	1.27
	1	Dimona	2,500	3	1.2	0.41
	1	Porto Alegre	1,400	2	1.4	0.5
	10	Colosso	3,240	2	0.6	0.12
	10	Dimona	5,200	1	0.2	0.06
	10	Porto Alegre	3,240	0	0	0
	100	Dimona	9,700	0	0	0
	100	Porto Alegre	7,080	5	0.7	0.24
	Continuous	Km 41	14,700	6	0.4	0.14
	Continuous	Dimona	3,300	1	0.3	0.1
	Total		**52,010**	**26**	-	-
2004	1	Colosso	3,900	2	0.5	0.18
	1	Dimona	2,900	2	0.7	0.24
	1	Porto Alegre	4,500	2	0.4	0.15
	10	Colosso	3,240	1	0.3	0.11
	10	Dimona	1,750	0	0	0
	10	Porto Alegre	5,040	0	0	0
	100	Dimona [c]	7,200	0	0	0
	100	Porto Alegre [c]	5,600	0	0	0
	Continuous	Km 41	13,000	1	0.1	0.03
	Continuous	Dimona	3,700	1	0.3	0.09
	Continuous	Cabo Frio	7,950	5	0.6	0.21
	Total		**58,780**	**14**	-	-

a: One detection is defined as one sight or hearing event. There were two events (*Colosso* and *Porto Alegre*) with two individuals and one (*Colosso*) with three; all events corresponded to a single individual.

b: Densities were estimated with *Distance Software* v. 4.1. See detailed explanation in the text.

c: Data for one-hundred hectare fragments were collected in 2005 instead of 2004.

TABLE VII: RESULTS FROM DISTANCE 4.1: SAMPLE SIZE FOR EACH
DATASET, BEST MODEL FUNCTION (ON THE BASIS OF THE SMALLEST
AKAIKE INFORMATION CRITERIUM), AND EFFECTIVE STRIP WIDTH USED
FOR DENSITY ESTIMATES

Species	Sites	Sample size	Model Function	ESW (m)
M. acouchy	All 1 and 10-ha fragments	30	Hazard-rate with no adjustments	15.7
M. acouchy	100-ha fragments	46	Uniform with one cosine adjustment	15.4
M. acouchy	Continuous Forest	62	Half-Normal with no adjustments	12.2
D. leporina	All	40	Uniform with one cosine adjustment	14.8

a)
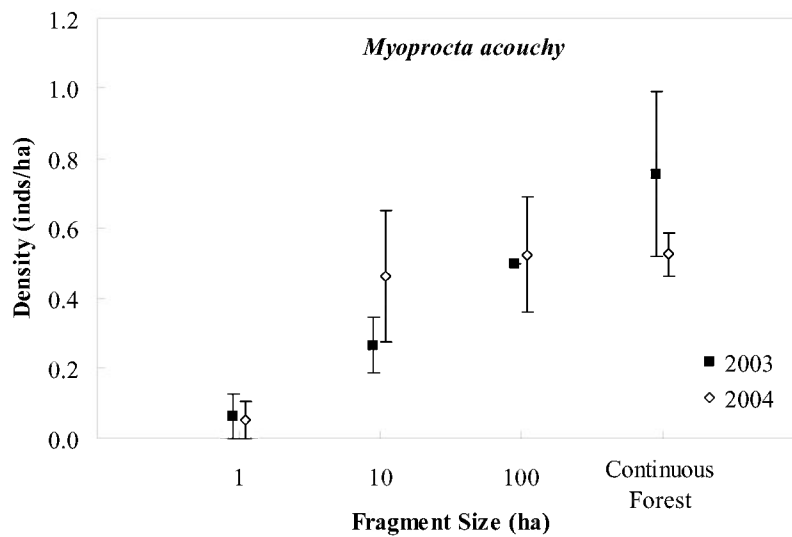
b)
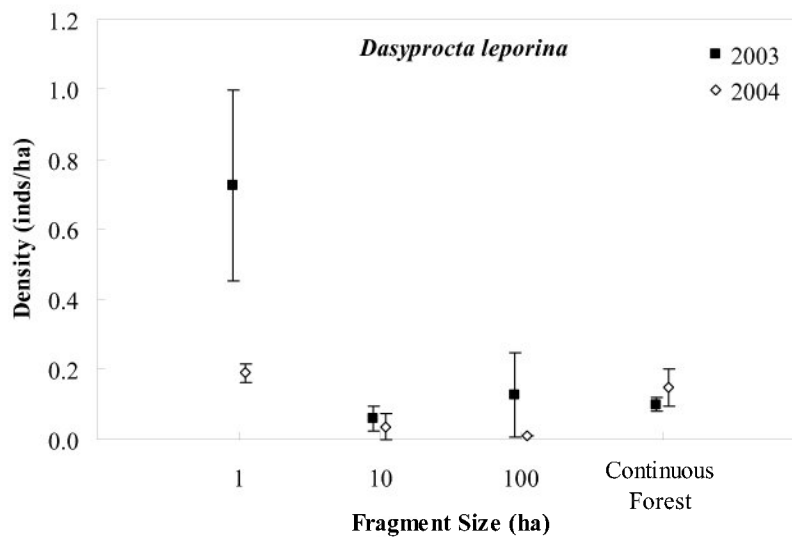
Figure 13: Average density (± SE) of (a) acouchies (*Myoprocta acouchy*) and (b) agoutis

(*Dasyprocta leporina*) in fragments of one, ten, one-hundred hectares and continuous

forest of the *Biological Dynamics of Forest Fragments Project*, Manaus, Brazil (one-way

analysis of variance with repeated measures, *Myoprocta*: $F_{3,6} = 6.46$, $p = 0.026$;

Dasyprocta: $F_{3,6} = 5.44$, $p = 0.038$).

The lack of significance when comparing agoutis in one-hectare fragments to hundred-hectare and continuous forest is probably due to the great decrease in densities in one-hectare fragments in 2004 (Figure 13b). Year effects were not significant for either genus (*Myoprocta*: $F_{1,6}$ = 0.022, p = 0.887; *Dasyprocta*: $F_{1,6}$ = 3.855, p = 0.097).

IV.5. <u>Discussion</u>

This study reveals that fragmenting the forest at *BDFFP* had opposite effects on populations of acouchies (*M. exilis*) and agoutis (*D. leporina*). Acouchies decreased in density in smaller forest fragments, whereas agoutis' density increased. The results are enlightening for two reasons. First, the response of agoutis was opposite of that shown previously (Asquith et al. 1997, Terborgh et al. 1997, Chiarello 1999). Second, agouti and acouchy responses were divergent despite their similar morphology and behavior (Morris 1962, Smythe 1978, Dubost 1988).

Agoutis' positive response, in contrast to what previous studies have shown, seems to be the result of different environmental contexts. In Venezuela (Terborgh et al. 1997), fragments are approximately the same age (10-20 years) and the same sizes (1-100 ha) of those at *BDFFP*, but they are surrounded by water and not vegetation. For rodents, water is an inhospitable matrix, leading to the expectation that negative effects should be more intense there. Indeed, agoutis were present in large and medium-sized fragments, but disappeared from small ones. In Panama (Asquith et al. 1997) fragments also have a comparable size range as those from *BDFFP*, but are much older (more than 100 years old), and surrounded by water. As in Venezuela, Panamanian agoutis were present in large and medium-size fragments, but absent from small ones. In this case, age and

matrix type may have acted in tandem to negatively affect populations of agoutis. The

work from Chiarello 1999 – Southeast Brazil) is the only other one in which the

fragments are surrounded by land. But Atlantic forest fragments of Southeastern Brazil

have suffered from poaching and human intervention for at least 150 years, accounting

for his report that agoutis disappeared from much larger fragments (200 ha). Moreover, in

all three previous scenarios, landscape levels of fragmentation are much worse than in

BDFFP, *i.e.*, the overall amount of primary forest left in a range of 1 km is much scarcer.

It seems that fragmentation levels at *BDFFP* in terms of age, matrix quality, and overall

presence of primary forest are still mild for populations of agoutis, and not yet sufficient

to negatively affect them.

Somewhat puzzling is why densities in one-hectare fragments greatly increased,

especially in 2003. It is unlikely that the animals present in the small fragments were

remnants of pre-isolation times (*BDFFP* fragments were about 20 years old when

surveyed for this study and maximum lifespan of *M. acouchy* and *D. leporina* are

approximately 15 and 18 years – http://genomics.senescence.info). Individuals' presence

in those fragments seems to reflect visitation rates of animals that wander through the

area and use the fragments as part of their home ranges. In continuous forests of

Southeast Amazon, agoutis' home ranges were unevenly used, with areas of greater

resource abundance used much more intensively than others (Jorge 2000). The

fragmented scenario of *BDFFP* may parallel what happens in continuous forest and

agoutis may have been using one-hectare fragments more intensively because of higher

abundance of their preferred food when compared to the surrounding matrix. The great

density difference observed in one-hectare fragments between 2003 and 2004 further

corroborates that idea. T. Viscarra (*unpublished data*) reported that fruit production in the secondary vegetation in 2003 was significantly lower than in 2004. As a consequence, agoutis may have searched for food more intensively in one-hectare fragments in that year.

Acouchies, in contrast, significantly decreased in density in smaller fragments. The divergent response of the two genera is surprising because they are evolutionarily close, and morphologically and behaviorally similar. Yet, in a recently fragmented forest, they have distinct responses, with agoutis being positively affected, and acouchies negatively affected. Previous studies (Dubost 1988, Voss et al. 2001) and personal observation revealed that agoutis cross and forage in forests at several levels of regeneration, in forest edges adjacent to open vegetation, and even dirt roads. On the contrary, acouchies are always restricted to the interior of mature forest. It is safe to assume that agoutis are better dispersers through habitats other than primary forest.

Body-size differences are the most probable explanation underlying distinct dispersal abilities (Gehring and Swihart 2003). The larger body size of agoutis may provide greater perceptual ability (Zollner 2000) allowing enhanced assessment of the heterogeneous landscape at greater distances and reduced vulnerability to predation. Behavioral attributes could be associated with acouchies' negative response to forest fragmentation. Acouchies responded similarly to forest fragmentation as did understory birds in the same area (Bierregaard and Stouffer 1997), but opposite to smaller rodents (Malcolm 1997). Acouchies and understory birds are both diurnal and probably depend on visual cues to avoid predation, whereas nocturnal animals such as smaller mammals, probably depend more on olfactory and acoustic cues. Therefore, a change in light intensity due to canopy

opening would most probably affect acouchies and understory birds and not necessarily nocturnal rodents. Looking at a broader, regional level, the responses of acouchies and agoutis to forest fragmentation at *BDFFP* may parallel differences in their geographic distributions (Figure 14) and the same ecological reasons could explain local as well as regional distributions. Agoutis may be more widespread regionally because they are better dispersers through sub-optimal habitats, the same reason why they are not affected by forest fragmentation at *BDFFP*.

This study enlightens the effects of forest fragmentation on mammals in two ways. First, it shows that species response to forest fragmentation is highly context-dependent. In this case, forest fragmentation at *BDFFP* is not yet sufficiently intense to negatively affect populations of agoutis. Unfortunately these levels of fragmentation are not the rule in Amazonian forests, and tend to get only worse (Laurance et al. 2001a). Therefore, increased fragmentation in the future will most probably also negatively affect agoutis.

Second, and more importantly, it shows that closely-related groups (agoutis and acouchies) respond differently to forest fragmentation and that body size seems to be an important factor in determining the differences. The smaller species (acouchies) was more negatively affected probably because individuals disperse more poorly through secondary vegetation, even at old stages of regeneration. If indeed Amazonian forests become completely fragmented, the disappearance of acouchies seems to be inevitable.
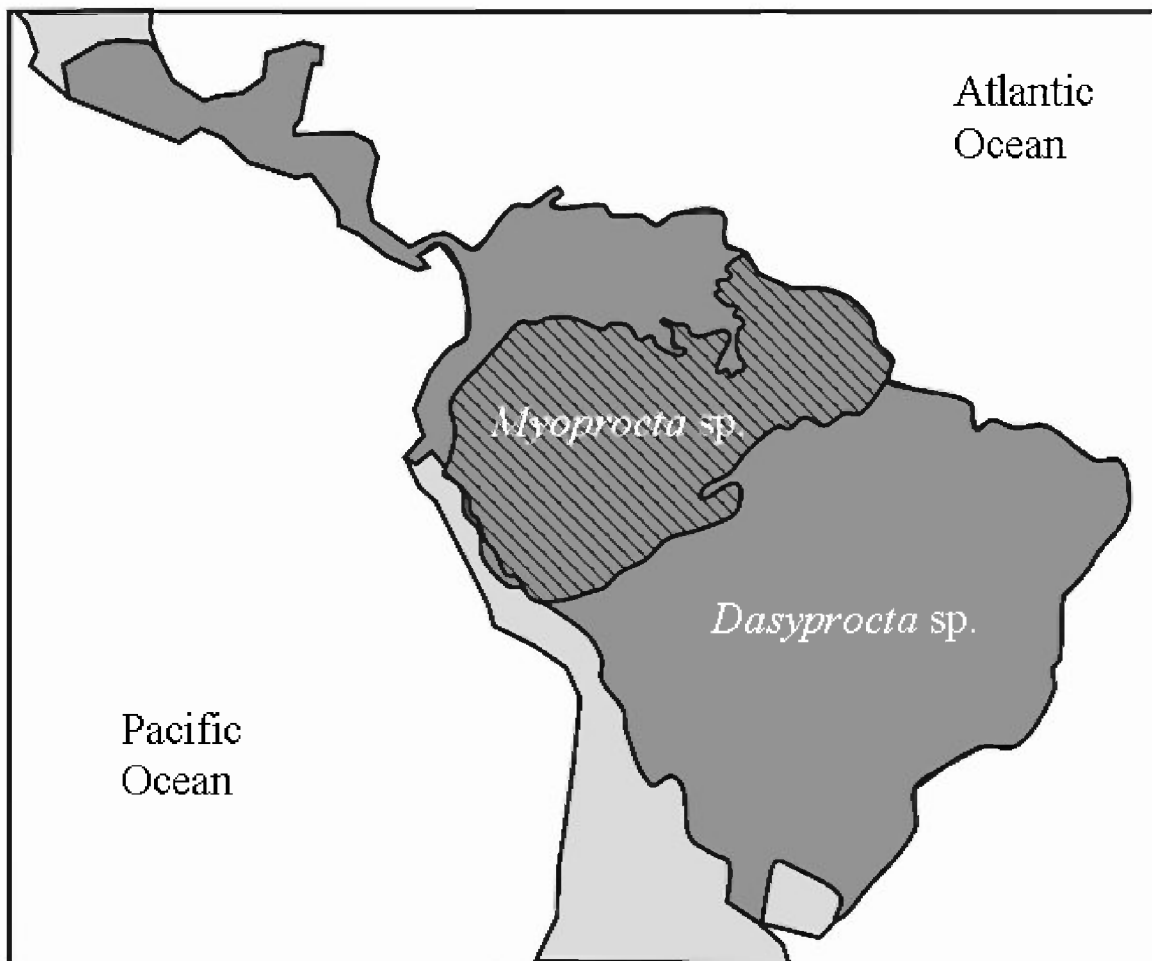
Figure 14: Geographic distribution of the genera *Myoprocta* spp. (hashed area) and

Dasyprocta spp. (dark grey area) in Central and South America. Both genera overlap at

the range of *Myoprocta* spp., which corresponds to the core area of the Amazonian forest.

V. EFFECTS OF FOREST FRAGMENTATION ON FRUIT PRODUCTION OF LARGE-SEEDED SPECIES AND CONSEQUENCES TO SCATTER-HOARDERS

V.1. **Introduction**

Agoutis (*Dasyprocta* spp.) and acouchies (*Myoprocta* spp.) are terrestrial rodents that inhabit Amazonian forests and eat fruits and seeds that fall on the forest floor (Henry 1999). Both species also scatter-hoard large seeds and harvest them later, when resource abundance is low (Morris 1962, Smythe 1978, Dubost 1988). Abundance of large-seeded fruits on the ground is therefore important for survival of these two rodents and to understand their scatter-hoarding dynamics. Scatter-hoarding is essential for recruitment large-seeded trees (Table I). Theimer (2005) proposes that fragmentation of the forest may disrupt the abundance of food resource to the animals and that it could further affect scatter-hoarding levels. In this chapter, I ask two questions. First, does fragmentation of the forest affect the production of large-seeded fruits available for these two rodents? Second, if so, how do changes in the abundances of fruits as well as the scatter-hoarders affect scatter-hoarding levels?

In order to answer the first question, I present results on the number of individuals fruiting and use it as an indication of fruit production. Therefore, hereafter, whenever I mention fruit production or fruit abundance, I always mean the number of individuals fruiting. To answer the second question, I correlate abundances of agoutis and acouchies (Chapter IV) with the abundance of the fruits, and correlate the abundance of fruits per animal with removal and scatter-hoarding levels of *A. aculeatum* (Chapter III)

There are a number of reasons why fruit abundance may change in forest fragments. First, it may happen by chance. Neotropical rainforests are highly diverse (Oliveira and Mori 1999, Gentry 1988, Valencia et al. 1994). Tree populations are usually present in densities lower than one individual per hectare (Pitman et al. 2001). Composition of forest fragments is expected to be very different from one another, and it may happen that some fragments have lower resource abundance than continuous forest by chance.

However, random variation of tree composition should not explain consistent changes. Consistent changes in fruit abundance due to changes in forest size may be related to changes in pollination patterns or differential tree mortality. Declines of native pollinators (Aizen and Feinsinger 1994) as well as declines in fruit production due to pollination disruption (Nason and Hamrick 1997) have been shown to occur for a few plant species. If this pattern proves to be more widespread, pervasive changes in fruit production are expected to happen as a consequence. Proximity to edges increases mortality rates of larger trees (Laurance et al. 2000) as a result of desiccation (Laurance et al. 1998) wind shear, and liana infestation (Laurance et al. 2001b). Trees that die at fragment edges are substituted by pioneer trees (Tabarelli et al. 1999). Pioneer trees produce smaller fruits and seeds that represent lower quality resources for rodents. The combination of those two factors – trees producing fewer or no fruits because of pollination disruption and large-seeded trees being substituted by smaller-seeded ones – may be sufficient to account for significant changes of resource abundance for agoutis and acouchies in forest fragments.

The question then becomes: if fruit production changes, will agoutis and acouchies respond by changing their abundances, or their scatter-hoarding levels? Changes in

abundance have been shown to occur with smaller rodents. For example, Central-American spiny rats (*Proechimys semispinosus*, Echymidae) increased in density when supplemented with extra food in small islands of the Panama Canal (Adler 1998). But abundances are not regulated solely by the amount of resources. Migration rates are known to disrupt mammal abundances in fragments as well (Laurance 1991). At *BDFFP*, I evaluate if changes in the abundance of agoutis and acouchies in the fragments (Chapter IV) and changes in their scatter-hoarding levels (Chapter III) may or may not be directly related to possible shifts in the abundance of their food.

V.2. <u>Data collection</u>

For the data collection of this chapter, I used the same sites used in Chapters III (Figure 7). At all nine sites (three one-hectare fragments, three ten-hectare fragments, and three areas of continuous forest), three parallel transects were sampled every month from mid-February to mid-August 2004, with the help of three field assistants. In the continuous forest, transects were 1000-meters long, and 200-meters apart from one another. In ten-hectare fragments, transects were 350-meter long, and 75-meters apart from one another. In one-hectare fragments, transects were 100-meter long, and 30-meters apart from one another.

To survey the transects, we walked at a slow pace (approximately one kilometer per hour) looking for fruits on the trail and the ground nearby (approximately one meter in each side). Upon encountering a fresh fruit, intact or partially eaten, we looked for more fruits outside the trail and looked for the plant source. We looked for the plant source because I did not want to include fruits that were carried from sources outside the vicinity

of the transects. I included fruit patches for which I did not find the source plant only if fruits clearly seemed to be falling from a plant (*e.g.* many fruits, some intact) and not carried by an animal (*e.g.* few fruits, pulp removed, bite marks).

A fruit sample was collected (ten or more fruits) for further information on fruit conditions and dimensions. Fruit condition was determined as: 1) immature or mature; 2) intact; pulp removed; seeds removed. Fruit and seed length, width and thickness were also measured. A digital photograph was taken of each fruit and, whenever possible, its seeds. When possible, family, genus and species were identified in the field. If not possible, further identification was attempted with the help of the botanic data bank from *BDFFP*, the plant field guide from Reserva Ducke, and specialists from the *Instituto Nacional de Pesquisas da Amazônia* (INPA). During the fruit survey, we collected all fruit types found on the forest floor. But for the present analyses, I included data from eleven plant families that produce large seeds (Arecaceae, Bombacaceae, Caryocaraceae, Chrysobalanaceae, Duckeodendraceae, Fabaceae, Humiriaceae, Lecythidaceae, Myristicaceae, Olacaceae, and Sapotaceae). These families are either known to be preferred by agoutis from the literature (Silvius and Fragoso 2003) or expected to be preferred by their seed characteristics (especially seed size) and anecdotal observation of field assistants.

V.3. <u>Statistical analyses</u>

V.3.a. Differences in number of individuals fruiting between months, sites and

fragment sizes

For the present analyses, I compared the number of plants fruiting per site per month and per fragment size. Sampling effort was unbalanced between sites and fragment sizes (Table VIII). Therefore, for each comparison, I corrected the values by dividing all the distances by the shortest distance walked (correction factor), then multiplying the number of individuals fruiting by the correction factor. For example, when comparing fragment sizes, I divided 41000 (distance walked in the continuous forest) by 6300 (distance walked in the one-hectare fragments). The result (correction factor = 0.154) was multiplied by the total number of individuals fruiting in the continuous forest (187 * 0.154 = 29 individuals).

I used a combination of analyses to detect significant differences between months, sites, fragment sizes, and significant interactions between these factors. First, I used chi-square tests with the corrected values to test for differences between months (mid-February to mid-August) sites (*Colosso-Km 41*, *Porto Alegre-Cabo Frio*, and *Dimona*) and fragment size (one hectare; ten hectares and continuous forest). Then I used a log-linear analysis with the raw data to identify significant interactions between the three factors (month, site and fragment size). I used SYSTAT v.11 for all statistical analyses.

TABLE VIII: DISTANCE MONTHLY WALKED IN EACH SITE FOR THE SURVEY OF NUMBER OF INDIVIDUALS FRUITING AT THE *BIOLOGICAL DYNAMICS OF FOREST FRAGMENTS PROJECT*, MANAUS, BRAZIL

Site	Fragment Size	February March	March April	April May	May June	June July	July August	Total
Colosso Km 41	1 ha	450	450	450	450	450	450	2700
	10 ha	1050	1050	1050	1050	1050	1050	6300
	Continuous Forest	2000	3000	3000	3000	3000	3000	17000
Porto- Alegre Cabo- Frio	1-ha	300	300	300	300	300	300	1800
	10-ha	1050	1050	1050	1050	1050	1050	6300
	Continuous Forest	3000	3000	3000	3000	3000	3000	18000
Dimona	1-ha	300	300	300	300	300	300	1800
	10-ha	1050	1050	1050	1050	1050	1050	6300
	Continuous Forest	1000	1000	1000	1000	1000	1000	6000
Total		10200	11200	11200	11200	11200	11200	66200

V.3.b. Correlation between fruit production, agouti and acouchy abundances, number of seeds removed and number of seeds cached

In all nine sites, I collected information on the number of large-seeded species fruiting (present chapter), the abundance of agoutis and acouchies (Chapter IV), the number of *Astrocaryum* seeds removed from artificial *seed stations*, and the proportion of seeds cached from the same stations (Chapter III). I used that information to identify if: 1) the abundances of the animals correlated with the abundances of their resources; 2) if the number of seeds removed correlated with the ratio of fruiting plants per animal; and 3) if proportion of seeds cached correlated with the ratio of fruiting plants per animals. For the abundance of fruiting plants and abundance of animals, I used number of individuals per kilometer walked (encounter rates). For the number of seeds removed and the proportion of seeds cached, I used the average number per site. Linear regressions were conducted to identify significant correlations. I used SYSTAT v.11 for all statistical analyses.

V.4. <u>Results</u>

V.4.a. Effects of season, site and fragment size on the number of individuals fruiting

Over the course of six months (mid-February to mid-August 2004), we walked 66 kilometers to survey the forest floor for fruit production (Table VIII). Among the 11 families included in this analysis, 294 individuals (Table IX) of 67 species (Table X) fruited over the six-month period.

TABLE IX: NUMBER OF INDIVIDUALS FRUITING OF 67 LARGE-SEEDED TREE SPECIES AT THE *BIOLOGICAL DYNAMICS OF FOREST FRAGMENT PROJECT*, MANAUS, BRAZIL.

Site	Fragment Size	February March	March April	April May	May June	June July	July August	Total
Colosso Km 41	1 ha	0	1	2	0	2	1	6
	10 ha	5	12	4	0	2	1	24
	Continuous Forest	13	13	18	3	9	4	60
Porto-Alegre Cabo-Frio	1-ha	6	3	1	2	1	0	13
	10-ha	10	7	8	5	3	7	40
	Continuous Forest	31	28	18	12	6	6	101
Dimona	1-ha	3	2	2	1	1	1	10
	10-ha	4	1	4	3	1	1	14
	Continuous Forest	5	7	3	5	1	5	26
Total		77	74	60	31	26	26	294

TABLE X: SPECIES PRESENT IN THE FRUIT SURVEY CONDUCTED IN 2004 AT
NINE RESERVES OF THE *BIOLOGICAL DYNAMICS OF FOREST FRAGMENT
PROJECT*, MANAUS, BRAZIL. THE SURVEY FOCUSED ON 11 FAMILIES OF
LARGE-SEED SPECIES.

Families/Species
Arecaceae
Attalea maripa
Euterpe precatoria
Oenocarpus bacaba
Oenocarpus bataua
Oenocarpus minor
Syagrus inajai
Bombacaceae
Scleronema micrantha
Caryocaraceae
Caryocar glabra
Caryocar villosum
Chrysobalanaceae
Couepia elata
Licania caudata
Licania heteromorpha
Licania impressa
Licania linoi
Licania reticulata
Licania sorthasea
Licania sp1
Licania sp2
Licania sp3
Licania sp4
Unidentified 01
Unidentified 02
Unidentified 03
Unidentified 04
Duckeodendraceae
Duckeodendrum cestroides
Fabaceae
Abarema jupumba
Abarema piresii
Abarema cochleata
Abarema sp1
Eperua glabriflora
Hymenolobium sp.
Inga sp. [a]
Peltogyne paniculata
Swartzia lanellata

TABLE X (CONTINUED)

Fabaceae (continued)
Unidentified 01
Unidentified 02
Humiriaceae
Duckesia verrucosa
Sacoglottis mattogrossensis
Vantanea parviflora
Unidentified 01
Unidentified 02
Lecythidaceae
Cariniana micrantha
Corythophora alta
Eschweilera cyathiformis
Eschweilera micrantha
Eschweilera wachenheimii
Eschweilera sp. [a]
Myristicaceae
Iryanthera elliptica
Virola calophylla
Virola pavoris
Olacaceae
Minquartia guianensis
Sapotaceae
Chrysophyllum pomiferum
Chrysophyllum sparsiflorum
Manilkara huberi
Micropholis venulosa
Pouteria cuspidata
Pouteria retinervis
Pouteria sp1
Pouteria sp2
Pouteria sp3
Unidentified 01
Unidentified 02
Unidentified 03
Unidentified 04
Unidentified 05
Unidentified 06
Unidentified 07

a: the genera *Inga* (Fabaceae) and *Eschweilera* (Lecythidaceae) probably include more species than listed here. It was not possible to separate them at the species level because fruit and seed characteristics are very similar within the genus.

The number of species is probably an underestimation because unidentified species of the genera *Eschweilera* (Lecythidaceae) and *Inga* (Fabaceae) were lumped together due to the difficulty to separate in morpho-species using fruit and seed characteristics (Table XI). Chrysobalanaceae, Fabaceae, and Sapotaceae were the most important families in richness and abundance (Figures 15d, h, and k).

Overall there was a significant season variation in fruit production. More individuals fruited during the rainy season, with a monotonic decrease towards the dry season (Figure 15a – $\chi^2_{d.f.=5} = 30.89$, p < 0.001). There was also temporal variation between families. Arecaceae and Duckeodendraceae spread their production over the entire sampling period (Figures 15b, and g). Bombacaceae, Caryocaraceae, Lecythidaceae, and Myristicaceae had a peak of production in the beginning of the wet season (Figures 15c, d, h, and j). Fabaceae had a peak of production late in the rainy season (Figure 15i). Chrysobalanaceae, Humiriaceae and Sapotaceae had a bimodal distribution, but with the largest production during the rainy season (Figures 15e, g, and l). Finally, Olacaceae fruited in the beginning of the dry season (Figure 15k).

There was also significant variation between sites. *Porto Alegre-Cabo Frio* had many more individuals fruiting than the other two sites ($\chi^2_{d.f.=2} = 12.50$, p < 0.05 – *Colosso-Km 41*: 49 individuals; *Porto Alegre-Cabo Frio*: 83 individuals; *Dimona*: 50 individuals). Local differences in the relative abundance of each family may explain the differences between the three sites. For example, two of the three overall most productive families (Chrysobalanaceae, and Sapotaceae) were overrepresented in *Porto Alegre-Cabo Frio* (Figure 16).
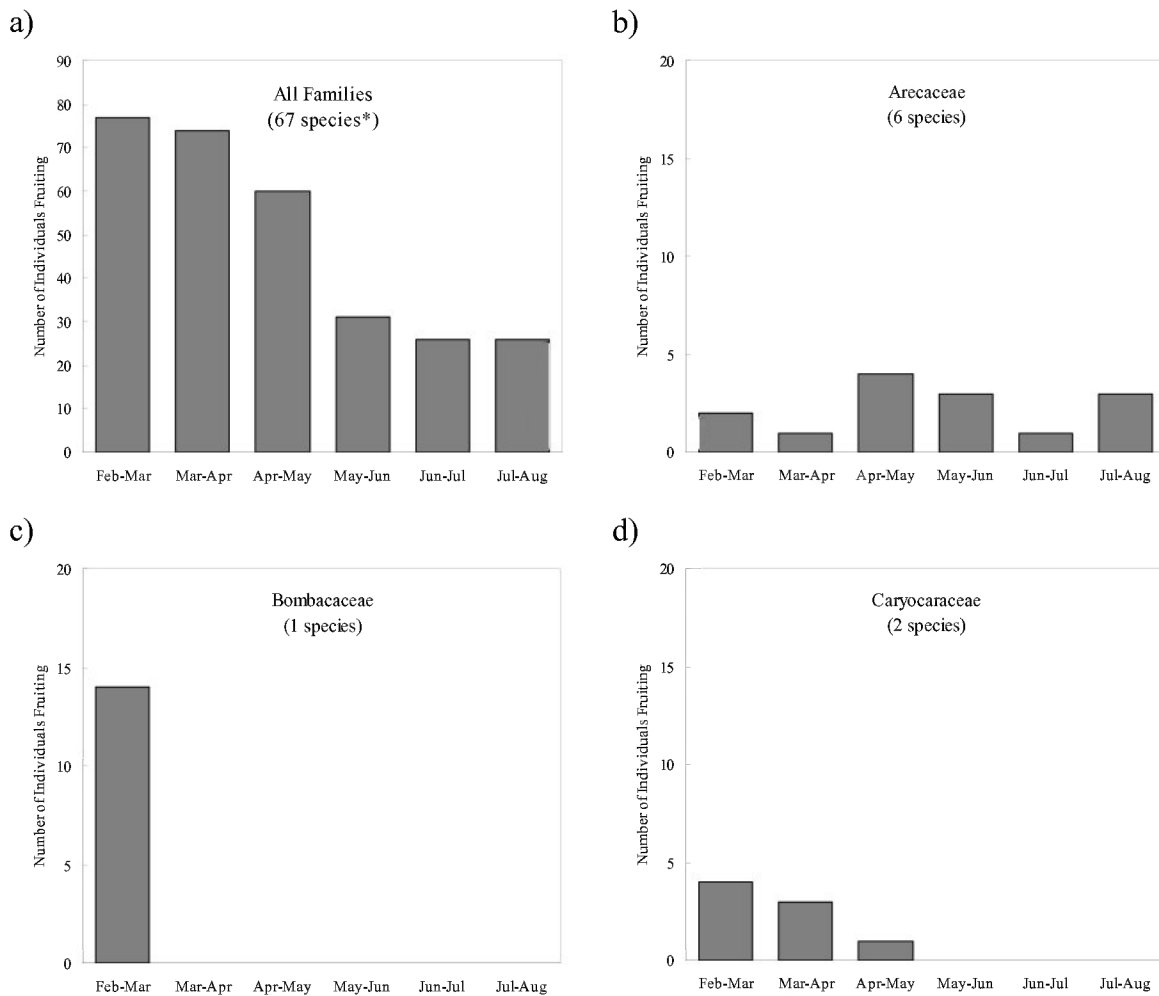
Figure 15: Number of individuals fruiting over the course of six months (mid-February to mid-August) at the *Biological Dynamics of Forest Fragment Project*, Manaus, Brazil. (a) There was a temporal variation in overall number of individuals fruiting ($\chi^2_{d.f.=5} = 30.89$, $p < 0.001$) as well as a variation among families (b – l).

e)

f)

g)

h)

Figure 15: (*Continued*).

i)

j)

k)

l)
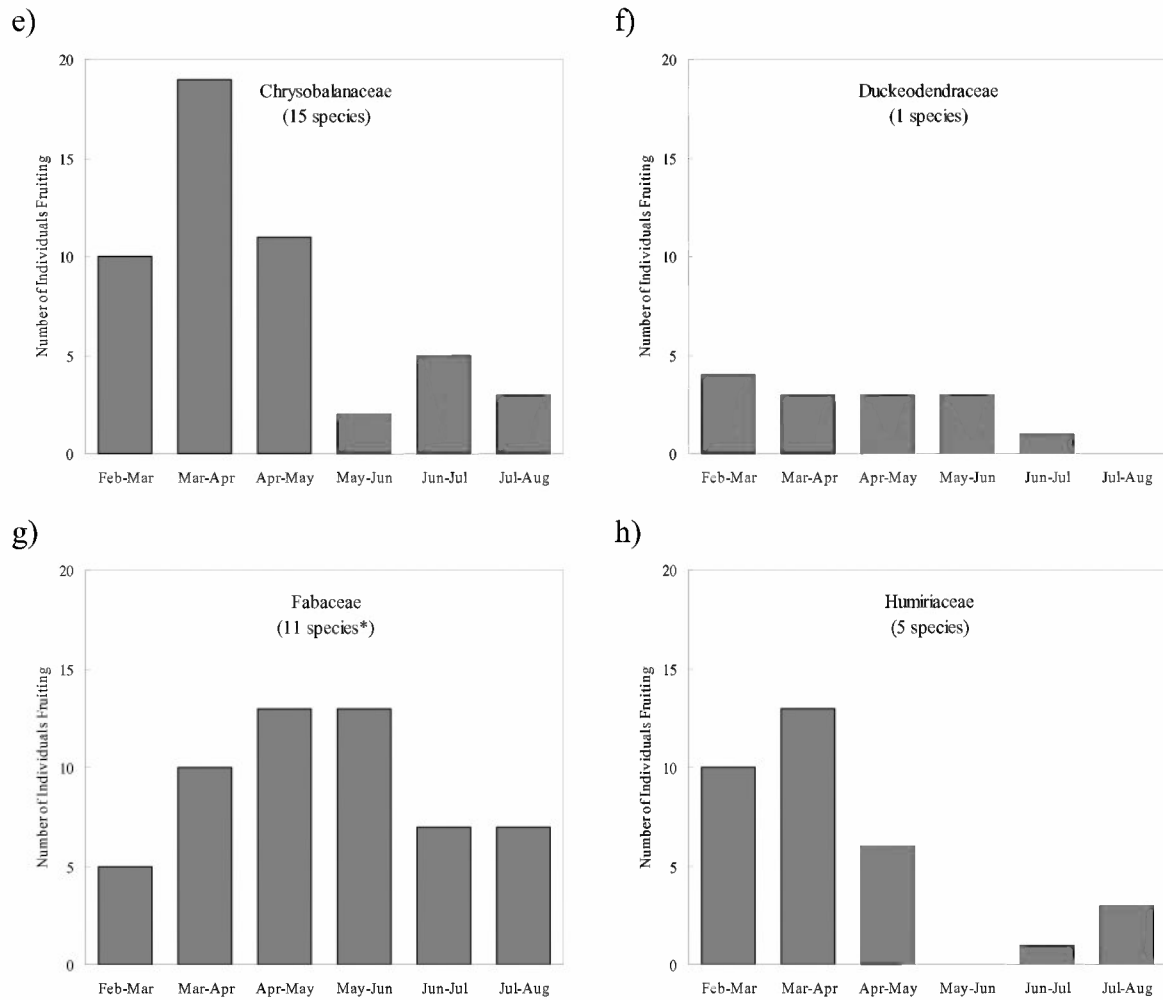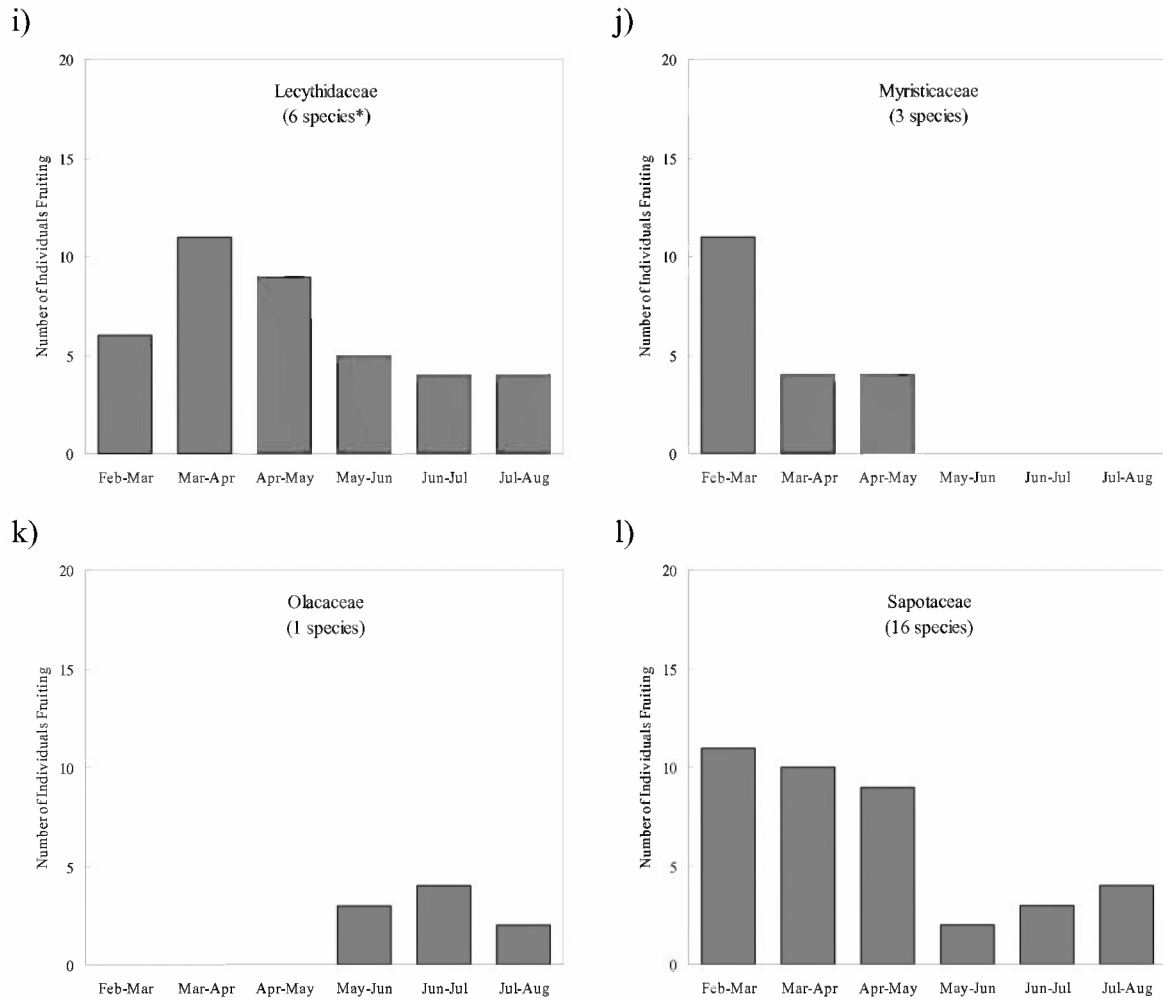
Figure 15: (*Continued*).
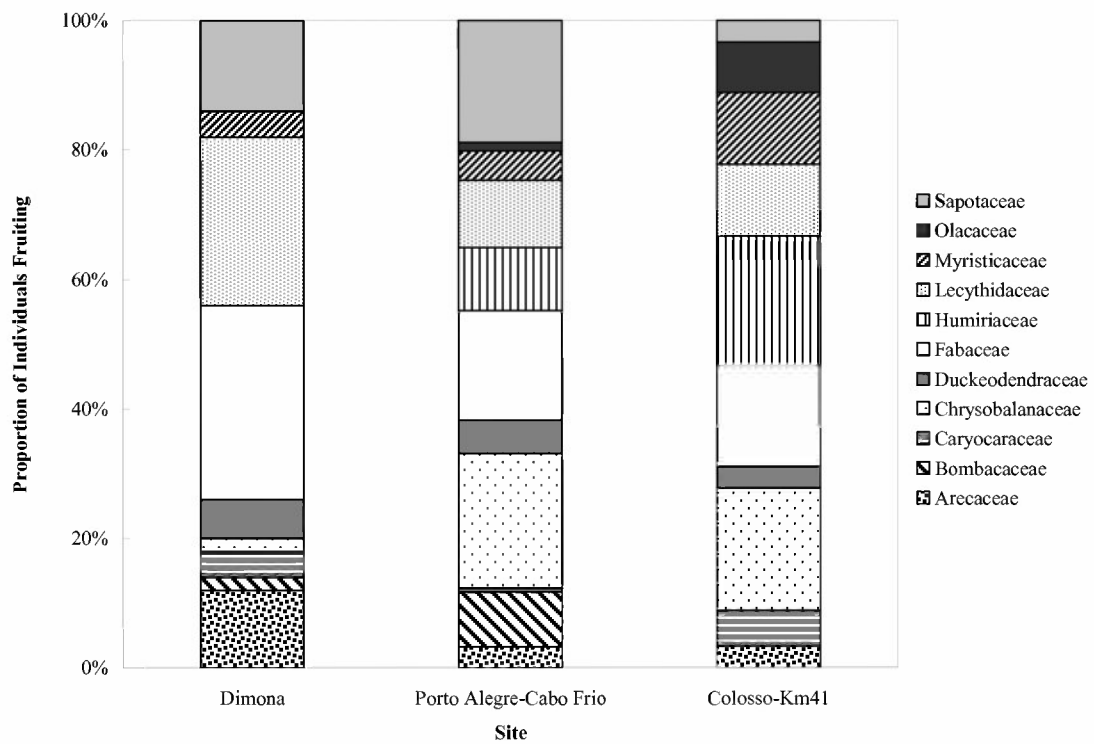
Figure 16: Proportion of individuals fruiting of eleven families of large-seeded species in three sites approximately five to ten kilometers apart from each other (see Figure 7 for detailed map). Data collected from the *Biological Dynamics of Forest Fragments Project*, Manaus, Brazil.

There was also a significant interaction between site and month ($\chi^2_{d.f.=2}$ = 12.50, p < 0.05). At *Porto Alegre-Cabo Frio*, fruit production monotonically declined from February to June, but started increasing again in July. At *Dimona*, the trend was very similar, but overall fruit production was much lower. At *Colosso-Km 41*, there were two peaks of fruit production, one at the late wet season, and another at the beginning of the dry season (Figure 17). Once again, local variation of families' relative abundance is the most probable explanation for the significant differences. For example, *Porto Alegre-Cabo Frio* had 7 individuals of Bombacaceae and 5 individuals of Sapotaceae fruiting in February-March, whereas *Dimona* had one of Bombacaceae and one of Sapotaceae and *Colosso-Km 41* had none of Bombacaceae and one of Sapotaceae. On the other hand, *Colosso-Km 41* had 4 individuals of Olacaceae fruiting between June and Augusts, whereas *Porto Alegre-Cabo Frio* had one and *Dimona* had none

Finally, the number of individuals fruiting was not significantly different between fragments of the two sizes and continuous forest ($\chi^2_{d.f.=2}$ = 0.198 – one-hectare: 29 individuals; ten-hectares: 26 individuals; continuous forest: 29 individuals), neither were the interactions between fragment size and month ($\chi^2_{d.f.=10}$ = 2.96; p = 0.982) and fragment size and site ($\chi^2_{d.f.=4}$ = 7.27; p = 0.122).
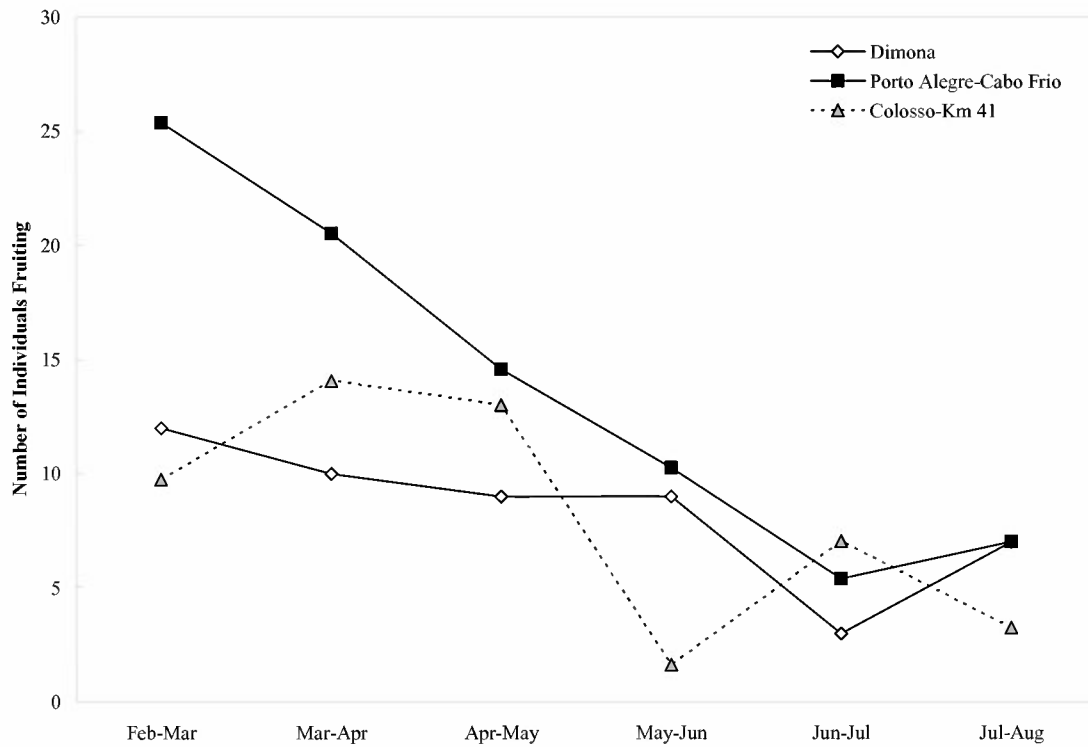
Figure 17: Temporal variation of number of individuals fruiting from 67 large-seeded species was significantly different ($\chi^2_{d.f.=2}$ = 12.50, p < 0.05) between three sites that are five to ten kilometers apart from one another (see Figure 7 for map details) at the *Biological Dynamics of Forest Fragments Project*, Manaus, Brazil.

Fewer families were represented in the one-hectare fragments (only six out of 11). But some of them had more individuals fruiting over the six months. For example, Arecaceae had four individuals fruiting in one-hectare fragments, but only one in ten-hectare and continuous forest. Lecythidaceae had six individuals fruiting in one-hectare, two in ten-hectare and four in the continuous forest. Finally, Sapotaceae had an unusually high number of individuals fruiting in one-hectare fragments (10 versus 4 in ten-hectare and 2 in the continuous forest).

V.4.b. Correlation between fruit production, agouti and acouchy abundances, number of seeds removed and proportion of seeds cached

With the data on fruit production, animal abundances and seeds removed and cached collected from the same nine sites during the same period (February to August 2004), it was possible to evaluate how much of the abundances of the animals was explained by fruit abundance and how much of the number of seeds removed and cached was explained by the fruit abundance per animal.

Animal encounter rates did not significantly vary with number of fruiting trees ($R^2_{n=9} = 0.008$, p = 0.82 – Figure 18a). Factors other than resource abundance seem to regulate animal abundances. The range of number of fruiting trees per animal varied from one (continuous forest of *Dimona*) 16 (one-hectare fragment of *Porto Alegre-Cabo Frio*). Surprisingly, the number of seeds removed did not vary with the number of fruiting trees per animal ($R^2_{n=9} = 0.138$, p = 0.32 – Figure 18b). Moreover, the proportion of seeds cached was negatively correlated with the number of fruiting trees per animal ($R^2_{n=9} = 0.545$, p = 0.02 – Figure 18c).

a)

b)

c)
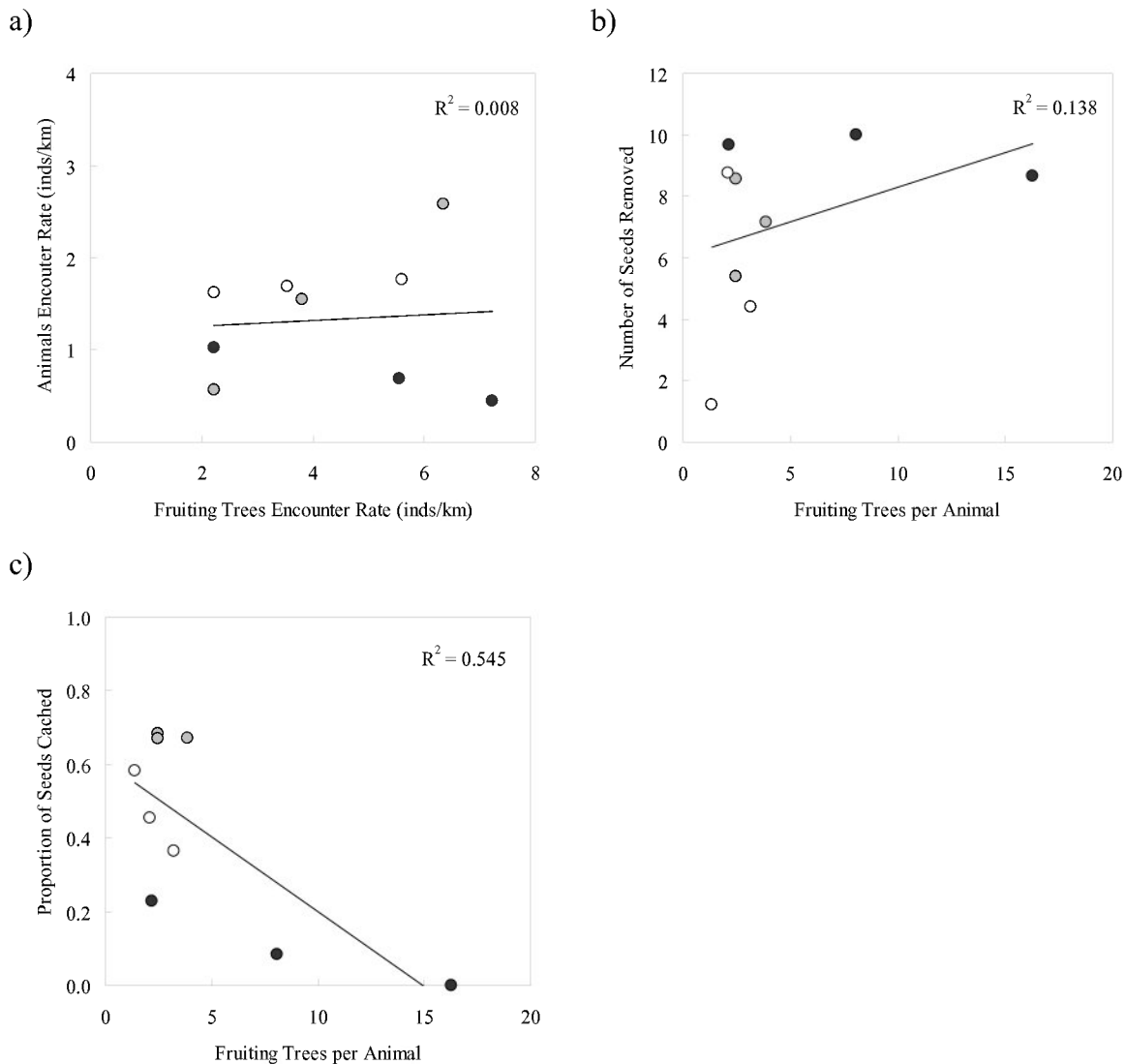
Figure 18: When all fragment sizes of all sites (N = 9) were included (a) the number of

acouchies (*M. acouchy*) and agoutis (*D. leporina*) did not significantly vary with the

number of fruiting trees of 67 large-seeded species (p = 0.82); (b) neither did the number

of seeds removed with number of fruiting trees per animal (p = 0.32); (c) on the other

hand, the proportion of seeds cached was negatively correlated with the number of

fruiting trees per animal (p = 0.02), at the *Biological Dynamics of Forest Fragments*

Project, Manaus, Brazil. Black circles correspond to one-hectare fragments; grey circles

correspond to ten-hectare fragments; and white circles correspond to continuous forest.

By taking a closer look at Figure 18c, it was possible to identify that most of the negative correlation was explained by the results from one-hectare fragments. At the one-hectare fragments, a fair amount of trees fruited, but only few agoutis sporadically visited the fragments. Therefore, the ratio of fruiting trees per animal was much higher than for the other sites. On the other hand, proportion of seeds cached was very low, resulting in a negative correlation.

When one-hectare fragments are removed from the analyses, animals' abundances nicely correlate with the number of fruiting trees ($R^2_{n=6} = 0.622$, $p = 0.06$ – Figure 19a). The results are marginally significant only because the sample size is small. Nevertheless, seeds removed and cached still do not correlate with fruit abundance per animal (seeds removed: $R^2_{n=6} = 0.145$, $p = 0.47$ – Figure 19b; seeds cached: $R^2_{n=6} = 0.003$, $p = 0.92$ – Figure 19c).

In summary, in one-hectare fragments, there is a high proportion of fruiting trees per animal, but that does not translate in more seeds being cached. On the other hand, in ten-hectare fragments and continuous forest, the abundance of animals nicely correlates with the abundance of fruiting trees. But in ten-hectare fragments, acouchies and agoutis are caching more seeds, independent of the levels of resource abundance per animal.

a)

b)

c)
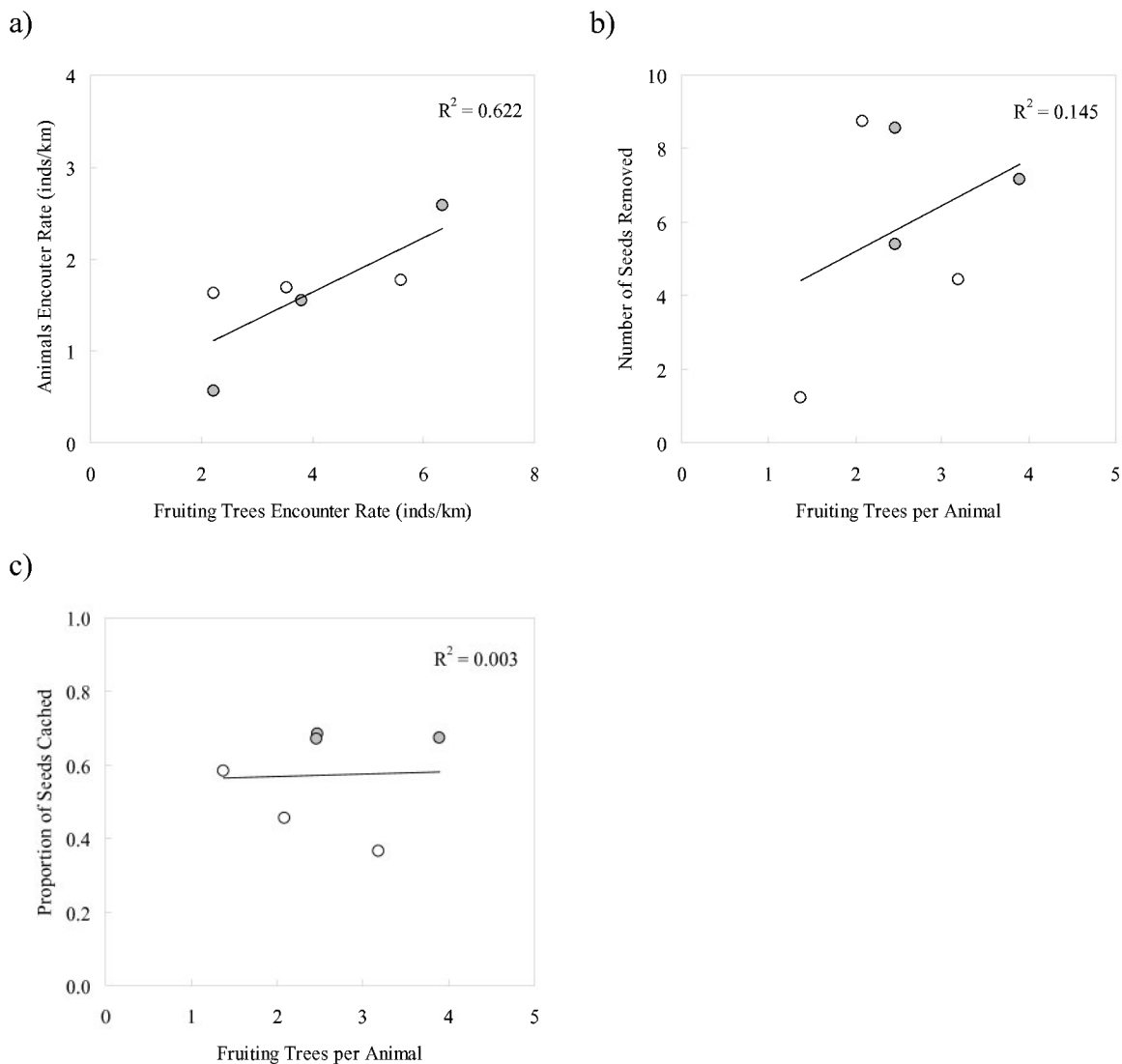
Figure 19: When one-hectare fragments were excluded from the analysis (N = 6) (a) the number of acouchies (*M. acouchy*) and agoutis (*D. leporina*) significantly varied with the number of fruiting trees of 67 large-seeded species (p = 0.06); (b) but the number of seeds removed with number of fruiting trees per animal did not (p = 0.47); (c) nor did the proportion of seeds cached with the number of fruiting trees per animal (p = 0.92), at the *Biological Dynamics of Forest Fragments Project*, Manaus, Brazil. Grey circles correspond to ten-hectare fragments; and white circles correspond to continuous forest.

V.5. <u>Discussion</u>

Neotropical trees support a wide array of animals through the production of their fruits and seeds. Nevertheless, fruit production is temporally and spatially variable (Foster 1982, Gentry and Emmons 1987, Fleming 1992, Forget et al. 2002) and animals need to adapt to this reality (Smythe 1986). Neotropical scatter-hoarding rodents are expected to cache seeds during the peak of fruit production, and use their hoardings later, when fruits and seeds are scarcer (Smythe 1978). Forget and colleagues (2002) showed that, in Barro Colorado Island (Panama), such temporal variation in scatter-hoarding behavior correlates well with temporal variation in fruit abundance However, their work was a compilation of results from four different studies, conducted with four different plant species and species-specific variations cannot be excluded as an alternative explanation.

The present study confirms that there is temporal variation in fruit production of eleven large-seeded species in a Central Amazonian forest. The study further shows a temporal correlation between fruit production and scatter-hoarding patterns. At *BDFFP*, large-seeded trees have more individuals fruiting during the peak of the rainy season (February-March), with a monotonic decrease until the dry season (July-August). As a response, agoutis (*D. leporina*) and acouchies (*M. acouchy*) scatter-hoard more seed of a palm tree (*A. aculeatum*) during the rainy season (March-April), and eat most of the seeds during the dry season (August-September). As expected, agoutis and acouchies are responding to changes in fruit abundance by shifting their scatter-hoarding levels depending on the availability of fresh food.

Fruit and seed production also vary locally in tropical forests (Loiselle and Blake 1993, Curran and Leighton 2000, Wright et al. 2005) mostly because of low density (Pitman et al. 2001) and the patchy distribution of many of the trees present in these forests. Once again, animals are expected to respond to such patchiness of resource distribution. However, as opposed to behavioral responses to temporal changes, responses to spatial variation in resource abundance are mostly in terms of numbers, as shown by Loiselle and Blake (1993) for understory frugivorous birds in Costa Rica, and myself (Jorge and Peres 2005) for agoutis and Brazil nut trees in Brazil. At *BDFFP*, I detected significant local variation in fruit production among three sites five to ten kilometers apart from one another and abundances of agoutis and acouchies responded accordingly.

Finally, the hypothesis that forest fragmentation may disrupt patterns of fruit abundance was not supported by the present study. The number of individuals fruiting of 67 species of large-seeded trees was similar in fragments of two sizes (one and ten-hectares) and continuous forest when numbers are corrected for area. Laurance and colleagues (2003) found similar results. Out of 11 tree species surveyed, only one (*Swartzia reticulata*, Fabaceae) showed negative effects of fruit production related to proximity to forest edges at *BDFFP*. This lack of effect may be the result of the age of the fragments. Fragments at *BDFFP* are only 25 years old and may be too young to show any disruption of fruit production. Moreover, it is important to point out that in the current chapter, I presented results only for the number of trees fruiting. It is possible that the number of fruits per tree is changing, and that should be assessed in order to have a more complete picture of the effects of forest fragmentation on overall fruit production.

Even though number of trees fruiting was not affected by forest fragmentation, animal abundances and scatter-hoarding levels were. Acouchies decreased in numbers as forest patch decreased in size, whereas agoutis did not. That seems to be a consequence of differential abilities of the two rodent species to cross and use the matrix. As for the seeds, the two rodent species ate more seeds of *A. aculeatum* in one-hectare fragments and cached more in ten-hectare fragments. Nevertheless, scatter-hoarding proportions do not correspond to the abundance of fruits per animal. So, it is still an open question as why agoutis and acouchies scatter-hoard fewer seeds in one-hectare fragments and more seeds in ten-hectare fragments.

To explain the distinct results from one-hectare and ten-hectare fragments, some possibilities can be raised. In one-hectare, agoutis are the only visitors of the two scatter-hoarding species. It is possible that they are eating most of the seeds inside the fragments, but still caching many of them outside the fragments. The other possibility is that indeed, the levels of hunger are so high that they cannot afford to cache some of the seeds that they find. On the other hand, in ten-hectare, most seeds are cached. A plausible explanation is that competition from other seed eaters (e.g. *Proechimys*) may be higher. By caching they may guarantee that the seeds will be available later. What is clear from the present study is that effects of forest fragmentation on scatter-hoarding dynamics are not trivial. Clearly, the important factors that influence the dynamics in ten-hectare fragments are not the same that influence the dynamics in smaller one-hectare fragments. To fully understand the influences of forest size on scatter-hoarding dynamics, it seems fundamental to look at other aspects of the dynamics, and not only the abundance of resources. Two aspects that may be playing important roles in the system studied here are

competitive pressure from other seed eaters (in ten-hectare fragments), and dynamics of

the matrix that surrounds the one-hectare fragments.

CITED LITERATURE

Achard, F., H. D. Eva, H. J. Stibig, P. Mayaux, J. Gallego, T. Richards, and J. P. Malingreau. 2002. Determination of deforestation rates of the world's humid tropical forests. Science **297**:999-1002.

Adler, G. H. 1998. Impacts of resource abundance on populations of a tropical forest rodent. Ecology **79**:242-254.

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons, Inc., New York.

Aizen, M. A., and P. Feinsinger. 1994. Habitat fragmentation, native insect pollinators, and feral honey-bees in Argentine Chaco Serrano. Ecological Applications **4**:378-392.

Almeida, S., and P. J. Dantas da Silva. 1997. As palmeiras: aspectos botânicos, ecológicos e econômicos. Pages 235-251 *in* P. L. B. Lisboa, editor. Caxiuanã. Museu Goeldi, Belém.

Asquith, N. M., J. Terborgh, A. E. Arnold, and C. M. Riveros. 1999. The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. Journal of Tropical Ecology **15**:229-235.

Asquith, N. M., S. J. Wright, and M. J. Clauss. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology **78**:941-946.

Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita. 2001. Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven.

Bierregaard, R. O., and P. C. Stouffer. 1997. Understory birds and the dynamic habitat mosaics in Amazonian rainforests. Pages 616 *in* L. W. F. and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management and conservation of fragmented communities. Chicago University Press, Chicago.

Brewer, S. W., and M. Rejmanek. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. Journal of Vegetation Science **10**:165-174.

Brewer, S. W., and M. A. H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. Oikos **93**:32-41.

Brodin, A., and C. W. Clark. 1997. Long-term hoarding in the Paridae: A dynamic model. Behavioral Ecology **8**:178-185.

Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. Trends in Ecology & Evolution **9**:214-217.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundances of biological populations. Chapman and Hall, London.

Chiarello, A. G. 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biological Conservation **89**:71-82.

Clark, C. W. 1994. Antipredator behavior and the Asset-protection principle. Behavioral Ecology **5**:159-170.

Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences of the United States of America **100**:14052-14056.

Curran, L. M., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. Ecological Monographs **70**:101-128.

Daly, M., L. F. Jacobs, M. I. Wilson, and P. R. Behrends. 1992. Scatter-hoarding by Kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. Behavioral Ecology **3**:102-111.

Damuth, J. 1981. Population density and body size in mammals. Nature **290**:699-700.

de Castro, E. B. V., and F. A. S. Fernandez. 2004. Determinants of differential extinction vulnerabilities of small mammals in Atlantic forest fragments in Brazil. Biological Conservation **119**:73-80.

Dearing, M. D. 1997. The manipulation of plant toxins by a food-hoarding herbivore, *Ochotona princeps*. Ecology **78**:774-781.

Diamond, J. L. 1984. "Normal" extinctions of isolated populations. Pages 191-246 *in* M. H. Nitecki, editor. Extinctions. University of Chicago Press, Chicago.

Dubost, G. 1988. Ecology and social-life of the red acouchy, *Myoprocta exilis*: comparison with the orange-rumped agouti, *Dasyprocta leporina*. Journal of Zoology **214**:107-123.

Dubost, G., and O. Henry. 2006. Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. Journal of Tropical Ecology **22**:641-651.

FAO 2005. Global forest resources assessment: Progress towards sustainable forest management. Food and Agriculture Organization.

Feer, F., C. Julliot, B. Simmen, P. M. Forget, F. Bayart, and S. Chauvet. 2001. Recruitment, a multi-stage process with unpredictable result: the case of a Sapotaceasae in French Guianan forest. Revue D'Ecologie-La Terre et La Vie **56**:119-145.

Fleming, T. H. 1992. How do fruit- and nectar-feeding birds and mammals track their food resources. Pages 355-393 *in* M. D. Hunter, T. Ohgushi, and P. W. Price, editors. Effects of resource distribution on animal-plant Interactions. Academic Press, San Diego.

Forget, P. M. 1990. Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. Journal of Tropical Ecology **6**:459-468.

Forget, P. M. 1991. Scatter-hoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparison with *Myoprocta exilis*. Tropical Ecology **32**:155-167.

Forget, P. M. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). Biotropica **24**:408-414.

Forget, P. M. 1993. Postdispersal predation and scatter-hoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. Oecologia **94**:255-261.

Forget, P. M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. Journal of Tropical Ecology **12**:751-761.

Forget, P. M., D. S. Hammond, T. Milleron, and R. Thomas. 2002. Seasonality of fruiting and food hoarding by rodents in Neotropical forests: Consequences for seed dispersal and seedling recruitment. Pages 241-266 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York.

Forget, P. M., and T. Milleron. 1991. Evidence for secondary seed dispersal by rodents in Panama. Oecologia **87**:596-599.

Forget, P. M., T. Milleron, and F. Feer. 1998. Patterns in post-dispersal seed removal by Neotropical rodents and seed fate in relation to seed size. Pages 25-49 *in* D. M. Newbery, P. H. T. T., and N. D. Brown, editors. Dynamics of tropical communities. Blackwell Science, Oxford.

Forget, P. M., E. Munoz, and E. G. Leigh. 1994. Predation by rodents and bruchid beetles on seeds of *Scheelea* Palms on Barro Colorado Island, Panama. Biotropica **26**:420-426.

Forget, P. M., and S. B. Vander Wall. 2001. Scatter-hoarding rodents and marsupials: convergent evolution on diverging continents. Trends in Ecology & Evolution **16**:65-67.

Foster, R. B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. Pages 151-172 *in* E. G. Leigh, A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical rainforest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington D.C.

Foster, S. A., and C. H. Janson. 1985. The relationship between seed size and establishment conditions in Tropical woody plants. Ecology **66**:773-780.

Gehring, T. M., and R. K. Swihart. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological Conservation **109**:283-295.

Gentry, A. H. 1988. Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Sciences of the United States of America **85**:156-159.

Gentry, A. H., and L. H. Emmons. 1987. Geographical variation in fertility, phenology, and composition of the understory of Neotropical forests. Biotropica **19**:216-227.

Gerber, L. R., O. J. Reichman, and J. Roughgarden. 2004. Food hoarding: future value in optimal foraging decisions. Ecological Modelling **175**:77-85.

Gilbert, L. E. 1980. Food web organization and the conservation of Neotropical diversity. Pages 11–33 *in* B. A. Wilcox, editor. Conservation Biology: An evolutionary-ecological perspective. Sinauer Associates, Sunderland.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19-34 *in* M. E. Soulé, editor. Conservation Biology: the science of scarcity and diversity. Sinauer Associates, Sunderland.

Guariguata, M. R., J. J. R. Adame, and B. Finegan. 2000. Seed removal and fate in two selectively logged lowland forests with contrasting protection levels. Conservation Biology **14**:1046-1054.

Guariguata, M. R., H. Arias-Le Claire, and G. Jones. 2002. Tree seed fate in a logged and fragmented forest landscape, northeastern Costa Rica. Biotropica **34**:405-415.

Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): The inheritors of guapinol (*Hymenaea courbaril*, Leguminosae). Pages 285-304 *in* A. Estrada and T. H. Fleming, editors. Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht.

Hammond, D. S., and V. K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet Neotropical forests. Ecology **76**:2544-2561.

Hammond, D. S., V. K. Brown, and R. Zagt. 1999. Spatial and temporal patterns of seed attack and germination in a large-seeded Neotropical tree species. Oecologia **119**:208-218.

Hansen, M. C., and R. S. DeFries. 2004. Detecting long-term global forest change using continuous fields of tree-cover maps from 8-km advanced very high resolution radiometer (AVHRR) data for the years 1982-99. Ecosystems **7**:695-716.

Henderson, A., G. Galeano, and R. Bernal. 1995. Field guide to the palms of the Americas. Princeton University Press, Princeton.

Henry, O. 1999. Frugivory and the importance of seeds in the diet of the orange-rumped agouti (*Dasyprocta leporina*) in French Guiana. Journal of Tropical Ecology **15**:291-300.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada **45**:1-60.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13**:201-228.

Howell, A. B. 1926. Voles of the genus *Phenacomys* II. Life history of the red tree mouse (*Phenacomis longicaudus*). North American Fauna **48**:39-64.

INPE 2002. Monitoramento da floresta amazônica brasileira por satélite. Instituto Nacional de Pesquisas Espaciais, São José dos Campos.

Jaeger, M. M. 1982. Feeding pattern in *Peromyscus maniculatus*: the response to periodic food deprivation. Physiology & Behavior **28**:83-88.

James, P. C., and N. A. M. Verbeek. 1984. Temporal and energetic aspects of food storage in Northwestern crows. Ardea **72**:207-215.

Jansen, P. A., M. Bartholomeus, F. Bongers, J. A. Elzinga, J. D. Ouden, and S. E. V. Wieren. 2002. The role of seed size in dispersal by scatter-hoarding rodent. Pages 209-226 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York.

Jansen, P. A., F. Bongers, and H. H. T. Prins. 2006. Tropical rodents change rapidly germinating seeds into long-term food supplies. Oikos **113**:449-458.

Jorge, M. L. S. P. 2000. Área de vida, atividade diária e densidade populacional de cotias na Estação de Pesquisas Pinkaiti - Amazônia oriental (SE-Pará). M.Sc. Thesis. Universidade de São Paulo, São Paulo.

Jorge, M. S. P., and C. A. Peres. 2005. Population density and home range use of red-rumped agoutis (*Dasyprocta leporina*) within and outside a natural Brazil-nut stand in South-eastern Amazonia. Biotropica **37(2)**:317-322.

Kawn, F., and J. Granville. 1992. Palms in forest ecosystems of Amazonia. Spring Verlag, Heidelberg.

Kollmann, J., and M. Buschor. 2003. Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. Plant Ecology **164**:249-261.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian Tropical rainforest mammals. Conservation Biology **5**:79-89.

Laurance, W. F. 2005. The alteration of biotic interactions in fragmented tropical forests. Pages 441-457 *in* D. F. R. P. Burslem, P. M. A., and H. S. E., editors. Biotic interactions in the Tropics: their role in the maintenance of species diversity. Cambridge University Press, Cambridge, UK.

Laurance, W. F., and R. O. Bierregaard. 1997. Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago.

Laurance, W. F., M. A. Cochrane, S. Bergen, P. M. Fearnside, P. Delamonica, C. Barber, S. D'Angelo, and T. Fernandes. 2001a. The future of the Brazilian Amazon. Science **291**:438-439.

Laurance, W. F., P. Delamonica, S. G. Laurance, H. L. Vasconcelos, and T. E. Lovejoy. 2000. Conservation - Rainforest fragmentation kills big trees. Nature **404**:836-836.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-De Merona, and S. G. Laurance. 1998. Rainforest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032-2040.

Laurance, W. F., J. Merona, A. Andrade, S. G. Laurance, S. D'Angelo, T. E. Lovejoy, and H. L. Vasconcelos. 2003. Rainforest fragmentation and the phenology of Amazonian tree communities. Journal of Tropical Ecology **19**:343-347.

Laurance, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001b. Rainforest fragmentation and the structure of Amazonian liana communities. Ecology **82**:105-116.

Leaver, L., and M. Daly. 1998. Effects of food preference on scatter-hoarding by kangaroo rats (*Dipodomys merriami*). Behaviour **135**:823-832.

Leaver, L. A. 2004. Effects of food value, predation risk, and pilferage on the caching decisions of *Dipodomys merriami*. Behavioral Ecology **15**:729-734.

Lima, S. L., and T. J. Valone. 1986. Influence of predation risk on diet selections - a simple example in the gray squirrel. Animal Behaviour **34**:536-544.

Loiselle, B. A., and J. G. Blake. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a Neotropical lowland wet forest. Vegetatio **108**:177-189.

Lucas, J. R., and L. R. Walter. 1991. When should chickadees hoard Food - theory and experimental results. Animal Behaviour **41**:579-601.

Mackay, W. P., and E. E. Mackay. 1984. Why do harvester ants store seeds in their nests. Sociobiology **9**:31-47.

Malcolm, J. R. 1997. Biomass and diversity of small mammals in Amazonian forest fragments. Pages 207-221 *in* W. F. Laurance and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago.

Morris, D. W. 1962. The behaviour of the green acouchy (*Myoprocta pratti*) with special reference to scatter-hoarding. Proceedings of the Zoological Society of London **139**:701-733.

Nason, J. D., and J. L. Hamrick. 1997. Reproductive and genetic consequences of forest fragmentation: Two case studies of Neotropical canopy trees. Journal of Heredity **88**:264-276.

Oliveira, A. A., and S. A. Mori. 1999. A Central Amazonian terra firme forest I. High tree species richness on poor soils. Biodiversity and Conservation **8**:1219-1244.

Peres, C. A. 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical Primates **7**:11-16.

Peres, C. A., and C. Baider. 1997. Seed dispersal, spatial distribution and population structure of Brazil-nut trees (*Bertholletia excelsa*) in southeastern Amazonia. Journal of Tropical Ecology **13**:595-616.

Pesce, C. 1985. Oil palms and other oil seeds of the Amazon. Algonac, Michigan.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist **132**:757-785.

Pitman, N. C. A., J. W. Terborgh, M. R. Silman, P. Nunez, D. A. Neill, C. E. Ceron, W. A. Palacios, and M. Aulestia. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology **82**:2101-2117.

Pravosudov, V. V., and J. R. Lucas. 2001. Daily patterns of energy storage in food-caching birds under variable daily predation risk: a dynamic state variable model. Behavioral Ecology and Sociobiology **50**:239-250.

Pruett Jones, M. A., and S. G. Pruett Jones. 1985. Food caching in the Tropical frugivore, Macgregor bowerbird (*Amblyornis macgregoriae*). Auk **102**:334-341.

Pulliam, H. R. 1974. Theory of optimal diets. American Naturalist **108**:59-74.

Salm, R. 2006. Invertebrate and vertebrate seed predation in the Amazonian palm *Attalea maripa*. Biotropica **38**:558-560.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio **108**:15-29.

Seeley, T. D. 1985. Honeybee ecology: a study of adaptation in social life. Princeton University Press, Princeton.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. Bioscience **31**:131-134.

Silvius, K. M., and J. M. V. Fragoso. 2003. Red-rumped agouti (*Dasyprocta leporina*) home range use in an Amazonian forest: implications for the aggregated distribution of forest trees. Biotropica **35**:74-83.

Smythe, N. 1978. The natural history of the Central American agouti (*Dasyprocta punctata*). Smithsonian Contributions to Zoology **257**:1-52.

Smythe, N. 1986. Competition and resource partitioning in the guild of Neotropical terrestrial frugivorous mammals. Annual Review of Ecology and Systematics **17**:169-188.

Smythe, N. 1989. Seed survival in the palm *Astrocaryum standlenyanum*: evidence for dependence upon its seed dispersers. Biotropica **21**:50-56.

Steele, M. A., S. Manierre, T. Genna, T. A. Contreras, P. D. Smallwood, and M. E. Pereira. 2006. The innate basis of food-hoarding decisions in grey squirrels: evidence for behavioural adaptations to the oaks. Animal Behaviour **71**:155-160.

Stevens, T. A., and J. R. Krebs. 1986. Retrieval of stored seeds by Marsh tits *Parus palustris* in the field. Ibis **128**:513-525.

Tabarelli, M., W. Mantovani, and C. A. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. Biological Conservation **91**:119-127.

Terborgh, J. 1974. Preservation of natural diversity: problem of extinction prone species. Bioscience **24**:715-722.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1923-1926.

Terborgh, J., L. Lopez, J. Tello, D. Yu, and R. Bruni. 1997. Transitory states in relaxing ecosystems of land bridge islands. Pages 256-274 *in* L. W. F. and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago.

Terborgh, J., E. Losos, M. P. Riley, and M. B. Riley. 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. Vegetatio **108**:375-386.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119-133 *in* M. E. Soule, editor. Conservation Biology: an ecological-evolutionary perspective. Sinauer, Sunerland.

Theimer, T. C. 2005. Rodent scatterhoarders as conditional mutualists. Pages 283-295 *in* P.-M. Forget, J. E. Lambert, P. E. Hulme and S. B. Vander Wall, editors. Seed fate. CABI International, Wallingford.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2003. Distance 4.1. Release 2. *in*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Thompson, D. C., and P. S. Thompson. 1980. Food habits and caching Behavior of urban grey squirrels. Canadian Journal of Zoology – Revue Canadienne de Zoologie **58**:701-710.

Toates, F. M. 1978. Circadian-rhythm of hoarding in hamster. Animal Behaviour **26**:631-631.

Uhl, C., and J. Dransfield. 1987. Genera Palmarum. Allen Press.

Valencia, R., H. Balslev, and G. P. Y. Mino. 1994. High tree alpha-diversity in Amazonian Ecuador. Biodiversity and Conservation **3**:21-28.

Vander Wall, S. B. 1988. Foraging of Clark nutcrackers on rapidly changing pine seed resources. Condor **90**:621-631.

Vander Wall, S. B. 1990. Food hoarding in animals. The University of Chicago Press, Chicago.

Voss, R. S., and L. H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bulletin of the American Museum of Natural History:3-115.

Voss, R. S., D. P. Lunde, and N. B. Simmons. 2001. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna - part 2. Non-volant species. Bulletin of the American Museum of Natural History:3-236.

Wenny, D. G. 1999. Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. Journal of Tropical Ecology **15**:481-496.

Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a Neotropical montane tree. Ecological Monographs **70**:331-351.

Wolff, J. O., and G. C. Bateman. 1978. Effects of food availability and ambient temperature on torpor cycles of *Perognathus flavus* (Heteromyidae). Journal of Mammalogy **59**:707-716.

Wright, S. J., and H. C. Duber. 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. Biotropica **33**:583-595.

Wright, S. J., H. C. Muller-Landau, O. Calderon, and A. Hernandez. 2005. Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. Ecology **86**:848-860.

Wright, S. J., H. Zeballos, I. Dominguez, M. M. Gallardo, M. C. Moreno, and R. Ibanez. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. Conservation Biology **14**:227-239.

Ximenes, G. E. I. 1999. Sistemática da família Dasyproctidae Bonaparte, 1838 (Rodentia, Histricognathi) no Brasil. M.Sc. Thesis. Universidade de São Paulo, São Paulo.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice Hall, New Jersey.

Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology **15**:523-533.

VI. APPENDICES

Appendix A: deriving caching isolegs for short-term caching

Here I derive the caching isoleg for the short-term caching scenario (Chapter II, *Three Scenarios* Section). In this scenario, as explained in the text (Chapter II, Scenario Description Section), total energy gained is defined by:

$$G_T(I) = G_1 + G_{2a} + G_{2b},$$ (A.I.1)

Where

$$G_1 = \frac{aR_1e_e\,(1-\mu)}{1 + aR_1[(1-\mu)h_e + \mu h_c]} * T$$ (A.I.2)

is the energy gained in period 1, after taking into account items cached (μ);

$$G_{2a} = \frac{aR_1e_c\mu}{1 + aR_1[(1-\mu)h_e + \mu h_c]} * T$$ (A.I.3)

is the energy gained in period 2 from the cached items; and

$$G_{2b} = \frac{aR_2e_e}{1 + aR_2h_e} * \left[T - \left(\frac{aR_1\mu h_e}{1 + aR_1[(1-\mu)h_e + \mu h_c]} * T \right) \right]$$ (A.I.4)

is the energy gained in period 2 from the environment.

To derive the isoleg, we evaluate the derivative of total energy gained with respect to caching: $\frac{\partial G_T(I)}{\partial \mu}$. Since the function of total energy gain is the sum of the energy gained

Appendix A (continued)

in the three harvesting functions (A.I.2, A.I.3, and A.I.4), the derivative of the total

energy gained is the sum of the derivative of the three harvesting functions:

$$\frac{\partial G_T(I)}{\partial \mu} = \frac{\partial G_1}{\partial \mu} + \frac{\partial G_{2a}}{\partial \mu} + \frac{\partial G_{2b}}{\partial \mu},$$

(A.I.5)

Taking the derivatives yields to:

$$\frac{\partial G_1}{\partial \mu} = -\frac{aR_1e_eT(1+aR_1h_c)}{\left[1+aR_1(h_e(1-\mu)+h_c\mu\right]^2},$$

(A.I.6)

$$\frac{\partial G_{2a}}{\partial \mu} = \frac{aR_1e_cT(1+aR_1h_e)}{\left[1+aR_1(h_e(1-\mu)+h_c\mu\right]^2},$$

(A.I.7)

$$\frac{\partial G_{2b}}{\partial \mu} = \frac{a^2R_1R_2e_eT(1+aR_1h_e)}{\left(1+aR_2h_e\right)\left[1+aR_1(h_e(1-\mu)+h_c\mu\right]^2}.$$

(A.I.8)

Adding the three derivatives (A.I.6, A.I.7, and A.I.8) yields to the derivative of the

total energy gained as:

$$\frac{\partial G_T(I)}{\partial \mu} = \frac{\left[\begin{array}{l} a^2R_1R_2e_eT(1+aR_1h_e)+ \\ (1+aR_2h_e)[aR_1T[e_c(1+aR_1h_e)-e_e(1+aR_1h_c)]] \end{array}\right]}{\left(1+aR_2h_e\right)\left[1+aR_1(h_e(1-\mu)+h_c\mu\right]^2}.$$

(A.I.9)

$\frac{\partial G_T(I)}{\partial \mu} = 0$ defines the maximum energy gain. At $\mu^* = 0$, $\left.\frac{\partial G_T(I)}{\partial \mu}\right|_{\mu=0} = 0$ defines the

curve that separates no caching from some caching, or the **some-caching isoleg**. When

<u>Appendix A (continued)</u>

$\left.\frac{\partial G_T(I)}{\partial \mu}\right|_{\mu=0} > 0$ the forager should eat everything, and when $\left.\frac{\partial G_T(I)}{\partial \mu}\right|_{\mu=0} < 0$ the forager

should cache some. At $\mu^* = 1$, $\left.\frac{\partial G_T(I)}{\partial \mu}\right|_{\mu=1} = 0$ defines the curve that separates some

caching from caching everything, or the **all-caching isoleg**. When $\left.\frac{\partial G_T(I)}{\partial \mu}\right|_{\mu=1} > 0$ the

forager should cache some, and when $\left.\frac{\partial G_T(I)}{\partial \mu}\right|_{\mu=1} < 0$ the forager should cache everything.

In this Scenario, $\frac{\partial G_T(I)}{\partial \mu} = 0$ is independent of μ, meaning that there is no interior

solution, or, in other words, no intermediate levels of caching. The best strategy is either

no-caching or **all-caching** with one isoleg defining the threshold between the two

strategies:

$$R_2 = \frac{e_e(1+aR_1 h_c) - e_c(1+aR_1 h_e)}{ah_e[e_c(1+aR_1 h_e) - e_e(2+aR_1(h_c+h_e))]}. \tag{A.I.10}$$

Appendix B: deriving caching isolegs for long-term caching

Here I derive the caching isoleg for the long-term caching scenario (Chapter II, Three Scenarios Section). In this scenario, total energy gained is defined by:

$$G_T(II) = G_1^{\alpha} * \left(G_{2a} + G_{2b}\right)^{\beta},$$ (A.II.1)

where G_1, G_{2a}, and G_{2b} are the same as for short-term caching (A.I.2, A.I.3, and A.I.4 respectively).

Following the same steps of *Scenario I*, I evaluate the derivate of total energy gained with respect to caching: $\dfrac{\partial G_T(II)}{\partial \mu}$. Nevertheless, in this *Scenario*, total energy gained is the product of the energy gained in each period. Therefore, the influence of caching on the forager's energy gain yields to a more complex derivative function:

$$\frac{\partial G_T(II)}{\partial \mu} = G_1^{\alpha-1}\left(G_{2a} + G_{2b}\right)^{\beta-1}\left[\alpha\left(G_{2a} + G_{2b}\right)\frac{\partial G_1}{\partial \mu} + \beta\, G_1\left(\frac{\partial G_{2a}}{\partial \mu} + \frac{\partial G_{2b}}{\partial \mu}\right)\right],$$ (A.II.2)

where $\dfrac{\partial G_1}{\partial \mu}$, $\dfrac{\partial G_{2a}}{\partial \mu}$ and $\dfrac{\partial G_{2b}}{\partial \mu}$ are the same expressions that were derived for short-term caching scenario (A.I.6, A.I.7, and A.I.8).

Once again, I evaluate $\dfrac{\partial G_T(II)}{\partial \mu} = 0$ and isolate $\mu*$ in order to determine the isolegs that will separate the **no-caching** from **some-caching** from **all-caching**:

Appendix B (continued)

$$\mu = \frac{(1 + aR_1h_e)\left[\beta R_1(e_c(1 + aR_2h_e) - e_e aR_2h_e) - \alpha\, e_e R_2(1 + aR_1h_c)\right]}{\beta R_1(1 + aR_1h_e)(e_c(1 + aR_2h_e) - e_e aR_2h_e) + \alpha(1 + aR_1h_c)\left[e_c R_1(1 + aR_2h_e) + e_e R_2(aR_1h_c + 2aR_1h_e)\right]}. \qquad \text{(A.II.3)}$$

At $\mu = 0$ (some-caching isoleg):

$$R_2 = \frac{\beta\, e_c R_1}{\beta\, aR_1h_e(e_e - e_c) + \alpha\, e_e(1 + aR_1h_c)}. \qquad \text{(A.II.4)}$$

And at $\mu = 1$ (all-caching isoleg):

$$R_2 = -\frac{e_c R_1}{aR_1(e_c h_e + e_e h_c - e_e h_e) + e_e}. \qquad \text{(A.II.5)}$$

As noticed from expression A.II.5, the **all-caching isoleg** is negative, and negative expressions have no biological meaning in the present model. Therefore only the **some-caching isoleg** will be further used to investigate the dynamics of caching behavior in long-term caching (Chapter II, Results).

Appendix C: deriving caching isolegs for caching under predation risk

Here I will derive the caching isoleg for the caching under predation risk scenario (Chapter II, Three Scenarios Section). In this scenario, total energy gained is defined by:

$$G_T(III) = e^{-T(q_1\gamma_1 + q_2\gamma_2)} * \left[G_1 + G_{2a} + G_{2b} \right],$$

(A.III.1)

where $\dfrac{\partial G_1}{\partial \mu}$, $\dfrac{\partial G_{2a}}{\partial \mu}$ and $\dfrac{\partial G_{2b}}{\partial \mu}$ are the same expressions that were derived for short-term caching (A.I.6, A.I.7, and A.I.8), and time spent searching in periods one and two are defined by:

$$q_1 = \frac{1}{1 + aR_1\left[h_e(1-\mu) + h_c\mu\right]},$$

(A.III.2)

$$q_2 = \left[\frac{1}{1 + aR_2 h_e} \right] * \left[\frac{1 + aR_1\left[h_e(1-2\mu) + h_c\mu\right]}{1 + aR_1\left[h_e(1-\mu) + h_c\mu\right]} \right].$$

(A.III.3)

Following the steps of *Scenario I* and *II*, I evaluate the derivate of total energy gain with respect to caching ($\dfrac{\partial G_T(III)}{\partial \mu}$) which yields to:

$$\frac{\partial G_T(III)}{\partial \mu} = e^{-(\gamma_1 q_1 + \gamma_2 q_2)}\left[\left(\frac{\partial G_1}{\partial \mu} + \frac{\partial G_{2a}}{\partial \mu} + \frac{\partial G_{2b}}{\partial \mu} \right) - T\left(G_1 + G_{2a} + G_{2b}\right)\left(\gamma_1 \frac{\partial q_1}{\partial \mu} + \gamma_2 \frac{\partial q_2}{\partial \mu} \right) \right],$$

(A.III.4)

Appendix C (continued)

where $\dfrac{\partial G_1}{\partial \mu}$, $\dfrac{\partial G_{2a}}{\partial \mu}$ and $\dfrac{\partial G_{2b}}{\partial \mu}$ are the same of those of for short-term and long-term

caching scenarios (A.I.6, A.I.7, and A.I.8), and the derivatives for search time are defined

as follows:

$$\frac{\partial q_1}{\partial \mu} = \frac{aR_1(h_e - h_c)}{[1 + aR_1(h_e(1-\mu) + h_c\mu]^2} ,$$ (A.III.5)

$$\frac{\partial q_2}{\partial \mu} = \frac{aR_1 h_e(1 + aR_1 h_e)}{(1 + aR_2 h_e)[1 + aR_1(h_e(1-\mu) + h_c\mu]^2} .$$ (A.III.6)

Due to exponential nature of energy gain in this scenario (A.III.1), $\mu*$ and the

derived isolegs are long and complex. Nevertheless, many terms are repeated through

out. Therefore, for simplicity of notation, they will be substituted as follows:

$A = aR_1 h_c;\ B = aR_1 h_e;\ C = aR_1 e_c;\ D = aR_1 e_e;\ E = aR_2 h_e;\ and\ F = aR_1 e_e.$

Once again, I evaluate $\dfrac{\partial G_T(III)}{\partial \mu} = 0$ and isolate $\mu*$ in order to determine the isolegs

that will separate the **no-caching** from **some-caching** from **all-caching**:

$$\mu = \frac{\begin{array}{l}T[D(1+E)+F(1+B)][\gamma_1(B-A)(1+E)-\gamma_2 B(1+B)]\\ -(1+B)(1+E)[(1+E)[C(1+B)-D(1+A)]-DE(1+B)]\end{array}}{\begin{array}{l}(A-B)(1+E)[(1+E)[C(1+B)-D(1+A)]-DE(1+B)]\\ -T[(C-D)(1+E)+F(A-2B)][\gamma_1(B-A)(1+E)-\gamma_2 B(1+B)]\end{array}} .$$ (A.III.7)

Appendix C (continued)

The function that defines $\mu*$ is quadratic; therefore each isoleg is defined by two functions. The **some-caching isolegs** (at $\mu = 0$) are defined by:

$$R_2 = \frac{\left(\begin{array}{l} -2e_c h_e (1+B)^2 \\ -\sqrt{e_e}(1+B) \\ \sqrt{ \begin{array}{l} e_e \left(\begin{array}{l} h_e(1+B) \\ -T\gamma_1(h_c - h_e) \end{array} \right)^2 + 2T\gamma_2 h_e \left(\begin{array}{l} h_e(1+B)(2e_c(1+B) - e_e(3+2A)) \\ +T\gamma_1 e_e (h_c - h_e)(1+2B) \end{array} \right) \\ +e_e (T\gamma_2 h_e)^2 (1+2B)^2 \\ +e_e \left(\begin{array}{l} h_e B(2(2+A) + 3T(\gamma_1 - \gamma_2)) + h_e(B)^2(1-2T\gamma_2) \\ +h_e(3+A(2-3T\gamma_1) + T(\gamma_1 - \gamma_2)) - T\gamma_1 h_c \end{array} \right) \end{array} } \end{array} \right)}{2ah_e \left(\begin{array}{l} h_e(1+B)(e_c(1+B) - e_e(2+A+B)) \\ +T\gamma_1 e_e (h_c - h_e)(1+2B) \end{array} \right)}$$

(A.III.8)

and

$$R_2 = \frac{\left(\begin{array}{l} -2e_c h_e (1+B)^2 \\ + \sqrt{e_e} \left(\begin{array}{l} (1+B) \\ \sqrt{ \begin{array}{l} e_e \left(\begin{array}{l} h_e(1+B) \\ -T\gamma_1(h_c - h_e) \end{array} \right)^2 + 2T\gamma_2 h_e \left(\begin{array}{l} h_e(1+B)(2e_c(1+B) - e_e(3+2A)) \\ +T\gamma_1 e_e (h_c - h_e)(1+2B) \end{array} \right) \\ +e_e (T\gamma_2 h_e)^2 (1+2B)^2 \end{array} } \\ + \sqrt{e_e} \left(\begin{array}{l} h_e B(2(2+A) + 3T(\gamma_1 - \gamma_2)) + h_e(B)^2(1-2T\gamma_2) \\ +h_e(3+A(2-3T\gamma_1) + T(\gamma_1 - \gamma_2)) - T\gamma_1 h_c \end{array} \right) \end{array} \right) \end{array} \right)}{2ah_e \left(\begin{array}{l} h_e(1+B)(e_c(1+B) - e_e(2+A+B)) \\ +T\gamma_1 e_e (h_c - h_e)(1+2B) \end{array} \right)}$$

(A.III.9)

Appendix C (continued)

And the **all-caching isolegs** (at $\mu = 1$) are defined by:

$$R_2 = \frac{\left(\begin{array}{l} a^3 R_1^2 h_e \left(h_c \left(e_e (2h_c + h_e) - 2e_c h_e \right) + T\gamma_2 h_e \left(e_e (h_e - h_c) - e_c h_e \right) \right) \\ - a^2 R_1 \left(\begin{array}{l} e_c h_e \left(2(h_c + h_e + T\gamma_1 (h_c - h_e)) + T\gamma_2 h_e \right) \\ + ee \left(T\gamma_1 h_c^2 + h_e^2 (T\gamma_1 - 1) + h_c h_e (T\gamma_2 - 2T\gamma_1 - 5) \right) \end{array} \right) \\ - a \left(2e_c h_e + e_e \left(T\gamma_1 h_c + h_e (T\gamma_2 - T\gamma_1 - 3) \right) \right) \\ - \sqrt{ \begin{array}{l} a^2 \left(\begin{array}{l} \left(e_c h_e \left(\begin{array}{l} 2 + 2aR_1 \left(\begin{array}{l} h_c + h_e + aR_1 h_c h_e \\ + T\gamma_1 (h_c - h_e) \end{array} \right) \\ + T\gamma_2 B(1+B) \end{array} \right) \right. \\ \left. + e_e \left(\begin{array}{l} T\gamma_1 (hc - he)(1 + A - B) \\ - h_e (1+A)(3 + 2A + B) \\ - T\gamma_2 h_e (1+B)(B - A - 1) \end{array} \right) \right) \\ - 4h_e \left(\begin{array}{l} \left(\begin{array}{l} h_e (1+A)(e_c (1+B) - e_e (2 + A + B)) \\ + T\gamma_1 (h_c - h_e)(e_e + e_e (A - B) + e_c B) \end{array} \right) \\ \left(e_c \left(1 + aR_1 \left(\begin{array}{l} h_e + h_c (T\gamma_1 + 1 + B) \\ + T h_e (\gamma_2 B + \gamma_2 - \gamma_1) \end{array} \right) \right) \right. \\ \left. - ee(1+A)^2 \end{array} \right) \end{array} \right) \end{array} } \end{array} \right)}{2a^2 h_e \left(\begin{array}{l} h_e (1+A)(e_c (1+B) - e_e (2 + A + B)) \\ + T\gamma_1 (h_c - h_e)(e_e (1 + A - B) + e_c B) \end{array} \right)} \tag{A.III.10}$$

and

Appendix C (continued)

$$R_2 = \frac{\left(\begin{array}{l} a^3 R_1^2 h_e \left(h_c\left(e_e\left(2h_c+h_e\right)-2e_c h_e\right)+T\gamma_2 h_e\left(e_e\left(h_e-h_c\right)-e_c h_e\right)\right) \\ -a^2 R_1 \left(\begin{array}{l} e_c h_e\left(2\left(h_c+h_e+T\gamma_1\left(h_c-h_e\right)\right)+T\gamma_2 h_e\right) \\ +ee\left(T\gamma_1 h_c^2+h_e^2\left(T\gamma_1-1\right)+h_c h_e\left(T\gamma_2-2T\gamma_1-5\right)\right)\end{array}\right) \\ -a\left(2e_c h_e+e_e\left(T\gamma_1 h_c+h_e\left(T\gamma_2-T\gamma_1-3\right)\right)\right) \\ \quad + \left|a^2 \sqrt{\left(\begin{array}{l}\left(e_c h_e\left(\begin{array}{l}2+2aR_1\left(\begin{array}{l}h_c+h_e+aR_1 h_c h_e \\ +T\gamma_1\left(h_c-h_e\right)\end{array}\right)\\ +T\gamma_2 B(1+B)\end{array}\right)\right.\\ \left.+e_e\left(\begin{array}{l}T\gamma_1\left(hc-he\right)(1+A-B)\\ -h_e(1+A)(3+2A+B)\\ -T\gamma_2 h_e(1+B)(B-A-1)\end{array}\right)\right)\\ -4h_e\left(\begin{array}{l}\left(\begin{array}{l}h_e(1+A)\left(e_c(1+B)-e_e(2+A+B)\right)\\ +T\gamma_1\left(h_c-h_e\right)\left(e_e+e_e(A-B)+e_c B\right)\end{array}\right)\\ \left(e_c\left(1+aR_1\left(\begin{array}{l}h_e+h_c\left(T\gamma_1+1+B\right)\\ +T\,h_e\left(\gamma_2 B+\gamma_2-\gamma_1\right)\end{array}\right)\right)\right)\\ -ee(1+A)^2\end{array}\right)\end{array}\right)}\right|\end{array}\right)}{2a^2 h_e\left(\begin{array}{l}h_e(1+A)\left(e_c(1+B)-e_e(2+A+B)\right)\\ +T\gamma_1\left(h_c-h_e\right)\left(e_e(1+A-B)+e_c B\right)\end{array}\right)} \qquad \text{(A.III.11)}$$

Expressions A.III.9 and A.III.11 only exist in the negative state space of R_1, with no biological meaning in this model. Therefore, they will not be further considered to evaluate the dynamics of caching under predation risk.

VII. VITA

NAME: Maria Luisa da Silva Pinto Jorge

EDUCATION: B.S., Biological Sciences, Universidade de São Paulo, São Paulo, São Paulo, Brazil, 1996

B.S., Secondary Education, Biological Sciences, Universidade de São Paulo, São Paulo, São Paulo, Brazil, 1996

M.Sc.. Ecology, Universidade de São Paulo, São Paulo, São Paulo, Brazil, 2000

Ph.D., Biological Sciences, University of Illinois at Chicago, 2007

TEACHING: Universidade São Francisco, Bragança Paulista, São Paulo, Brazil, Paleontology for Undergraduates, 2000

Escola Estadual Mauro de Oliveira, São Paulo, SP, Brazil, Biology for High School Students, 2000, 2001

Universidade Federal do Amazonas/Instituto Nacional de Pesquisas Amazônicas, Manaus, Brazil, Field course *Fragmentation in the Amazonian Landscape* for Undergraduates:, 2004

Biological Dynamics of Forest Fragments Project – Instituto Nacional de Pesquisas Amazônicas/Smithsonian Institution, Manaus, Brazil, Internship Program for Undergraduates, 2004

Department of Biological Sciences, University of Illinois at Chicago, Chicago, Illinois:
Evolution for Undergraduates, 2002;
Biology of Cells and Organisms for Undergraduates, 2002;
Biology of Populations and Communities for Undergraduates, 2003;
Laboratory of General Ecology for Undergraduates, 2005;
Ecology and Evolution for Undergraduates, 2006, 2007

FELLOWSHIPS: Conselho Nacional de Ciência e Tecnologia, Brazil, B.A. fellowship, 1993-1995

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, M.Sc. fellowship, 1997-1999

Conselho Nacional de Ciência e Tecnologia, Brazil, Ph.D. fellowship, 2001-2005

GRANTS: World Wildlife Foundation-Brazil, 1997

University of Illinois Provost Award, 2003

Biological Dynamics of Forest Fragment Project, Manaus, Brazil, 2003-2005

HONORS: 3rd International Symposium of Frugivory and Seed Dispersal, São Pedro, São Paulo, Brazil, Best poster presentation, 2000

Department of Biological Sciences, University of Illinois at Chicago, Research Achievement, 2006, 2007

MEMBERSHIP: Association of Tropical Biology and Conservation

SERVICE: Journal of Mammalogy, Scientific Reviewer

PUBLICATIONS: Jorge M.S.P. and Peres C.A. 2005. Population density and home range use of red-rumped agoutis (*Dasyprocta leporina*) within and outside a natural Brazil nut stand in South-eastern Amazonia. *Biotropica* 37(2):317-320

Jorge, M.L.S.P. and Velazco P.M. 2006. Mammals. *In* T. S. Schulenberg, C. Vriesendorp, J. I. Rojas, and D. K. Moskovits (editors): *Peru: Sierra del Divisor*. The Field Museum: Rapid Biological Inventories Report Number 17