

Effects of poaching on seed-predatory interactions
of a Neotropical palm.



Consequences for density-dependent mortality?

2007

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The results presented in this report are preliminary. See Jansen et al. (*in prep*) for the definite results of experiments described in this report.

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Abstract

Hunting and poaching have become a major problem in tropical forest conservation (Redford 1992). Many forests have lost most if not all large bird and mammal species and more species may disappear in the future, if human activities like hunting and habitat fragmentation don't decrease (Hughes *et al.* 1997, Thiollay 1999). Because most of the large-bodied species have important ecological functions such as dispersal and predation, their decrease may have major effects on other species present in the same food web. The impact of these effects depends on the complexity of the food web; complex food webs are more stable and will have other species in the same functional group to compensate, while simple food webs might not have this option. A reduction in one species can result in shifts in population sizes of the other species in the same web (Christianou & Ebenman 2004, Borrvall *et al.* 2000). Predators form an important functional group in food webs, because they prevent their prey species from gaining dominance. In tropical forests, seed predators cause the density-dependent mortality that is thought to maintain high tree diversity (Janzen 1970, Connell 1971).

The aim of this study was to assess the effects of mammal poaching on seed predatory interactions in the palm species *Astrocaryum standleyanum*. The web involves one resource, one frugivore and four seed-predators. I determined (1) the functioning of this food web, (2) how reduced mammal abundance affected the interactions within the food web, and (3) how reduced mammal abundance affected the total level of density-dependent seed mortality caused by the seed predators. In the Neotropical forest in Panama, I compared interactions at 3 high and 3 low palm density plots at each of two sites, one without poaching and one with high poaching intensity.

Besides indirect interactions among seed predators via the shared resource, I found complex direct interactions among the frugivore and the seed predators in the food web.

Reduction in mammal abundance changed the infestation rates of three other seed predators. The infestation rate of one predator, a bruchid beetle, increased, while infestation rates of two other predators, scolytid beetles and fungi, decreased. Seed survival increased, as the bruchid beetle did not compensate for the reduction in seed predation by mammals due to poaching. Evidence was found for density-dependent mortality due to a higher seed viability, but could not be lead back to the three non-mammalian seed predators. Thus, hunting indirectly relieved seed predation and reduced density-dependence of seed mortality in this palm species. Enhanced seedling recruitment could lead to an increase in population size of this palm at the cost of other species, and result in a decrease in biodiversity.

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Introduction

Poaching intensity.

Hunting and poaching have become a major problem in the conservation of Neotropical forests (Redford 1992, Peres 2000). Many large herbivores have already gone extinct (Janzen *et al.* 1982a) and a lot more forest fauna is going to disappear in the future, if human activities like hunting and habitat fragmentation don't decrease (Hughes *et al.* 1997, Thiollay 1999, Galetti *et al.* 2006). The estimated number of killings in Neotropical forests by hunters and poachers is around 60 million each year. Although only a third is actually eaten or used for leather, most are wounded through traps and can't be found by the poachers (Redford 1992, Peres 2000).

Preferred game species in the Neotropics are birds and mammals that weigh > 1 kg (Wright 2003), such as monkeys, caiman and herbivores like the capybara, otters, peccaries, deer and agouties (Redford 1992).

Many of these game species have important ecological functions such as dispersing seeds – which allows plant species to escape mortality and colonize new sites – or predating seeds – which may prevent competitive tree species from gaining dominance. A decline in game species populations may change plant population dynamics, which ultimately can result in changing whole ecosystems, its functions and a decrease in biodiversity (Borrvall *et al.* 2000, Silman *et al.* 2003, Wright 2003).

The impact of poaching

The impact of poaching on the community depends on the complexity of the food web these game species are part of. It depends on species richness, the function of the game species and on the number and strengths of the interactions between the species in the same food web (Jonsson & Malmqvist 2003, Christianou & Ebenman 2004).

Complex food webs, compared to simple ones, are usually more stable due to a higher species richness and higher connectivity among them. Many interactions are present, with multiple strong and weak links. An example of a complex food web is the web surrounding the Scotch broom, *Cytisus scoparius* (Memmott *et al.* 2000).

Losing species with many strong interactions usually has a bigger impact than species with fewer, weaker interactions. Disappearance of a single important species with many strong links to other species in the food web can change the entire system (Borrvall *et al.* 2000, Christianou & Ebenman 2004).

To determine the vulnerability of a food web we can start with partitioning the species into two components: the number of functional groups and the number of species per group. A complex food web with more species usually has several species per group. If one species is not able to perform its function, another from the same group will compensate. If species richness is low, there might not be a species present to compensate, a decrease or disappearing of one species could result in losing an entire function. This can lead to shifts in populations of other species in the food web and can even lead to secondary extinctions (Borrvall *et al.* 2000, Eklöf & Ebenman 2006).

When species are lost from a food web, species richness and the number of interactions in the food web decreases, the web loses complexity and becomes more vulnerable to species loss in the future (Eklöf & Ebenman 2006). The food web has entered a negative feedback loop.

Food webs and its important functional groups.

A food web shows the pattern of energy or nutrient flow throughout a community (Chapman & Reiss 1999). It is built up from several functional groups surrounding one or more autotrophic organisms called the primary producer or resource (R). Herbivores (H) consuming the resource are usually preyed upon by one or more Predators (P), which will in turn be preyed upon by other predators. A food web can also contain other functional groups, such as dispersers (D) and parasites (P). The number of species per group determines the complexity of the food web. Predators play an important role in a food web by controlling the population size of their prey species and preventing them from becoming superabundant. Predators can prey on insects or mammals, but also on plants, in which case we refer to them as herbivores (H). Herbivores can prey on the adults, on seedlings or seeds. Herbivores feeding solely on fruit pulp are referred to as frugivores (F).

Seed predation can occur before seeds are dispersed, also called pre-dispersal predation, and after seeds are dispersed, called post-dispersal predation (Janzen 1970). Pre-dispersal predation usually happens before the seeds are completely ripened and the predator can reach the seeds while they are still present in the trees. Examples of pre-dispersal predators in the Neotropics are arboreal invertebrates and mammals like monkeys (Janzen 1970, Whencke *et al.* 2003). Post-dispersal predation happens after the seeds have ripened and dropped to the forest floor, usually by invertebrates and terrestrial mammals such as rodents (Janzen 1970, Smythe 1970).

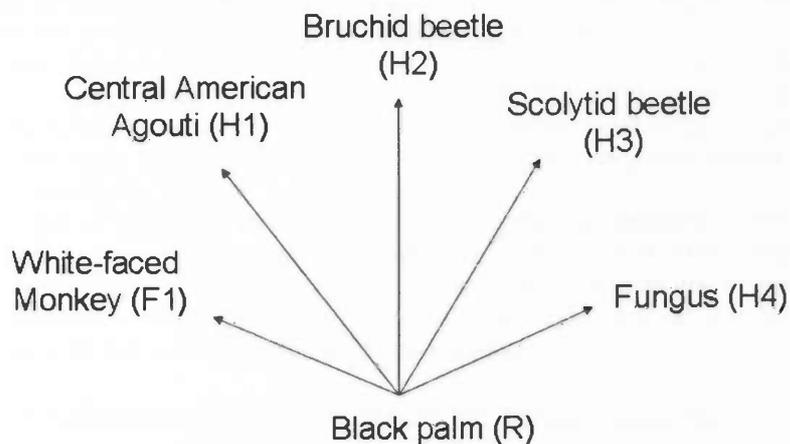
Density-dependent mortality

Seed predators are considered important for maintaining the diversity in tropical forests. Density-dependent mortality caused by seed predators may explain how many different species can co-exist together on a small area without one "strong" species gaining dominance, out-competing all the other species (Connell 1978).

Several mechanisms of density-dependent mortality have been proposed, which all result in preventing the potentially dominant species from monopolizing entire areas (Penfold & Lamb 1999). One mechanism proposed is the accumulation of host-specific pathogens and predators near the adult trees, also called the Janzen-Connell hypothesis (Janzen 1970, Connell 1971, Adler & Muller-Landau 2005). Seeds and seedlings near adults have more chances of being killed by these natural enemies, compared to seeds and seedlings farther away from the tree. This means seeds and seedlings of other species will have a higher survival rate at these sites, resulting in a higher species diversity in the forest. This effect will increase with a species' density; as more adults and consequently more seeds are available at one site, more natural enemies will accumulate, decreasing the chances of survival even further (Janzen 1970).

This study

Here, we study how poaching affects the functioning of a relatively simple seed-predatory food web. Our study system is the Neotropical palm species *Astrocaryum standleyanum* and its fruit- and seed-centered food web, i.e. the species feeding on the seeds/fruits and their interaction with each other (figure 1). This web contains one autotrophic organism as the resource, one frugivore and three seed herbivores. The frugivore and one of the herbivores are mammals. Our aims were (1) to determine how the food web members interact, (2) to determine how a decrease of the two mammals, due to poaching, will affect these interactions, and (3) to determine whether density-dependent seed mortality is affected by the mammal abundance. We did our study in Panama, where high levels of poaching exist. The agouti, an important mammalian seed predator and disperser in this food web, is one of the major game species (Wright *et al.* 2000). White-faced monkeys, the frugivore in the food web, are also hunted heavily (Wright *et al.* 2000). Population levels of these species are seriously reduced at sites with poaching. In this study we conducted two experiments with each several sub-questions, to ultimately answer the main questions.



**Figure 1: the food web of the Neotropical palm species *Astrocaryum standleyanum*.
R=Resource, F=Frugivore and H = Herbivore.**

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Experiment 1: The effect of agouties and monkeys on the scolytid beetle, bruchid beetle and fungus infestation and their interaction.

1. Does pulp removal by white-faced monkeys affect the proportion of bruchids hatching?
2. Does pulp removal increase the accessibility of seeds to scolytid beetles and fungus?
3. Does burial by the agouti affect scolytid and fungus infestation?
4. Does scolytid beetle presence affect the proportion of bruchids hatching?
5. Does the presence of fungus affect the bruchid beetle and scolytid beetle development / infestation?
6. Does poaching and palm abundance have an effect on bruchid, scolytid and fungus infestation?

Expectations:

1. Pulp removal will have a positive effect on the proportion of seeds with hatching bruchids, because the moist fruit pulp keeps the seed from drying which has a negative effect on bruchid larvae development.
2. We expect higher infestation rates in seeds without fruit pulp, the accessibility will increase for both scolytids and fungus.
3. Burial will decrease the accessibility for both scolytid beetles and fungus.
4. The proportion of seeds infested with bruchid beetles decreases as scolytid infestation increases, because the scolytid beetles colonizing the seeds will feed on both the endosperm and on bruchid larvae if present.
5. We expect fungus to access the seeds through the holes drilled by both beetles. This means the fungus infests the seeds after the bruchids have developed and hatched and will not affect the number of bruchids hatching. Scolytids drill holes before the eggs are laid and they will experience a negative effect from the fungus presence.
6. The number of scolytid infestations will be negatively correlated with the palm density, assuming a homogeneous distribution of scolytids. More seeds are available which results in a decrease in the percentage of infestation. If the distribution of scolytids isn't homogeneous, then the number of scolytids will increase with the palm density and infestation rate will increase as well.

Experiment 2: The effect of monkeys and age of the fruits/seeds on the removal time by rodents.

7. Does pulp removal affect the probability of seeds being removed and hoarded by rodents?
8. Does the presence of old, rotting pulp affect seed removal by rodents?
9. Is the removal time affected by palm and mammal abundance?

Expectations:

7. The rodents will consider the mesocarp as a quick bite and will prefer the seeds with the mesocarp still attached.
8. We expect a decrease in preference of the rotting pulp because it's inedible for the rodents.
9. The removal time will decrease with higher palm abundance and increase with mammal abundance.

Methods

Research location

This study was conducted in the Neotropical moist forest in the Republic of Panama. Two sites, separated by the Panama Canal, and located approximately 15 km apart were used for our experiments (figure 2).

The first site was Barro Colorado Island (BCI; 9°09'N, 79°51'O), located in Lake Gatun within the Panama Canal. The second site was Pipeline Road (PLR; 9°10'N, 79°45'W) located on the mainland in Parque Nacional de Soberanía.

Both sites are highly similar in terms of climate, forest composition and structure. They support secondary evergreen forests with 20-30 m tall vegetation and are classified as lowland moist forest in a wet climate (Wright & Duber 2001). The area has an average temperature of 27°C and an average annual rainfall between 2100-2600 mm, of which 90% during the wet season (Dietrich *et al.* 1982, Rand & Rand 1982). Each year has a distinct wet (April-November) and dry season (December-March). The production of fruits and seeds peaks between March and June, and between September and October. Between June and September there's a mild food shortage, but between November and February the shortage is quite severe (Foster 1982).

The main difference between both sites is the poaching intensity. BCI is effectively protected against poachers, while poaching is severe in the poorly protected Parque Nacional de Soberanía (Ibanez *et al.* 2002).

Major game species, like agouties and pacas, are more abundant on BCI than on the mainland, with the exception of white-lipped peccaries, which are absent on both (Glanz 1982).

BCI was formed when the Chagres River was dammed during the construction of the Canal in 1914. The water raised and Lake Gatun was formed, thereby isolating a large hill from the mainland. This became BCI and is the largest Island (1500 Ha) in Lake Gatun. It became a research site for biologists in 1916 and in 1923 was BCI designated as a biological reserve.

Together with the neighbouring islands was BCI declared a nature monument in 1979, forming the BCNM, the Barro Colorado Nature Monument.

BCI has undergone several human disturbances, especially during the construction of the Canal. During the 19th century, the French cleared parts of the hilltop, and half of the island was used for shifting agriculture (Dietrich 1982). Although forest has been regenerating since, it is still considered as young forest, approximately 100 years old. The other half of the island consist of old-growth forest, approximately 400 years old (Foster 1982). At BCI, we worked in an existing 25 ha plot (Appendix A).

Parque Nacional de Soberanía is approximately 19.700 hectares large and is under the supervision of ANAM, the national environmental authority of Panama.

During railroad and canal construction in the 19th and early 20th century, large parts of the forests surrounding the Panama Canal were cleared. Still some old-growth forest exists, e.g. around the Fort Sherman canopy crane research and along pipeline road (Ibanez *et al.* 2002). Pipeline road runs through the park from the south-east to the north-west (figure 2). We did our experiments in forests along the first 6 km starting from the beginning of the road in the south (Appendix A).

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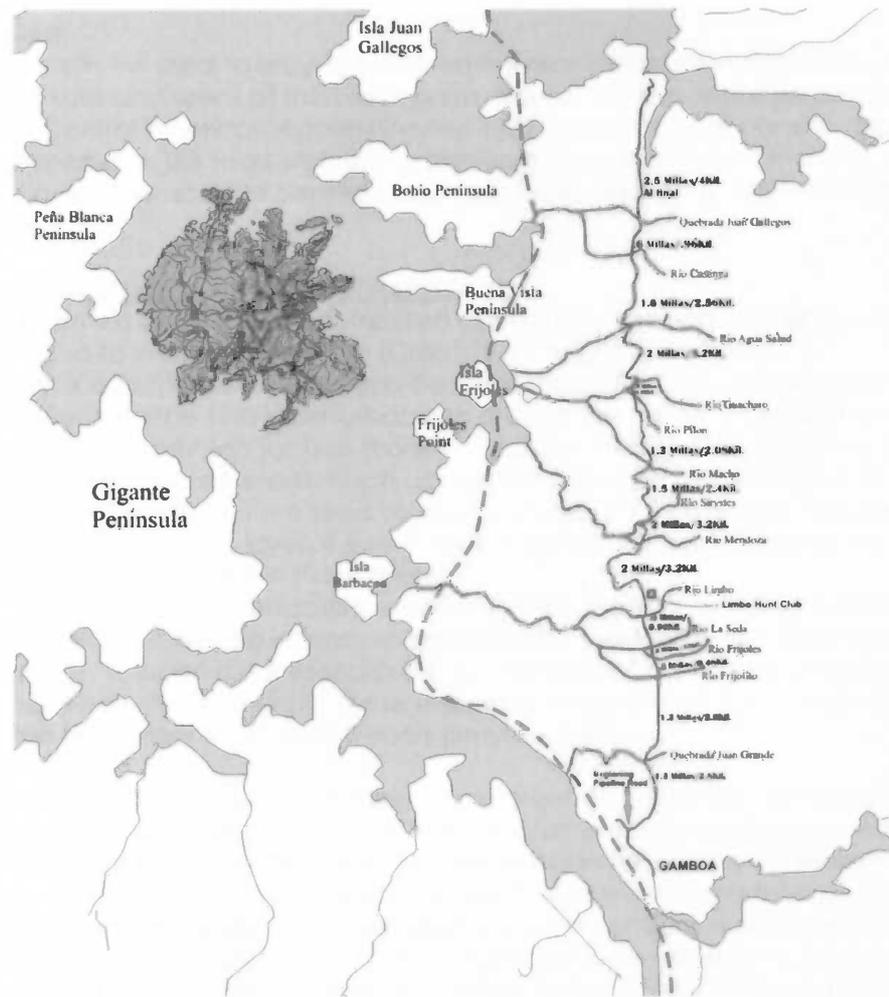


Figure 2: Location of the study sites. In green (on the left) is BCI and the red line indicates Pipeline Road on the mainland.

Study system

The study system we used to answer our questions was based on a single resource species, the fruits and seeds of the black palm. One of the important predators of the seeds is the Central American Agouti (Smythe 1989), which is an important disperser as well. Other species in this food web are: a frugivore, the white-faced monkey, and three other seed predators, scolytid beetles, bruchid beetles and fungi. We will introduce them one by one.

The black palm (*Astrocaryum standleyanum*).

The black palm is a palm species distributed abundantly throughout Central America, from Nicaragua to Western Colombia (Croat 1978, Wright *et al.* 2000).

The single trunk and the below sides and bases of the leaves are covered with 50-200 mm long spines (Smythe 1989), presumably to protect the fruits from predation by rodents and other mammals such as monkeys (Janzen 1982b). One adult tree can produce up to six infructescences, each containing between 100 and 300 fruits (personal observations). Within the fruit is a seed of approximately 2 x 3 cm in size, covered with a soft fleshy edible mesocarp layer, 4-5 mm thick (Smythe 1989). Surrounding the mesocarp is a thin but tougher pericarp < 1 mm present.

The seed itself consists of an endosperm covered by a resistant endocarp, approximately 1.5 – 3.0 mm thick. Usually the endocarp protects one seed, although (rarely) it can be 2 or even 3 seeds. To open the endocarp a force between 223 – 321 kg (between two flat plates) is necessary (Smythe 1989). These endocarps decay very slowly and can remain visible on the forest floor for at least 3 years (Smythe 1989).

When the fruits have ripened they change from green to bright orange and drop on the forest floor, underneath the parent tree. The fruits start producing ethanol, creating a strong penetrating smell (Dudley 2004). Fruit fall peaks in the period between March and June, although at PLR it seems to peak approximately 2 weeks later than at BCI. Both the seeds and fruit pulp are consumed by several vertebrate and invertebrate species. Vertebrates consuming the fleshy fruit pulp include opossums (*Didelphis marsupialis*, *Philander opossum*, *Caluromys derbianus*), pacas (*Cuniculus paca*), coatis (*Nasua nasua*), howler monkeys (*Alouatta palliata*), white-faced monkeys (*Cebus capucinus*) and possibly others (Smythe 1989, personal observations). Few vertebrates are able to penetrate the tough endocarp to feed on the endosperm: the agouti (*Dasyprocta punctata*), peccaries (*Tayassu pecari*, *T. tajacu*), squirrels (*Sciurus granatensis*), and spiny rats (*Prochimys semispinosus*) (Smythe 1989, Hoch & Adler 1997). Three of these species are known to scatterhoard the seeds: agouties (Smythe 1989), spiny rats (Hoch & Adler 1997) and squirrels (Heaney & Thorington 1978), but the agouti is considered as the most important scatterhoarder (Smythe 1989). Invertebrate species preying on the seeds include a scolytid beetle (*Coccotrypes palmarum*) and a bruchid beetle (*Pachymerus bactris*).

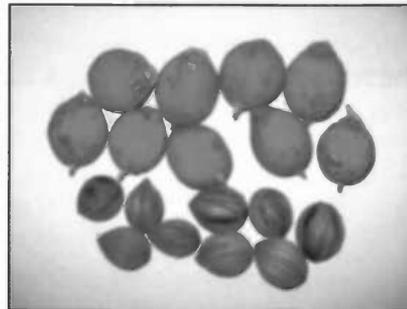


Figure 3: an *Astrocaryum standleyanum* tree (left) and *Astrocaryum* fruits and peeled seeds (right).

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Central American Agouti (*Dasyprocta punctata*)

Agouties are caviomorph rodents (fig. 4) weighing approximately 3 - 5kg, and native to most of the Neotropical broad-leaved forest (Smythe 1989). They are scatterhoarders: they bury seeds in times of seed abundance to eat them in times of scarcity. They collect the seeds underneath the trees after which they peel off the fruit, carry the seed a certain distance away from the tree, and bury the seeds in carefully dug holes 2-4 cm in the soil (Smythe 1989).

Smythe (1989) hypothesized agouties remove the fruit pulp to remove bruchid larvae present in the fruit pulp as well. If they would leave the fruit pulp present, the larvae would crawl into the inside of the seed and feed on the endosperm. By removing these larvae they make sure the endosperm remains intact when the agouti comes back to collect the seeds.

The agouti disperses and predated many large-seeded tree species, including *Astrocaryum standleyanum*, *Pouteria sapota*, and *Scheelea zonensis* (Smythe 1989, Brewer & Rejmanek 1999, Forget *et al.* 1994, Wright *et al.* 2000).

White-faced monkey (*Cebus capuchinus*)

White-faced monkeys are relatively small primates weighing approximately 3 kg. They are distributed from Honduras to Ecuador and live in permanent social groups of approximately 5 - 25 individuals.

Their diet consists mostly of fruit (65%) and the group moves through the forest remaining around 10 minutes at one fruiting tree, after which they move to the next one.

Observations conducted on BCI showed they feed on as much as 95 different fruiting trees. If seeds are relatively small, they swallow them together with the fruit thereby being an important disperser for the trees (Whencke *et al.* 2003). If fruits contain bigger seeds, like the *Astrocaryum standleyanum* seeds, the fruit pulp is peeled of and eaten, the seeds are disposed of beneath the parent tree (Whencke *et al.* 2003, personal observations).

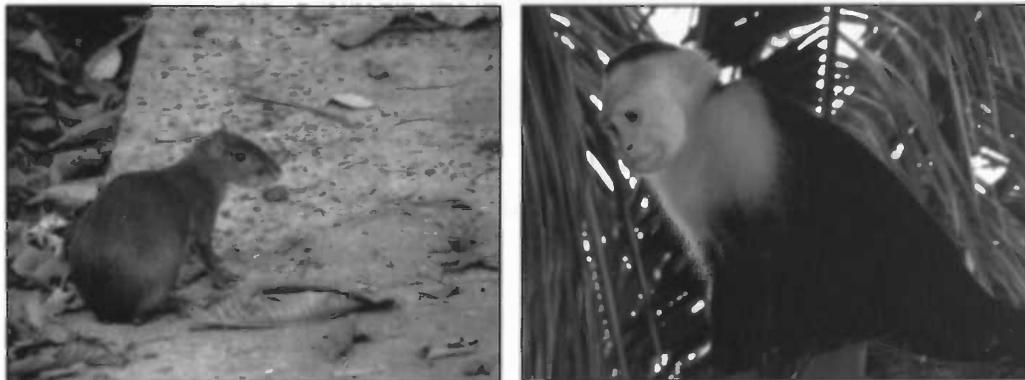


Figure 4: Central American Agouti (left) and white-faced monkey (right).

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Bruchid beetle (*Pachymerus bacticis*)

The bruchid beetle family (coleoptera: bruchidae) is widely distributed. The family consists of 1300 species divided in 56 genera and placed in 5 subfamilies. They exist in every continent except Antarctica, although most are present in the old and new world tropics (Southgate 1979). The beetles are host specific and are usually restricted to a one or a few tree species to reproduce (Southgate 1979, Delobel *et al.* 1995). *Pachymerus bacticis* is specialized to seeds of ca. 20 palm species, including *Astrocaryum standleyanum* (P.A. Jansen, pers. comm.).

The adult lays her eggs on the outside of the fruit or pod. After the larvae hatch they will crawl through the fruit pulp and bore themselves through the endocarp into the seed where they develop into adults. Larvae pupate inside the seed and adults leave a distinct exit hole (Southgate 1979, Janzen 1972). Unlike other palm bruchids that lay eggs on fruits that are present on the forest floor and prefer handled fruits with damaged or partially removed fruit pulp (Silvius & Fragoso 2002, Wright 1990), *P. cardo* infests *A. standleyanum* seeds when still up in the palm crown.

Although the larvae causes a lot of damage to seeds it is (in many occasions) still possible for the seed to germinate. This probably has to happen soon after the beetle left, as the seed becomes more vulnerable to fungus infestation due to the hole in the endocarp.

In *Astrocaryum* seeds, usually only one larvae (figure 5) pupates per seed, unless more seeds were present in the endocarp. In these rare occasions we usually saw multiple beetles hatching. This indicates most seeds can receive several eggs, but only one larva develops per seed (personal observations).



Figure 5: a bruchid beetle larvae in an *Astrocaryum* seed (left) and a bruchid beetle adult (right).

Scolytid beetle (*Coccotypes palmarum*)

Scolytid beetles (Coleoptera: Scolytidae) are beetles specialized in foraging on bark and 119 different species have been assigned to this genus so far. Although they are called bark beetles, only some of these species live exclusively on bark. Some are specialized in reproduction on seeds, fruits, leafstalks, phloem and the pitch of twigs, usually in a wide range of trees (Jordal *et al.* 2002). The scolytid beetles observed in this study forage and reproduce on *Astrocaryum* seeds (figure 6). As other members of the *Coccotypes* genus, they bore a small hole (approximately 0.5 - 1 mm) in the endocarp after which they lay their eggs in the endosperm (Janzen 1972). Each beetle colonizing the seed will make its own entrance hole (Zeledon unpublished).

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Their eggs have a sex-ratio biased towards females (Jordal *et al.* 2002, Janzen 1972). After the beetles hatched and developed will the females mate with one of the males inside the seed – often siblings – before dispersing (Jordal *et al.* 2002). Offspring remains present in the seed until all the endosperm has completely disappeared and the seed is killed (personal observations). *Coccotrypes* may cause a predation rate of almost 100% of the seeds remaining on the forest floor (Janzen 1972).

Previous studies have shown that bark-feeding Scolytids can produce a kind of pheromone once they have found a suitable host, usually a weak or ill tree susceptible to the attack of bark beetles. Other beetles will be attracted to the smell and will attack the same host (Byers 1996). This is to the advantage of the beetles because the tree might try to restrain the attack by producing toxic resin. One beetle might not survive the resin, but a joined attack by many beetles has a higher chance of being successful (Byers 1996). A recent study by Zeledon showed seeds located in an area with high palm abundance are more likely to have a higher infestation rate, indicating the beetles accumulate where most seeds are available (Zeledon unpublished).

Fungi

Several different kinds of fungus were found to infest the seeds. Most common was a bright yellow, smelly kind of fungus (figure 6 on the bottom of the picture), but several others were found as well. Figure 6 also shows the other most common kinds of fungus we found inside the seeds. We did not identify the fungi we found.

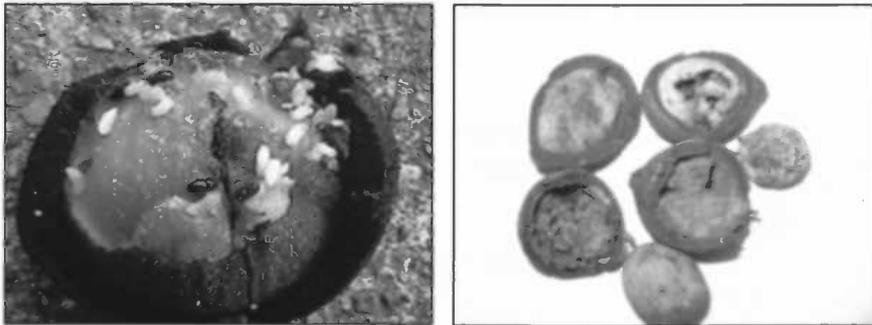


Figure 6: an *Astrocaryum* seed infested by scolytid beetles and larvae (left) and several species of unidentified fungus that were found in the seeds (right).

Experimental set-up

Our experimental approach was to compare seed fate between locations with contrasting mammal abundance and palm density. At each of the two sites, one with and one without poaching, we established six 100x100m plots, three with high and three with low palm density (fig. 7). In each of these 12 plots, two experiments were set up.

Experiment 1: The effect of agoutis and monkeys on the scolytid beetle, bruchid beetle and fungus infestation and their interaction.

The fruits were collected directly from the palm trees. From each tree the ripest infructescence was chosen and cut down with special scissors on a 10 m long stick. To gather enough fruits we used the fruits of several trees (approximately 8 different trees along the first 5 km of pipeline road).

In the lab all the collected fruits were mixed to avoid tree-specific differences (e.g. in fruits or in bruchid infestation rates among trees), and they were randomly divided in two piles. For half of the seeds, pericarp and mesocarp were removed with a pocket knife (Smythe 1989) to mimic the handling of fruits by the white-faced monkeys.

To determine the effect of this pulp removal treatment on the bruchid beetle infestation, we incubated peeled and non-peeled seeds in plastic boxes. In total we had 11 boxes per treatment, each containing 20 seeds. The boxes were kept in a shade house, at ambient temperature and humidity.

After 4 months of incubation, the endocarps were opened with a hammer and presence/absence of developing bruchid beetle larvae was scored.

With this data we could determine the average proportion of seeds infested by bruchids and the effect of pulp removal on the number of bruchids hatching.

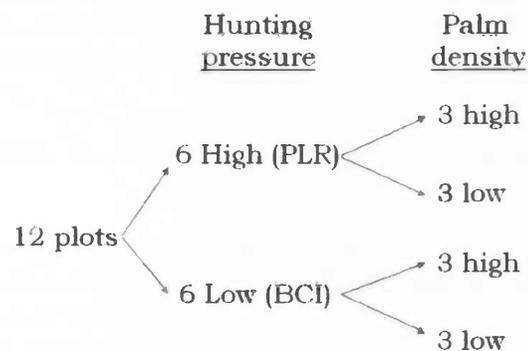


Figure 7: the experimental set-up of the plots.

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To determine the effects of seed peeling and seed burial on seed infestation by scolytid beetles, bruchid beetles and fungi, we carried out a field experiment with fruits and seeds. With this experiment we could also determine the interactions between these species. Fruits and peeled seeds were laid out in wire mesh exclosures, to exclude the rodents and avoid them dispersing or predated on the seeds.

To determine the effects of monkeys (peeling) and agouties (peeling and burial), fruits were divided into four treatments:

- 1: peeled and unburied
- 2: peeled and buried
- 3: unpeeled and unburied
- 4: unpeeled and buried

The seeds/fruits were buried approximately 2-4 cm under the soil surface (depth of seed burial by agouti, Smythe 1989), while the seeds/fruits with unburied treatment were laid on top of the soil layer.

To measure the effect of palm density and hunting, exclosures were set up in both research areas and in all the plots. Each plot received eight exclosures to which the four treatments were randomly assigned, i.e. each treatment had two wired mesh exclosures per plot. 96 exclosures were set up in total.

After 4 months the seeds were collected and opened with a hammer. While opening the seeds several measurements were taken.

First the outside of the seeds was examined for the presence of bruchid beetle exit holes and scolytid entrance holes. Bruchid exit holes are round holes approximately 5 mm in diameter (Figure 8). Scolytid holes are much smaller and are approximately 1 mm in diameter (Figure 8). Because these holes are so tiny, we used a needle to determine whether the hole went through the entire endocarp, indicating a colonization.

Hole presence and number were determined. Each scolytid beetle will make its own hole, so every hole indicates one colonization. Furthermore, we determined whether the seed had germinated.

After scoring the outside, the endocarp was opened and several other measurements were taken:

- Bruchid presence: larvae, pupae or adult,
- number of Scolytids present: both adults and larvae together,
- fungus presence: yes or no,
- viability of the seed: yes or no, and
- percentage of endosperm still intact.

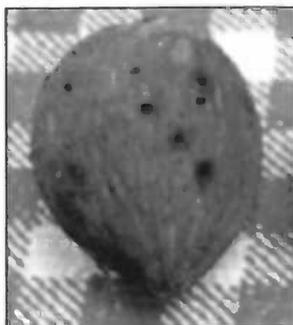


Figure 8: an astrocaryum seed with scolytid entrance holes (left), and (from top to bottom) an intact seed, seed opened with the endosperm visible, a seed with a bruchid beetle exit-hole and only the endosperm (right).

Effects of poaching on seed-predatory interactions of a Neotropical palm.

Experiment 2: The effect of fruit peeling and age on the time till seed removal by rodents.

To determine the effects of fruit peeling and age of the fruits/seeds on agouti behaviour, a field experiment was set up to measure the removal time of seeds with several different treatments. To determine the effect of peeling, we offered seeds with and without the fruit pulp present. The fruit pulp was removed the same way as in the experiments described above.

If a seed remains on the forest floor for a longer period of time, the fruit pulp will rapidly get populated with fly larvae, which will cause the fruit pulp to decay. We want to determine whether the rotting pulp made the seeds less attractive to the rodents and delayed seed removal.

In total we had four treatments that were presented simultaneously:

1. fresh seed with fruit
2. fresh seed without fruit
3. old seed with fruit
4. old seed without fruit

Old fruits were obtained by placing fresh fruits in an enclosure during two weeks. During this time, the fruits became very soft and you could smell the fermentation of ethanol in the fruit pulp very well (Dudley 2004). The fruits turned dark orange and partially black. Fresh fruits were collected from underneath palm trees on the forest floor just before the start of the experiment. We removed the fruit pulp of half of the old and half of the fresh fruits.

In each plot, we randomly selected 4 palms, around each of which we placed one station for each of the four treatments (fig. 9). Each station consisted of 16 seeds placed in a grid like manner at approximately 4 m from the palm to the North, East, South and West (figure 9). A small white ribbon was attached to a small tree or branch near the seeds to make sure the location could be found again.

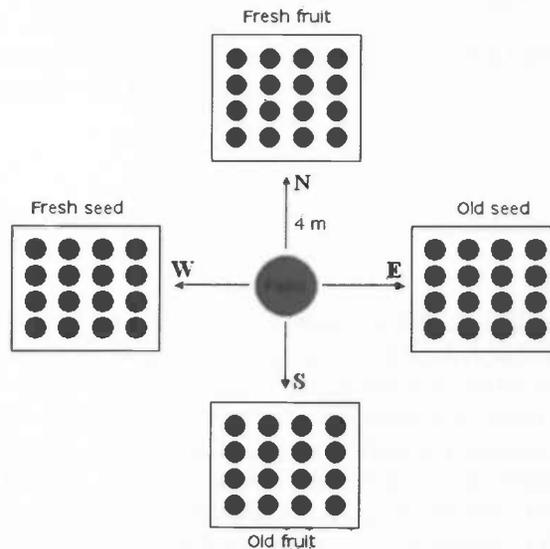


Figure 9: the experimental set-up of the cafeteria experiment.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

The stations were checked at logarithmic time intervals: at day 1, 2, 4, 8, 16 and 32. Each time the numbers of seeds still present were counted. This experiment was conducted on both PLR and BCI and at both high and low density plots to determine whether poaching and palm density affected seed removal rates and rodent selectivity.

Additionally, we used data collected with two other experiments:

Experiment 3: The scolytid, bruchid and fungus infestation after 11 months in the field.
In each plot on both PLR and BCI five fruiting *Astrocaryum* trees were randomly selected and exclosures were placed within a distance of 5 m from the tree. Seeds and fruits were collected with nets suspended below each tree and a random sample was placed within the exclosures in May 2005. Each exclosure received between 10-40 seeds, reaching a total of 1331 seeds. After 11 months of exposure in the field these seeds were collected and the same measurements were taken as in experiment 1.

Experiment 4: The effects of peeling by the agouti on the bruchid beetle development.
To determine whether seed peeling by agoutis would affect bruchid beetle infestation by "intercepting" larvae before those would penetrate the endocarp (Smythe 1989), we peeled fruits at different time intervals immediately upon fruit fall. Fruits were collected daily with nets suspended below palms. Fruits were placed on the ground below the palms in wire exclosures for 0, 1, 2, 4 and 8 days after fruit fall. Immediately upon collection from the exclosure, the fruit pulp was removed. The peeled seeds were incubated in plastic containers for three months and bruchid beetle presence was determined. For this experiment only fruits from PLR were used.

Statistical analyses

The greenhouse experiment consisted of binomial data (the bruchid beetle is present or not) which were analyzed with logistic regression. Beetle presence was the dependent factor and pulp presence was the predictor variable. We used the Wald- test to determine whether differences in beetle infestation were significantly different between seed with and seeds without fruit pulp.

Data from the experiments were nested. To account for the hierarchical structure, we analyzed these data with the Pearson Chi² test.

$$\text{Chi}^2 = \sum \frac{(o - e)^2}{e}$$

o = observed variable

e = expected variable

If $X^2 < 0.05$, it indicated the factor had a significant effect. This analysis worked with binomial data or categories only, meaning we had to divide the number of colonizations and number of individuals found into classes before we could analyze them.

If we had to analyze more than two factors we could not use a simple Chi² test anymore. It had to be analyzed with Log-linear multiple frequency tables, used for frequency tables with multiple factors. As the analysis becomes more difficult with more factors, we had to determine the simplest model which could still explain the observed frequencies. Once the best model was predicted we tested the residuals, if these were not significantly different from the expected residuals, the model fitted well.

The data of the scatterhoarding time is analyzed with a generalized linear model (GLM) with a poisson distribution. The log (time) is used as offset because not all seeds had disappeared on the last day the experiment was checked. With the Wald test we could determine whether the removal time was significantly different between treatments.

Results

The food web.

We will first consider all the interactions between the species to determine the structure of the food web, before considering the differences between the experimental treatments.

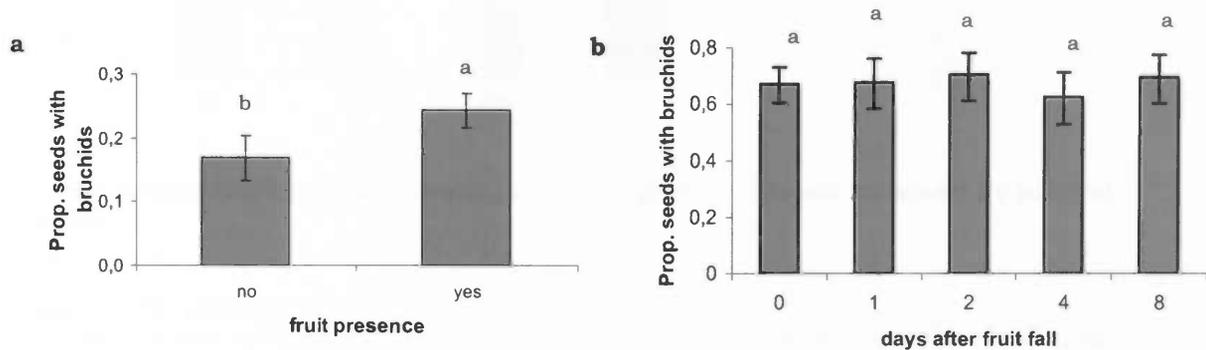


Figure 10a: Proportion of seeds with bruchid beetles developing depending on pulp presence, using unripe fruits cut from the parent tree and b: Infestation of freshly fallen fruits collected underneath the parent tree.

White-faced monkey/agouti – bruchid beetle interaction.

First we determined the effect of peeling by white-faced monkeys on bruchid beetle development. The proportion of bruchids developing and hatching was higher for seeds with fruit pulp compared to seeds without (figure 10a). The proportion of seeds with a developing bruchid beetle was approximately 16% for seeds without fruit pulp, compared to 24% for seeds with pulp present. Because the environment in the greenhouse was homogeneous and both treatments were mixed randomly, this difference can only be the result of the mesocarp presence. The difference in proportions between treatments was significant (GLM with binomial errors: Wald = 4.608, df = 2, p = 0.032).

This result was apposite to our expectation. We expected fruit pulp presence to effect the development negatively, but it seems the opposite happened.

When fruit pulp was removed after fruit fall, such as agoutis removing seeds would do, this no longer had an effect on the proportion of beetles developing and hatching (figure 10b).

Effects of poaching on seed-predatory interactions of a Neotropical palm.

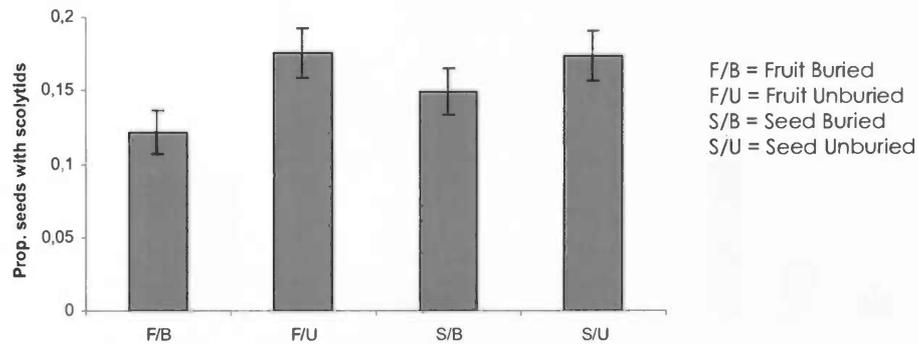


Figure 11: Effects of burial and peeling on the proportion of seeds colonized by scolytid beetles.

White-faced monkey/agouti – scolytid interaction

To see whether fruit presence and burial had an effect on the accessibility of seeds to scolytid beetles, we determined scolytid presence per seed in all four treatments. Burial seemed to affect scolytid presence negatively ($\text{Chi}^2 = 6.07$, $\text{df} = 1$ $p = 0.01$), while fruit pulp presence had no effect at all ($\text{Chi}^2 = 0.64$ $\text{df} = 1$ $p = 0.43$). This is not what we expected; we expected burial and pulp presence to decrease the accessibility of the seeds. Although we tried to determine the effects of burial on bruchid beetle development and the effect of burial and peeling on fungus presence, the numbers of seeds with bruchids and fungus present after 4 months were too low to test for treatment effects. Of the 2037 seeds used in this experiment only 12 had a bruchid beetle or larvae present and only 16 had fungus present.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

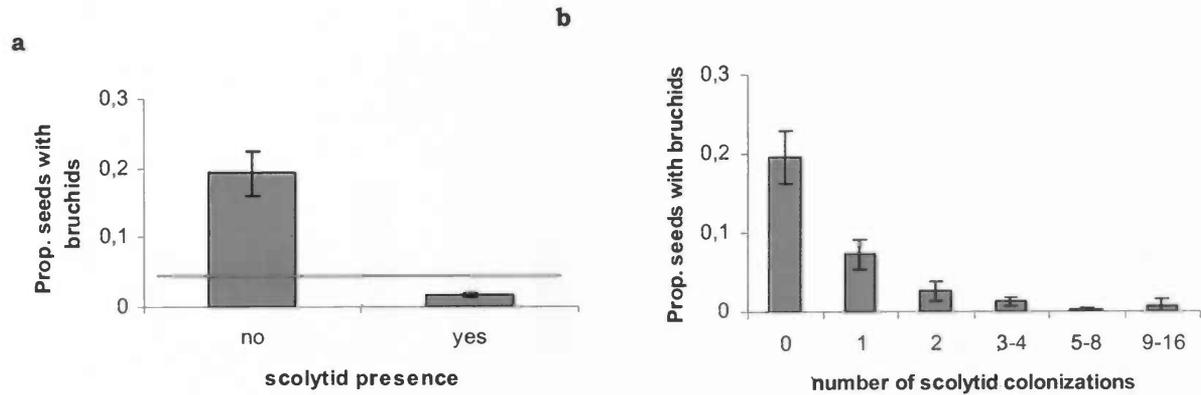


Figure 12: The proportion of seeds with bruchid present depending on the scolytid presence (a) and number of scolytid colonizations (b) after 11 months. The red line in the left graph represents the average proportion of bruchids present.

Bruchid beetle – scolytid beetle interaction

To determine how scolytid beetles affect bruchid beetle development we related bruchid presence in seeds to scolytid presence and number of colonizations. The proportion of bruchids developing and hatching was lower if scolytid beetles were present (fig. 12a; $\text{Chi}^2 = 105.38$, $\text{df} = 1$, $p < 0.001$). The proportion of bruchids also significantly decreased when the number of colonizations by the scolytid beetle increased (fig. 12b; $\text{Chi}^2 = 124.75$, $\text{df} = 5$, $p < 0.001$). This is in line with what we expected; we expected the scolytid beetle to affect the bruchid beetle development negatively due to predation on present bruchid larvae by scolytid beetles and larvae.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

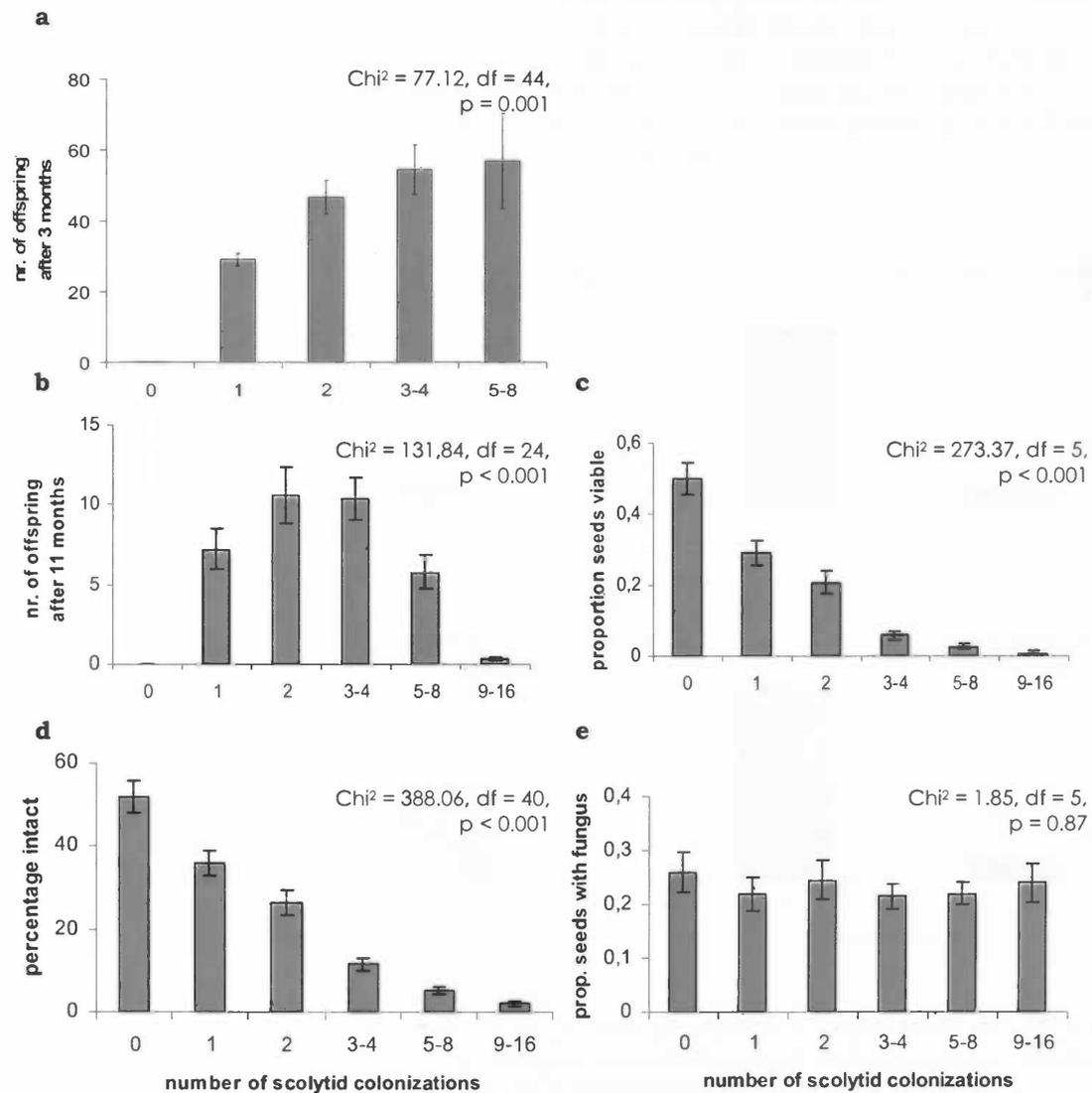


Figure 13: The number of adults and larvae present in the seed after 3 months (a) and after 11 months (b) in the field. c) the proportion of seeds infested with fungus, d) the proportion of seeds still viable and e) the percentage endosperm still intact, all dependent of the number of scolytid colonizations after 11 months in the field.

Fungus - scolytid interaction, and the characteristics of scolytid infestations.

To determine the effects of scolytid beetles on the survival of *A. standleyanum* seeds, we related the number of offspring in the seeds, the percentage endosperm still intact and the proportion of seeds still viable to the number of colonizations. We also wanted to determine how colonization by scolytids affected fungus presence.

The number of scolytids (both adult and larvae together) present in the endosperm increased with the number of colonizations (figure 13a). However, among seeds that had been in the field for 11 months the number of individuals decreased again after 3-4 colonizations (figure 13b; the analysis includes only seeds with scolytid infestation

Effects of poaching on seed-predatory interactions of a Neotropical palm.

present). A negative correlation existed between the proportion of seeds viable (figure 13c) and the number of scolytid colonizations. The same trend was seen in the percentage of endosperm still intact (figure 13d), which decreased as the number of colonization increased. The proportion of seeds infested by fungus did not depend significantly of the number of scolytid colonizations. Even if no colonization occurred, the proportion of seeds infested was still the same (figure 13e).

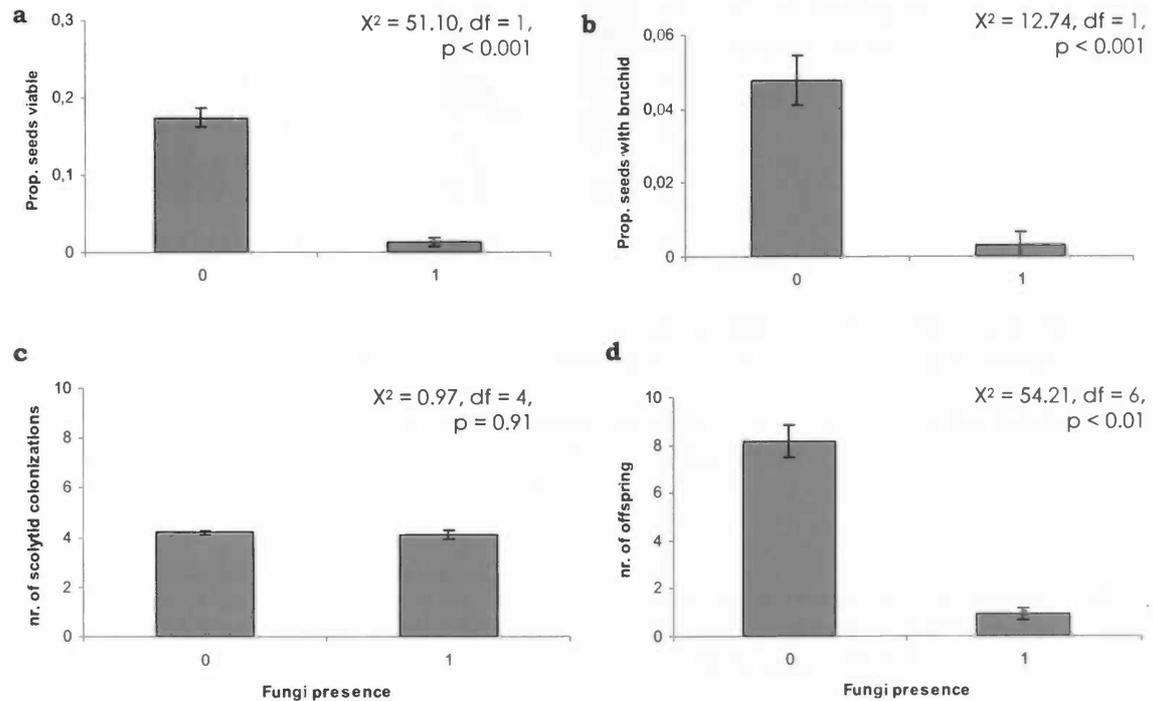


Figure 14: The proportion of seeds viable (a), the proportion of seeds infested with bruchid beetles (b), the average number of scolytid colonizations (c) and the number of scolytid offspring present in the endocarp (d) all depending of the presence of fungi.

Scolytid/bruchid beetle – fungus interaction, and the characteristics of a fungus infestation.

When we considered the effects of fungus presence on both the seed survival and infestation of both invertebrate predators, we found that the proportion of seeds viable after 11 months was significantly lower under the presence of fungus. The number of bruchids developing in fungus-infested seeds was significantly lower as well. The number of colonizations by the scolytid beetles did not depend significantly on the presence of fungus, but the number of individuals present inside the endocarp was significantly lower with fungi presence. Both analyses included only seeds with scolytid infestation.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

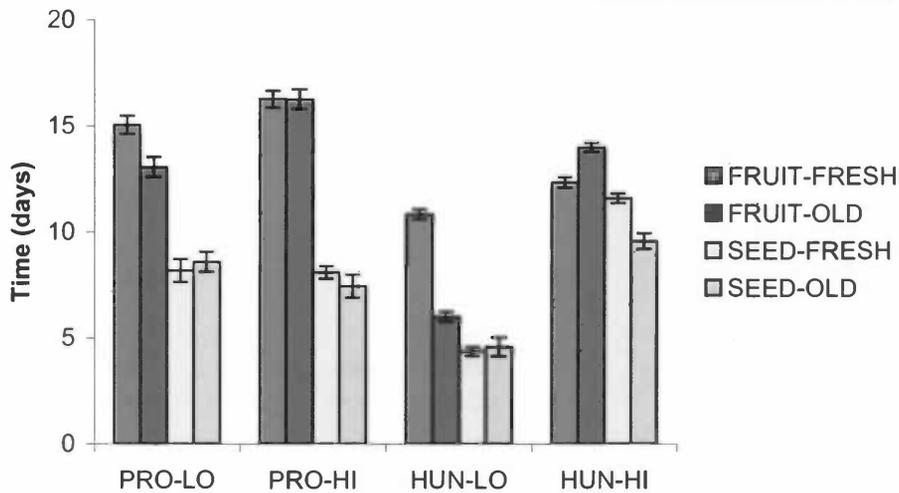


Figure 15: The average removal time of fresh fruits/seeds and old fruits/seeds by the Central American agouti. Removal time is compared between contrasting areas.

PRO-LO = Protected and low palm density plots, PRO-HI = Protected-high palm density plots, HUN-LO = Hunted-low palm density plots and HUN-HI = Hunted-high palm density plots.

White-faced monkey-agouti interaction

The age of the seeds and fruit had no significant effect on the removal time (Wald = 2.29, df = 5, p = 0.13). Fruit presence resulted in a significant decrease in removal time (GLZ poisson regression; Wald = 27.72, df = 1, p < 0.00). This was opposite to the expected preference for fresh fruits.

Hunting (Wald = 6.57, df = 1, p = 0.01) and fruit abundance (Wald = 15.20, df = 1, p < 0.001) both had a significant effect as well. A significant interaction between hunting and fruit abundance (Wald = 14.67, df = 1, p < 0.001) indicated that differences were significant between high and low fruiting density on PLR but not on BCI.

Effects of mammal reduction and palm abundance on a food web.

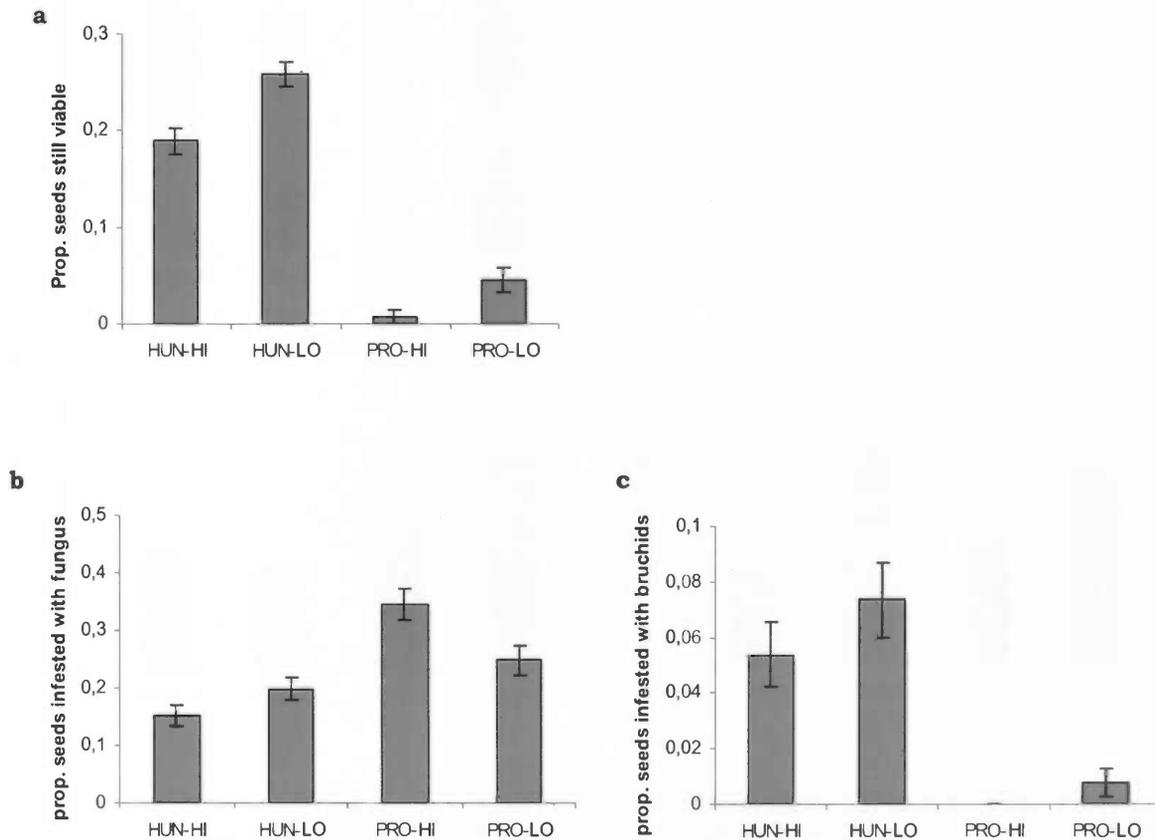


Figure 16: The proportion seeds viable (a), infested by fungus (b) and infested by bruchid beetles (c) after 11 months in contrasting areas.

Effects of mammal and palm abundance on viability of the seeds and on fungus and bruchid beetle infestation.

The proportion seeds still viable was significantly higher at the hunted sites compared to the protected site ($\text{Chi}^2 = 126.59$, $\text{df} = 1$, $p < 0.001$) and was significantly higher in the low palm density plots than at the high palm density plots ($\text{Chi}^2 = 9.43$, $\text{df} = 1$, $p = 0.002$).

The infestation of fungus was significantly higher in the protected site than at the hunted site ($\text{Chi}^2 = 28.59$, $\text{df} = 1$, $p < 0.001$). An interaction between density and hunting ($\text{Chi}^2 = 8.94$, $\text{df} = 1$, $p = 0.003$) indicated the difference between high and low density was only significant at the protected site and not at the hunted site.

The proportion seeds infested with bruchids was lower at the protected site ($\text{Chi}^2 = 38.16$, $\text{df} = 1$, $p < 0.001$), but is not significantly different between fruit densities.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

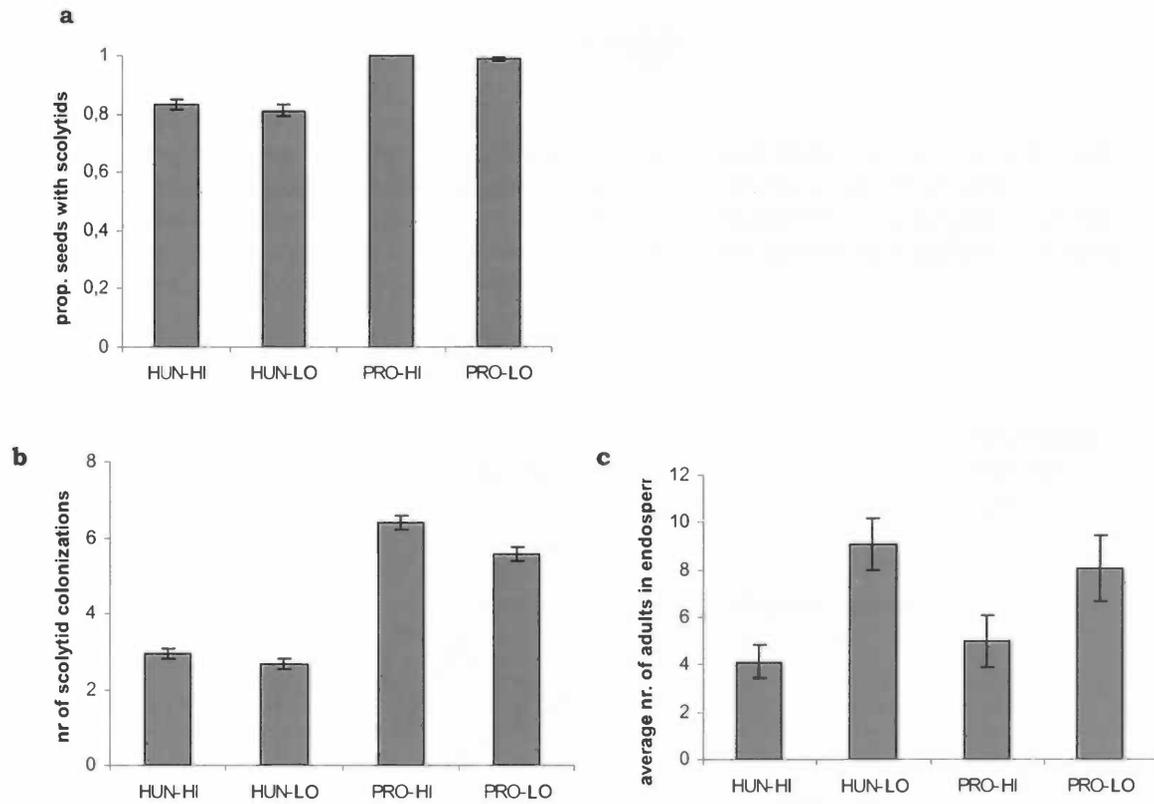


Figure 17: Scolytid presence (a), average number of colonizations (b) and average number of adults inside the endosperm (c) in contrasting area's after 10 months.

Effects of mammal and fruit abundance on scolytid infestation, the number of colonizations and the number of offspring.

The proportion seeds infested with scolytid beetles was higher at the protected site than at the hunted site ($\text{Chi}^2 = 134.93$, $\text{df} = 1$, $p < 0.01$) but not different between high and low fruit density ($\text{Chi}^2 = 1.12$, $\text{df} = 1$, $p = 0.23$). The number of colonizations was higher as well ($\text{Chi}^2 = 406.37$, $\text{df} = 6$, $p < 0.001$), but the number of offspring found in the endosperm was significantly different between the palm densities ($\text{Chi}^2 = 37.20$, $\text{df} = 6$, $p < 0.001$) and did not significantly depend on the hunting intensity. This is not what we expected; we expected higher infestation rates on the hunted site due to higher seed availability.

Discussion

The food web

To determine the effects of mammal abundance and palm density on a food web, we first had to determine in more detail how the species within the study food web interacted with each other. Looking at a simple food web like the web surrounding the *A. standleyanum*, containing one resource, four herbivores (or seed predators) and one frugivore, we already see many interactions (figure 18).

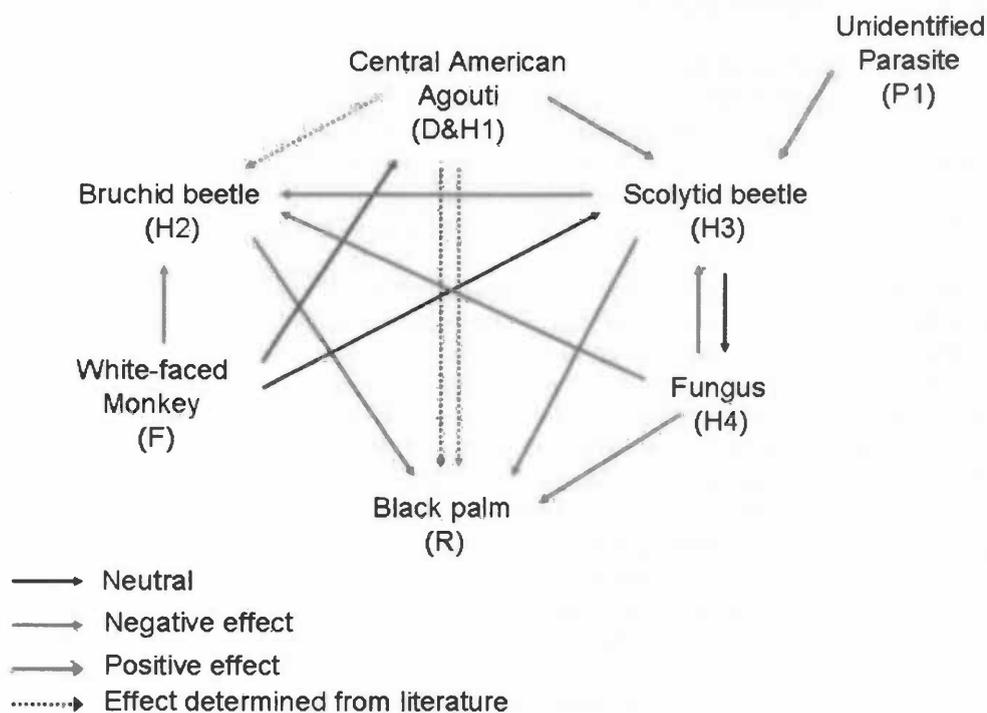


Figure 18: the interaction scheme of the food web surrounding the *Astrocaryum standleyanum*. R = Resource, H = Herbivore, D = Disperser, F = Frugivore and P = Parasite.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

Now we will take a closer look at our food web and examine each interaction carefully.

White faced monkey/agouti – bruchid beetle interaction

As both mammal species (agouti and white-faced monkey) remove the fruit pulp of the seeds, this might affect other species predating on the same seeds. When fruit pulp is removed it can increase the accessibility of the seeds to invertebrate predators (Silvius *et al.* 2002) or decrease the survival of invertebrate larvae present in the pulp (Smythe 1989).

Bruchid beetles usually lay their eggs on the outside of the fruit and the larvae have to reach the inside of the seeds by crawling through the fruit pulp (Southgate 1979).

In a study on bruchid beetle development in *A. standleyanum* seeds, Smythe (1989) hypothesized that agouties remove the fruit pulp before caching the seeds to remove bruchid larvae and thereby ensuring seed survival.

However, when we removed fruit pulp before the fruits fell naturally (simulating fruit handling by white-faced monkeys) it did result in a decrease in the proportion of bruchids developing and hatching. But when fruit was removed after the fruits had ripened completely (simulating fruit handling by agouties) it did not affect the proportion of bruchids developing and hatching anymore, contradicting the theory of Smythe. Apparently, the bruchid larvae have already entered the endocarp at the time of fruit fall.

Timing of the fruit removal seems to be the key factor in affecting the bruchid beetle development. Many species of bruchids lay their eggs on the outside of the fruit after the seeds have ripened and dropped on the forest floor (Forget *et al.* 1994, Delgado 2002), but this study showed the eggs or larvae were already present in fruits directly collected from tree crowns. When we removed fruit pulp at this point we might have removed the larvae with it. As more time passed and the fruits dropped from the trees, the larvae might have had enough time to reach the inside of the seeds and pulp removal had no effect anymore. A second possible explanation is that the larvae did manage to reach the inside of the seeds, but were still in a very vulnerable instar phase. Changes in physiology of the seeds, e.g. moisture level, might have a negative impact on the development of the larvae, increasing the mortality rate. As more time passed and the fruits dropped to the ground, the larvae developed beyond the instar phase, and were not vulnerable to these changes anymore.

Smythe based his hypothesis on an experiment comparing buried/peeled seeds with unpeeled/unburied seeds (Smythe 1989). As we showed in this experiment fruit removal by the agouti had no effect, but the burial treatment may have caused the difference Smythe found. We could not determine the effects of burial on bruchid beetle development in this experiment due to a low level of bruchid infestation.

Scolytid beetle/fungus – bruchid beetle interaction

Another mortality factor for the bruchids was the presence of scolytid beetles, which colonized seeds present on the forest floor. The seeds infested by scolytids had a significantly lower number of bruchids developing than seeds without scolytids. When the number of colonizations increased the number of bruchids decreased further, indicating the scolytids have a clear negative effect. We suppose that the decrease is due to the scolytid offspring feeding on the bruchid larvae next to feeding on the endosperm. When the colonization rate is high, the amount of endosperm intact is reducing fast and any bruchid larvae present must have been encountered by the scolytid larvae. If the colonization rate is low and the bruchid larva is developing on the opposite site of the endosperm, it might have enough time to develop and hatch.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

A third mortality factor for the bruchid beetle is the presence of fungi. The proportion seeds containing a bruchid beetle decreased from almost 5% if no fungus was present to less than 1% if fungus was present.

White-faced monkey/agouti – scolytid beetle interaction

Peeling (by agouties or white-faced monkeys) had no effect on the scolytid beetle infestation rate, but burial (by agouties) caused a significant decrease. Scolytid beetles apparently have more trouble reaching the seeds when they are buried. This means seeds not only benefit from agouties by carrying seeds a certain distance away from the parent tree, but seeds also become less vulnerable to infestation by scolytids when agouties bury them.

As the number of colonizations increased, the number of offspring present in the seed increased as well. Seeds that were in the field for 4 months showed an increase per extra colonization, but seed left in the field for 11 months showed an increase up to 2 colonizations, after which the number of offspring inside the endocarp decreased again. This is probably due to the amount of endosperm still intact. More colonizations and subsequently more offspring results in a faster exhaustion of the endosperm. After the endosperm is eaten entirely, the beetles likely leave the seed to find another seed to feed and reproduce on. This would explain the low numbers of beetles we found in seeds with many colonizations after 11 months.

Scolytid beetle – fungus interaction

No correlation was found between the presence of fungus and the number of colonizations by scolytid beetles. We expected fungus to enter seeds after other beetles drilled holes through the hard endocarp, decreasing the protective value of the endocarp. But seeds without a scolytid infestation had the same chances of being infested as seeds with one or more colonizations. What we did find was a decrease in survival of the offspring if fungus was present in the seed.

One possibility is that scolytids are unaware of fungus presence when they drill a hole in the endocarp, but, once having reached the inside of the seed, restrain from laying eggs. Alternatively, the fungus may infest the seeds after scolytids already colonized the seeds and kill the eggs and larvae present, explaining the decrease in offspring.

Bruchid beetle/scolytid beetle/fungus – black palm interaction

All three non-vertebrates, bruchids, scolytids and fungi, negatively affected the survival chances of *Astrocaryum* seeds. Most lethal to the *Astrocaryum* seeds seemed to be fungi, as survival chances of the seeds decreased to 1%.

Seeds with scolytids present had a survival chance of 10%, while 48% of the seeds with bruchid infestation were still viable after 10 months (appendix B), indicating that after fungi, scolytids are most lethal followed by bruchids.

White-faced monkey – agouti

Agouties had a preference for seeds without fruit pulp present. Although we expected them to prefer seeds with fresh fruit to feed on, they removed the seeds without pulp a lot faster. Apparently, the handling of fruit by white-faced monkeys was beneficial for the palm as it increased the chances and speed of seed removal by rodents.

Now we know how our food web is interacting, we can focus on how mammal and palm abundance affected this food web.

Food-web effects of poaching

With many interactions between species in a food web, a change in the population size of one of them could result in changing directly and indirectly the population sizes of all the other species in the same web (Wright *et al.* 2000, Feeley & Terborgh 2006). Before determining whether this also occurs in this food web, we will first have to determine a reduction of mammal abundance is present between both study sites. Our seed removal experiment showed no significant difference in activity between sites, but if we look at other recent studies conducted in the same areas it shows a clear decrease in several game species on the mainland compared to Barro Colorado Island (Wright *et al.* 2000). On the mainland the population of agouties and white-faced monkeys has reduced substantially (Wright *et al.* 2000, Wright & Duber 2001, Van Eijk unpublished). A possible reason why we did not find the same trend are differences in the background availability of fruits and seeds between the two sites at the time of the experiment. If on BCI, most naturally available seeds were already removed or infested by other animals, this would increase removal chances of our seeds. Due to the reduction in numbers of white-faced monkeys on the hunted site, fewer fruits were eaten and more fruits fell to the ground intact (personal observations).

Several studies have shown that a reduction in numbers of the main disperser of a palm species resulted in a decrease in seed dispersal, fewer seeds killed by rodents, more seeds remaining underneath the adults, and higher proportions of seeds infested by invertebrate predators (Forget *et al.* 1994, Wright *et al.* 2000, Galetti *et al.* 2006). In *A. standleyanum*, more seeds remain underneath the adults under hunting pressure as well (Wright *et al.* 2003). This indicates fewer seeds are dispersed and that other species known to disperse *A. standleyanum* seeds (Heaney & Thorington 1978, Hoch & Adler 1997) do not compensate for the function of the agouti as a disperser. The question then is whether compensation occurs due to increased seed predation by invertebrates.

The most important mortality factor of seeds remaining underneath the parent tree was the scolytid beetle *Coccotrypes palmarum*. Approximately 80% of the seeds got infested at the hunted sites, while the infestation rate was near 100% at the protected site. The number of colonizations was a lot higher at the protected site as well.

Because more seeds are available for scolytids at hunted sites (Wright *et al.* 2000) one would expect an increase in population size of the scolytids and thereby a higher or equal infestation rate of seeds. A possible reason why we found a lower infestation rate is satiation.

Seeds on BCI are removed by agoutis fast, and therefore almost no seeds remain on the forest floor (Wright *et al.* 2000, Sharrot 2006). Since burial decreases the accessibility of seeds to scolytids, this suggests that scolytids will first infest seeds present on top of the soil, before infesting seeds buried by agouties. The high infestation rates that we found on BCI may thus be an artefact of the seeds experimentally placed in exclosures being among the very few surface seeds available, hence these seed patches may have been attracting disproportionate numbers of scolytids.

High and low palm density plots showed comparable infestation rates, but we found lower numbers of offspring inside seed in high palm density areas. This could be explained by the presence of another predator or parasite, preying on the offspring. Higher palm density results in higher seed availability and more scolytids present (Zeledon unpublished). Parasites preying on Scolytid offspring could accumulate here (Janzen-Connell hypothesis, Janzen 1970), causing a decrease in offspring number per seed. As many more seeds remained on the forest floor at the hunted site and the scolytid population is suppressed by a parasite, then the number of seeds available per beetle increases and the beetle population gets satiated.

Effects of poaching on seed-predatory interactions of a Neotropical palm.

The proportion seeds infested with fungus also decreased with hunting intensity. We speculate that this trend might be due to differences in environmental factors instead of a result of differences in mammal abundance between the two sites.

The proportion of seeds in which bruchids developed showed the exact opposite of both scolytids and fungus: the infestation rate was higher at the hunted site compared to the protected site, which was also found in several other palms interacting with bruchid beetles (Wright *et al.* 2003, Galetti *et al.* 2006).

We can explain this with the interactions between the bruchid beetle, the scolytid beetle and the fungus. Both fungus and scolytids had a negative effect on the bruchid beetle development. As the infestation rates of both were higher on the protected site, more bruchid larvae were killed and a decrease in the number of bruchids was found.

Because these data are based on seeds collected in situ, it is also likely that the bruchid beetle population is smaller at the protected site. Because the infestation of scolytids and fungus of the seeds on top of the soil was higher on the protected site and most seeds were buried – causing a decrease in bruchid beetle development as well (Smythe 1989) – the population size of bruchids at BCI may have been much smaller and the results we found could reflect this.

When we opened the seeds we determined whether we thought the seeds were still viable at that point. The proportion seeds still viable was significantly higher on the hunted site, indicating there was no complete predator compensation for the decrease in population size of the agouti. Although the population size of bruchids increased it is not enough to compensate for the reduction in agouti abundance.

To come to a realistic conclusion, one would have to take all the seeds and seed fates in account. Although most seeds on the hunted site remain on the soil surface, most seeds on the protected site are taken away from the parent tree and buried immediately. To determine what happens to these seeds we can use the results of a study conducted on the same sites in 2005, in which numbers and fates of seeds present in the soil were determined at several distances from adult trees for the same 12-plot set-up used in this study (Sharrot, unpublished). The results are (partially) shown in appendix E. While seed density in the soil is almost independent of the distance away from the palm at the protected site, a decrease in seed density with increasing distance from the palm at the hunted site was found. This supports the theory that more seeds remain near the parent tree when mammals have reduced in numbers. Seed fate differs between sites as well, with a healthy population of mammals more seeds are eaten by rodents and less seeds are infested by scolytids. Seed survival decreased with palm density on the protected site, but was invariant to palm density at the hunted site.

Overall seed survival above and below ground together increased as mammal abundance decreased and this could lead to an increase in the population size of the black palm. As more seeds remain near the parent tree an aggregation of the black palm might occur if, due to density dependent mortality, seed and seedling mortality doesn't increase with density.

Consequences of poaching for density-dependent mortality

To determine the presence of density dependent mortality and the effects of poaching on this mechanism we will compare the results between high and low density plots. High density plots have significantly more seeds per hectare than low density plots (Eijk van, unpublished). When we look at the effects of the palm and fruit density on the population sizes of the three seed predators: the bruchids, scolytids and fungus, we can determine whether we find evidence for density-dependent mortality and whether mammal abundance affects this mechanism.

According to the Janzen-Connell hypothesis, an accumulation of pathogens and species-specific predators near parent trees will suppress seed survival and seedling recruitment in areas with a high increase in palm density, preventing the species from gaining dominance. Thus, we should find an increase of host-specific predators and pathogens on the high density plots compared to low density plots resulting in higher seed mortality (Janzen 1970, Connell 1971).

The protected site showed an increase in fungus infestation rates with increased palm density, which is in line with the Janzen-Connell hypothesis. The hunted site, in contrast, showed no increase in fungus presence with palm density. Why this difference exists is uncertain. Possibly, the fungus depends on another species to enter the seeds and if the population levels of these species do not increase, then the fungus infestation rates cannot increase either. Another possible cause are environmental factors, like soil moisture, which differed between the two sites (see also the section explaining the interactions between the species in this food web). The bruchid beetle and scolytid beetle infestation did not significantly differ between densities on either hunted or protected site. We expected an increase in infestation rate due to an accumulation of predators at higher density plots.

We did find evidence for density-dependence of the viability of the seeds. The proportion seeds viable decreased with increasing density, which is in line with the Janzen-Connell hypothesis. Thus, although we found no evidence of an increase in population size of any of the seed predators in this study, the resulting viabilities suggest that seed survival was negatively density-dependent.

Poaching did not seem to have an effect on this mechanism: the viability decreased equally between the high and low density plots, independent of mammal abundance. Possible explanations why seed viability decreased without one of the predators increasing are that there is another predator or pathogen which does accumulate at higher density plots, but this is not likely as we did not see any other mortality factor when we were opening the seeds. A second explanation is the time it takes the predators to find the seeds. If predators (especially scolytids) can find the seeds easier if they are more abundant, they will have infested these seeds earlier than seeds underneath palms when they are rare. As we determined the viability of the seeds by estimating the proportion endosperm still intact, seeds with earlier infestation will have a lower amount of endosperm still intact compared to seeds infested late. This could result in the negative correlation we found between viability and palm density.

Previous studies showed that a decrease in mammal abundance resulted in a decrease in density-dependent mortality of palm seeds (Wyatt & Silman 2004). Thus, if seed mortality does not increase or even decreases when mammal abundance is reduced, the density-dependent mortality mechanism will not be able to compensate for the increase in survival of the seeds when an important disperser/predator decreased in abundance.

Conservation implications

Anthropogenic disturbances, such as poaching, can have a major impact on the functioning of a food web and consequently the diversity of the tropical forest. Although poaching has been receiving more attention in the last few years (e.g. Peres 2000, Wright 2003, Forget & Jansen 2007), more research needs to be done.

The reduction of game species and the potential loss of their functions can decrease seed dispersal and affect seed survival and seedling recruitment. *Astrocaryum standleyanum* showed an increase in seed survival in an environment with reduced mammal abundance in this study. Similar trends have been found for several other palm species, such as *Attelea butyraceae* and *Astrocaryum murumuru*. (Wright *et al.* 2000, Silman *et al.* 2003, Galetti *et al.* 2006). In these studies, an important disperser/predator had decreased or disappeared resulting in an increase in the population size of the palm species they dispersed or predated upon. Other studies have shown the opposite for non-palm species: a reduced mammal abundance decreased the survival of the seeds or reduced the seedling recruitment, decreasing the population size of the species (Asquith *et al.* 1997, Forget & Jansen 2007).

Density dependent mortality is regarded a key factor keeping the population sizes of tree species in tropical forests in balance, thereby maintaining the high diversity of the forest (Janzen 1970, Connell 1971). This study showed that this mechanism is not enough to compensate for the increase in seed survival resulting from reduction in mammal abundance. If seed survival and seedling survival increase, the population size is likely to increase as well. As one species is a better competitor than others, an increase of one species will result in a decrease in other species, thereby decreasing the diversity of the forest (Connell 1983). If the seed survival and/or seedling recruitment is negatively affected, this will result in a decrease in the population size, thereby decreasing diversity as well. To preserve the Neotropical forests with its high diversity we will have to control hunting, before more species will go extinct.

Future research

It is difficult to determine all the effects that poaching has on the plant community, as many game species interact directly as well as indirectly with many plant species at the same time and poaching may alter the seedling regeneration of these other species as well (e.g. the Central American agouti which is an important predator and/or disperser for several palm species simultaneously (Brewer & Rejmanek 1999, Forget *et al.* 1994, Wright *et al.* 2000)).

The effects of poaching on *Astrocaryum standleyanum* we found in this study may provide a good example for other food webs in the Neotropical forest, but it is very important to realize we probably examined only a part of the actual food web surrounding the black palm. We did not determine all the parasites and pathogens affecting the herbivores, like the agouti, and we may have missed other less dominant seed-predators, which may play a more important role than we think (Memmott *et al.* 2000). More research on this food web as well as research on other food webs might provide us with more (essential) information in how we should preserve the Neotropical forests as best as we can.

Secondly, we need to take in account the mortality rates of the seedlings. Other predators predated on the seedlings may compensate for the increase in survival of the seeds we have found in this study.

A long-term study, investigating the survival of the seedlings until they become adults would show whether my expectations will come true.

What is the function of fruit pulp?

Our experiments allow us to also evaluate the function of fruit pulp in *Astrocaryum standleyanum*. Fruit pulp has been the subject of many studies, and can have many different functions (Mack 2000, Tiffney 2004).

The transition from ripening seeds to established seedlings is a critical stage with high mortality rates. In response to these high rates, plants have evolved a diverse array of morphological, anatomical and physiological traits that enhance the chances of survival of their offspring. One of these traits is the production of fruit pulp (Webber & Woodrow 2004). Several theories have been proposed on how the presence of fruit pulp enhances the survival of the seeds.

One possible function of fruit pulp is protection of the seed against predators and/or pathogens. The mortality of some seeds can reach up to a 100 % due to predation by insects (Janzen 1972) and by decreasing the accessibility of the seeds for insects and pathogens by producing fruit pulp, the chances of survival of the seeds would increase (Silvius & Fragoso 2002, Mack 2000). Protection of the seed against predators and pathogens can be further enhanced by producing pulp that contains lethal toxins (Cippollini & Stiles 1992, Cippollini & Levey 1997, Schaefer *et al.* 2003). Especially unripe fruits contain toxins to prevent the fruits from being eaten before the seeds have ripened and are ready to be dispersed. After the seeds have ripened the toxins disappear and the fruit pulp can be eaten by the dispersers. Sometimes, however, the pulp remains toxic even after seed ripening. Then, the presence of the pulp may mainly serve for protection against insects and pathogens, making it harder for them to infest the seeds (Cippollini & Levey 1997).

In this study, the presence of fruit pulp in *Astrocaryum* did not affect seed colonization by scolytid beetles. Although we expected a lower infestation rate due to fruit pulp presence, no significant difference was found. Fruit presence did not seem to affect bruchid infestation either. In this study, bruchid larvae were present in seeds that we had collected directly from the trees, with the fruit pulp intact. This indicates infestation by bruchid beetles did not depend on handling of the fruits by other vertebrates and pulp presence did not protect the seed against bruchid beetle infestation.

A second possible function is the attraction of seed dispersers. By embedding the seeds in fruit pulp that is attractive to mammals, seeds are more likely taken and dispersed, and chances of survival of these seeds will increase. Plants offer fruit pulp as food for the animal and the animals in turn will disperse the seeds in their faeces, by handling or by scatterhoarding.

In case of scatterhoarding, the fruit is believed to be present to satiate the animal and, consequently, reduce seed predation and thereby enhancing the chances of the seeds to be hoarded. The presence of edible pulp is considered as a reward for the animal. This is also called the quick meal hypothesis (Smythe 1989, Guimaraes *et al.* 2006).

In this study, we found that the Central American agouti, the current main disperser of the black palm, preferred seeds without fruit. The average removal time of seeds without fruit pulp was significantly lower compared to seeds with fruit pulp present and age had no effect on the removal time at all. Peeled pieces of fruit pulp were found on the forest floor at the location of the stations, indicating fruit was removed before they took the seeds with them (personal observations). This indicates the agouti considered the fruit pulp a nuisance rather than a food reward.

We didn't determine seed fate in this experiment. It remains possible that seeds without fruit pulp are more likely eaten than seeds with fruit pulp, making fruit presence beneficial

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to the survival chances of the seeds and consequently the reproductive success of the tree. A study on feeding habits of the red-rumped agouties shows the chances of being eaten or cached does not depend on the presence of fruit pulp (Guimaraes *et al.* 2006) and it is likely the central American agouti will have the same behavioural traits.

As several researchers have observed the agouti removing the fruit pulp and this is not meant for feeding, why would they remove the fruit? Smythe (1989) hypothesized the fruit is removed to remove the bruchid larvae as well, but our experiments indicate that this is not true. Another possible explanation is the production of ethanol (Dudley 2004). This process produces a very distinctive penetrating smell (Dudley 2004, personal observations), which might attract other predators to the buried seeds. Removing the fruit will decrease the likelihood of food competitors finding the seeds.

As fruit pulp removal by white-faced monkeys did have a negative effect on the bruchid beetle development this might explain why agouties have a preference for seeds without fruit present. If seed survival is higher of the seeds which had the fruit pulp removed, the agouties benefit from taken these seed opposed to seeds with fruit pulp which have higher chances of being eaten by the bruchid beetles while the agouties had cached the seeds.

Some people believe the fruit pulp is often not an adaptation for attracting current dispersers, but that it coevolved with larger new world herbivorous mammals, which have gone extinct (Janzen 1982a, Janzen 1984). In the Pleistocene, until around 10.000 years ago, the mammalian mega fauna in the new world could be compared to the mega fauna present in Africa. Fossils are found of big herbivores, e.g. gomphotheres (mastodon-like proboscidiens), ground sloths and several others (Janzen 1982a). The fruit pulp was produced to attract these species, which feed on the entire fruit, and defecate the seeds somewhere away from the parent tree. Since most of these mammals have gone extinct, the fruit pulp might not have a purpose anymore, it has become an anachronism.

Janzen compared the fruiting trees from the old world with the new world, to determine similarities between the fruits dispersed by large herbivores in the old world with fruits in the new world. Most large herbivores are still present in the old world and he determined the traits of the fruits and fruiting trees they disperse. He listed several traits that would indicate a tree co-evolved with large herbivores as the main disperser and listed several species in the Neo-tropics that have the same traits. Janzen mentions the black palm as one of them. The black palm has a tough endocarp to ensure the seed can pass the gut of a large herbivore unharmed, and a sweet smelling fruit to attract these large herbivores. Janzen also mentions that the crop size is too large for the current dispersers to handle and most of the seeds will remain rotting underneath the tree.

On BCI, however, with a healthy population of agouties, fruits of the black palm were removed fast and no fruits were left underneath the trees for a longer time period (personal observations), indicating the crop size of the black palm is not too large for the agouties to handle.

If the fruit was present to attract the large herbivores, the same is probably happening with the rodent as the current dispersers. The smell and bright colour will make it easier for the agouti to locate the fruits. As agouties are not interested in actually eating the fruit, while the pulp is edible, this might indicate the fruit pulp has co-evolved with large herbivores that were interested in feeding on the pulp. If the large herbivores used to be the most important dispersers of the black palm, the agouties took over the function of dispersing after they went extinct, thereby making fruit presence less important.

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During the experiments we also observed a scarab beetle burying the fruits underneath the trees in shallow tunnels. Usually these dung beetles feed and reproduce on dung, rolling dung in a small ball and bury it, after which they lay their eggs in the dung. As dung is less available in rainforests compared to other areas, e.g. savannah, dung beetles specialized in feeding and reproducing on fruits instead of dung (Davis & Sutton 1997). An experiment in the lab with a fruit feeding and reproducing scarab, *Oxysternon festivum*, showed one beetle burying 5 intact fruits in just a few hours (Silvius & Fragoso 2002).

As burial decreased the accessibility of seeds to the scolytid beetle this scarab has a positive effect on the survival chances of the seeds. As the beetles bury the seeds on the same spot where the fruit has fallen this will be mostly straight underneath the parent tree. Due to the accumulation of pathogens near the parent tree, seed dispersal away from the parent tree is probably important to the parent tree, making it unlikely that the function of fruit is to make sure the seeds get buried by the scarabs. The scarabs probably adapted to the fruits and the black palm has no major benefit from their presence.

It seems the fruit does not protect the seeds from insect predators like the bruchid beetle or the scolytid beetle, and it is not present to satiate the most important scatterhoarder, the agouti. It is not entirely sure whether the fruit pulp protects the seeds against fungus infection, although it's more likely the fruit is present for dispersal means and not for protection. The fruits contain a massive amount of sugars (Dudley 2004) which is usually meant to attract herbivores (Cippolini & Stiles 1992) and as the fruits ripen, the sugar is fermented into ethanol, inducing a penetrating smell and it will act as an appetitive stimulant (Dudley 2004). The appetitive effect of the ethanol indicates a species feeding on the fruit pulp is stimulated to eat more and the only way the tree will profit from this is if the species disperses the seeds at the same time. Next to attracting the dispersers by offering them fruit pulp as a food source, can fruit pulp attract the dispersers by smell and colour as well, making it easier for the dispersers to detect the fruits. Currently this seems to be the most important function of the fruit pulp of the black palm.

As the production of fruit pulp is quite a massive investment by the tree, it seems a waste of resources to create this amount of pulp (42% of the fruit; Dudley 2004) as the black palm does. Unless other functions are found in the future, I am convinced the fruit has originally co-evolved with larger herbivores and fruit pulp has become, at least partially, an anachronism.

If the only function left of the fruit pulp is to make it easier for the agouti to find the seeds, this might be enough to keep the trees producing the pulp. If one tree stops producing the pulp, the fruits of other trees will have a higher chance of being dispersed and will reproduce more successfully. This will ensure the fruit pulp remains present even though its most important function has disappeared.

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Appendix B: The average damage to a seed and the proportion of the seeds still viable, after the seed is infested by bruchid beetles, scolytid beetles or fungus.

seeds infested by:	prop. endosperm still intact	prop. seeds still viable
Fungi	0.02	0.01
Scolytid beetle	0.19	0.12
Bruchid beetle	0.47	0.48

Appendix C: The visitation rates by the agouti and removal time of *Astrocaryum* seeds in high and low palm density plots on the hunted and protected sites (Eijk van 2005).

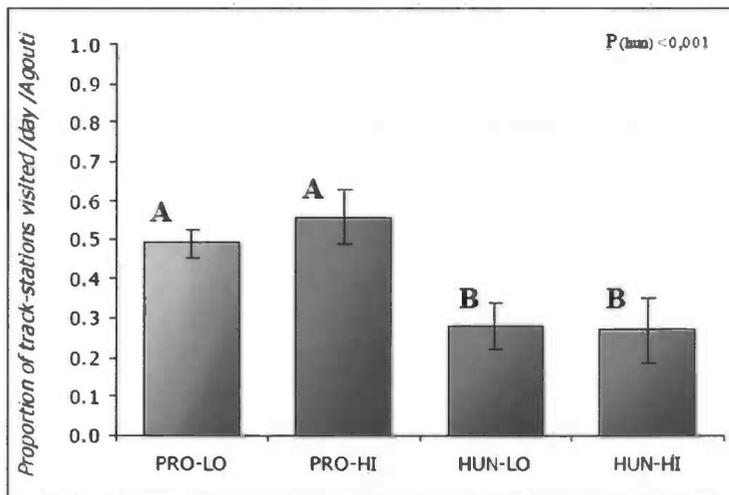


Figure 4.2. The average proportion of track stations visited per day by Agoutis in different treatments ($n = 12$).

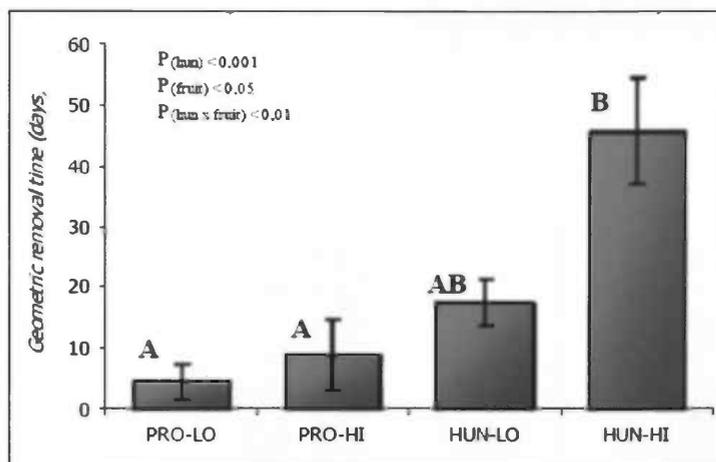
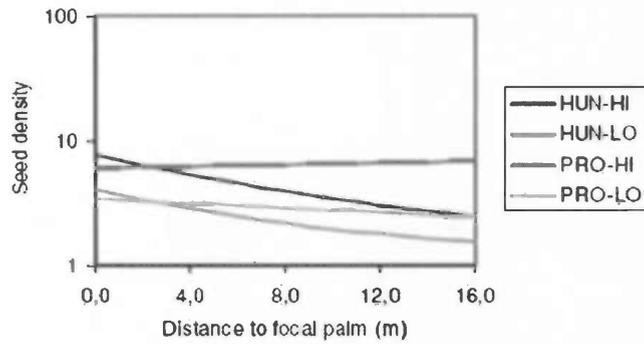


Figure 4.4. Average geometric seed-removal time (days) in different treatments ($n = 12$).

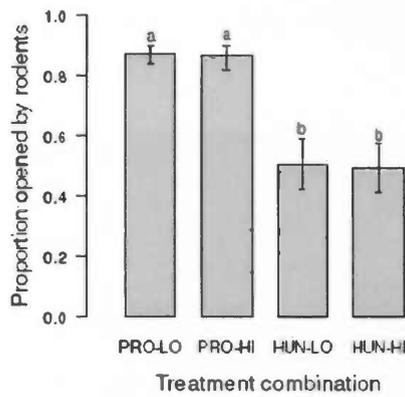
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Appendix D: Results of the study conducted on BCI and PLR by Heleen Sharrot in 2005.

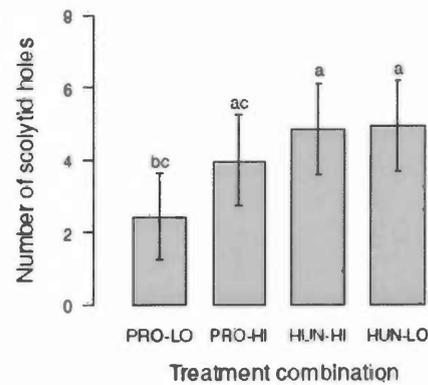
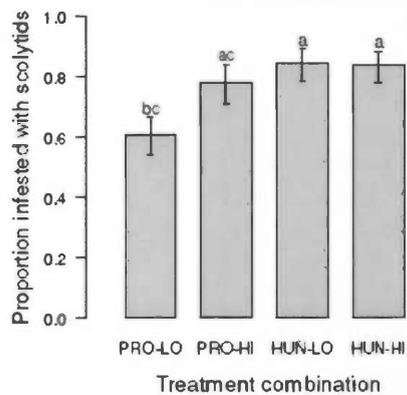
The seed density found in the soil depending of the distance away from the tree:



Proportion seeds eaten by rodents in contrasting areas:

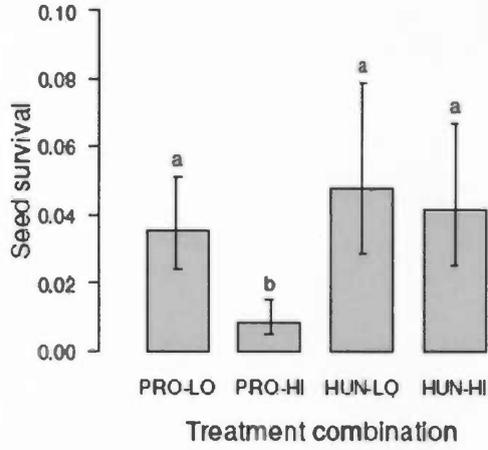


Proportion of seeds infested by scolytids and average number of scolytid holes in contrasting areas:



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Proportion of seeds still viable in the soil depending of seed density:



Appendix E: Scarab beetles observed to bury *Astrocaryum* fruits underneath the adults.

