Food caching by the Red acouchy, *Myoprocta acouchy* : a test of scatterhoarding models

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Acknowledgements

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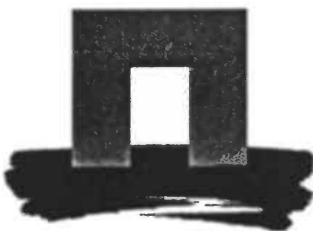
CONTENTS

INTRODUCTION: Factors influencing scatterhoarding patterns

Animals in areas with periodic food shortage have several options to solve this problem. Different mechanisms have evolved ranging from e.g. migration to hibernation and temporal weight loss. Hoarding food during times of food abundance is also a strategy to overcome temporal food shortages (Klosinska, 1994). A great number of bird, mammal and insect species have this strategy (for an extensive overview see Vander Wall, 1990). The stored food reserves are the major food source during times of food scarcity (Wauters & Casale, 1996). Whether food hoarders have a better body condition, higher survival rate and eventually a higher future reproductive success compared to non-hoarding animals depends on the retrieval rate of hoarded food items in terms of extra energy or nutrient availability (Andersson & Krebs, 1978; Waite, 1990; Nillson et al., 1993; Wauters et al., 1995).

Optimal foraging theory (Krebs et al., 1983) predicts that a hoarding animal will maximise cache yield. Factors that influence the yield are: the nutritional value of the food items, the rate of retrieval of the food items, the loss of food due to decomposition (or in the case of seeds, germination), the loss of food items due to cache robbers and the energy spent on hoarding and retrieving the food item (Vander Wall, 1990).
Cache robbing has an important influence on the spacing of food items by the hoarding animal. Keeping them in one or several clumps together (larder-hoarding) creates a risk of attracting robbers and losing a big amount of the stored food. Animals that cannot defend their stores effectively should therefore spread food items far enough from each other to diminish attraction to cache robbers. The hoarding activity is called scatterhoarding when every food item or small groups of food items are cached elsewhere.
More spacing from each other will decrease the chance of cache robbing (Stapanian & Smith, 1978; Sherry et al., 1982). However, spacing out means also that larger distances have to be covered and more energy and time have to be spent.

The scatterhoarder has to find an optimum in the balance between on the one hand more spacing, and on the other hand energy and time spent, to maximise cache yield. Stapanian & Smith (1978) and Clarkson et al. (1986) developed models for optimal spacing by scatterhoarding animals around a central food source. Both models assume that the loss of caches is mainly influenced by the amount of empty space around a cache i.e. the density at which caches are made.
The optimal density model (ODM) of Stapanian & Smith (1978) predicts that the animal minimises travelling costs and maximises the distance between two items. The optimum will be reached when items are cached at a density that discourages competitors from searching a second cache after finding a first.
Clarkson et al. (1986) suggest a model whereby the animal has to work with a time restraint (time restraint model, TRM). In this case the animal has to find an optimum between minimising cache robbery due to higher densities and minimising time spent in caching the food item.

These models lead to several predictions concerning the optimal spacing of caches (e.g. Vander Wall, 1990).
a) The first items are cached close to the source with subsequent caches at increasing distances (ODM) or both near and at increasing distances (TRM).
b) Nearest neighbour distances of cached food items with the same value are constant in the caching area (ODM) or increase with distance from the food source (TRM).
c) Mean nearest neighbour distances vary proportionately with the value of the food being cached (both ODM and TRM).
d) Caching occurs in a 360° arc around the source. The distance between the source and cached item increases when the arc used to cache decreases, e.g. due to inaccessibility (both ODM and TRM).
Several studies have tested one or more of these predictions for fox squirrels (*Sciurus niger*) (Stapanian & Smith, 1978), eastern grey squirrels (*S. carolinus*) (Kraus, 1983), red squirrels (*Tamiasciurus hudsonicus*) (Hurley & Robinson, 1987; Rice-Oxley, 1993), magpies (*Pica pica*) (Clarkson et al., 1986), marsh tits (*Parus palustris*) (Sherry et al., 1982; Cowie et al., 1981) willow and crested tits (*P. nantenus* and *P. cristatus*) (Jokinen & Suhonen, 1995) and kangaroo rats (*Dipodomys merrioni*) (Lisa & Daly, 1998). The models have not been tested in a tropical environment (Vander Wall, 1990).

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In this study, we will test both models' predictions for cache spacing pattern in a natural tropical habitat. The previously mentioned studies consisted mostly of experiments in artificial conditions or were done using unnatural sources. We will test predictions a, b and d mentioned before. Hypothesis c will be tested although our experimental set-up is not designed to test this hypothesis. In addition, we will test some predictions about factors that are typical of caching in a natural system.

Firstly, source robbery. Source robbery has not been included in the two models but is an important factor that can affect cache behaviour. The probability that a robber discovers a source will be higher, the longer the source is not fully depleted by the caching animal. On the other hand, the loss will be bigger, when the source is discovered early during caching. We will test the hypothesis

e) that animals anticipate the risk of source robbery by caching more quickly when the source still contains a large quantity of food.

Another factor that can influence cache spacing pattern in a natural system is the variation in food value between food items within a source. Natural sources will often consist of items of different food values arising from differences such as seed weights. The models make predictions (hypothesis (c)) about different values, however they are only valid when comparing sources composed of items with the same value in a source, not for sources with items of different values. These predictions have been tested for several animal species (Jokinen & Suhonen, 1995; Lisa & Daly, 1998).

We offered sources with items of a range of values so we could test if the animal makes any decision concerning food value. We tested the following predictions:

f) Higher valued items are cached first.
g) Higher valued items are cached at lower densities.
h) Higher valued items are cached at larger distances.
i) Animals spend more time in hiding higher valued items.

Eventually, we want to come to a model that describes cache spacing patterns adequately under natural conditions.

We did our study in a neo-tropical rainforest where transport of seeds by large animals is very important for the dispersion of plant species (Forget, 1990; 1991). We studied the caching pattern of the red acouchy. This animal caches several large fruit species that are often easy to weigh and mark.

METHODS

Research area
The study was conducted around the Station des Nouragues in French Guyana. It is situated 100 km south of Cayenne in a natural reserve. The area consists of slightly sloping primary evergreen tropical rainforest without human interference. Annual precipitation is around 3000 mm with a distinct dry season from September-October. Mean elevation is about 100 m above sea level. The well-drained clayey and sandy-clayey ferralitic soils lay on weathered granite rock material (Van der Meer & Bongers, 1996).
About 100 ha around the camp are divided in squares of 100 x 100 m by a grid of pathways. In these squares most trees with a diameter bigger than 10 cm have been assigned a specific number. Of these trees the co-ordinates are known.
Through the area runs a small river, which divides the area in two. Two rather flat surfaces of the area were used in this study; north of the river the Petit Plateau with shallow granitic soils and south of it the Grand Plateau with deeper ferralitic soils.

Animal species
The study focuses on the red acouchy, *Myoprocta acouchy* (Erxleben, 1777), also named *M. exilis* (Wayler, 1831). This terrestrial caviomorph rodent of the dasyproctidae family reaches a length of 33-39 cm and weighs 1.05-1.45 kg (Emmons & Feer, 1990). Acouchis are territorial scatterhoarders and bury individual seeds in shallow caches. They are known to use seeds and fruits from a large number of tree species and are therefore considered to be important dispersers in the Amazonian forests (Forget, 1994; 1996). Acouchis are diurnal with their greatest activity in the early morning and evening. They live solitary or in little family groups with overlapping territories (Dubost, 1988).
Species which are seen to be source robbers and are probably capable of cache robbing, are the red-rumped agouti (*Dasyprocta agouti*) and two species of peccaries, the collared peccary (*Tajassu tajacu*) and the white-lipped peccary (*Tajassu pecari*). The agoutis are also important scatterhoarding rodents of the dasyproctidae family (Hallwachs, 1986; Forget, 1996) but are about 3-5 times as big as the acouchy. The peccaries are very similar in behaviour and appearance as their related wild pigs *(Sus scrofa)* but slightly smaller. All species are active during the day.
Insects, especially moths, infesting seeds can also be considered as cache and source robbers but were not important in our study.

Tree species
We used seeds of *Carapa procera* (Meliaceae) in this study. The large brown quadrangular seeds are 2-5.5 cm long and weigh on average 18.4 g (range 8.5-30) (Forget, 1996). They are highly attractive to a great number of mammals because of their high fat content of about 50% (Siepel, 1998). The fruit consists of 5 husks covering 1- 20 seeds. The fruit breaks open and the seeds are scattered several meters around the tree when the fruit falls on the forest floor. The fruiting season is from February until June. 1999 was a year with a low production not only for *Carapa procera* but also for other fruiting trees and thus overall food abundance seemed to be quite low.

Experiments
The main experiment was done in April and May of 1999 in the rainy season when the *Carapa* trees produce seeds. Seeds used in the experiment were caught in nets beneath producing trees and stored for 1–7 days. Seeds of different weights, without signs of infestation or deterioration, were selected. The seeds were marked after weighing by attaching a 1 m long nylon thread with a needle to one of the edges of the seeds. A brightly coloured piece of flagging tape was attached to the far end of the thread to facilitate recovery (exp. 3-11). Every individual seed was marked by a unique bar code on the far end of the thread.
11 plots were established. Every plot was placed under or close to a fruiting *Carapa* tree (except exp. 1). Dubost (1988) measured a maximum territory width of about 100 m. Therefore, the plots were situated at least 100 m from each other so that they were likely to be in different acouchy territories (Dubost, 1988). 5 plots were placed on the Petit Plateau and 6 on the Grand Plateau. 49 marked seeds with different weights were placed in random order in a square of 70 x 70 cm with 10 cm distances in every experiment. Threads were placed so that the probability of tangling was low.

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A surveillance camera (Philips VCM 6250) in a waterproof housing (Videor VHL-2EC) connected to a time-lapse video recorder (Panasonic AG-1070 DC) and a 12-volt car battery was placed around 1.5 m above the plot. We recorded in 24 hour mode (3 pictures per second) from dawn till dusk without changing videotape or battery. The plots could be made in the evening in the dark because all large terrestrial seed-eating mammals in the area are diurnal.

From the videotapes, we derived the order in which the seeds were taken, the time at which the animal came into view, the time when the animal picked up a seed, when the animal went away, in which direction it went and which species it was. The day after (almost) all seeds were taken away (mostly after one day, sometimes two or three), the area around the plot was thoroughly searched until as many seeds as possible were found again. The number, the condition (buried, eaten, etc.) and the direction and distance from the plot or a numbered tree were recorded for every seed found. In this way, the distance and direction a seed was taken from the food source could be computed from the known co-ordinates. Buried seeds were left in place for further study of cache management, which is not discussed in this paper.

We computed the nearest neighbour distance of all cached seeds as a measure of density. Caching speed was computed by dividing cache distance by cache time (the time between walking off with a seed and coming into view again without it). Only data from seeds where cache time was less than 600 s and speed up to 1 m/s were used. A few unlikely values originating from errors in measurements or disturbances in behaviour were discarded in this way.

Analyses.

Analysis of the results was done by linear regression between pairs of factors, since the Spearman rank correlation tests did not result in different conclusions and linear regression quantifies relations more clearly. We determined the regression factor β with linear regression for each individual plot for relations that we were interested in. We used a t-test at $\alpha = 0.05$ to test if relations were significant for all plots together. The β's, weighed with the inverse of the square of their standard error to account for the different numbers of data and variance in each plot, were tested for a significant difference from zero (G.Gort, pers. comm.).

Analysis of uniformity around the 360° arc was done with a Raileigh-test (Zar, 1996).

Because we were only interested in the scatterhoarding pattern by acouchis, only data of seeds cached by an acouchy were used.

Analyses were performed with the statistical program SPSS.

RESULTS: The scatterhoarding pattern of the red acouchy

538 seeds were placed in the 11 plots (table 1). 1.1% were left on the source. 9.1% were taken by source robbers in 3 experiments; white-lipped peccaries (exp. 6), collared peccaries (exp. 10) and an agouti (exp. 9). 89.8% had been removed by an acouchy. We found 87.6% of the threads of these seeds on the first day of searching; 8.4% of the threads were broken with no seed attached anymore, 70.6% were attached to a cached seed and 9.8% of the threads had seeds removed or had only a part of the hull attached. The last category was considered as being eaten. The rest (11.2%) was found in different states such as entangled or not buried.

The acouchy started with only 35 seeds in plot 10, because the first 14 were eaten by collared peccaries. Although the pattern was expected to be different for this plot, especially cache distances (see discussion), discarding the data did not change conclusions, except for the relation between mean weight and mean cache distance. Data from this plot is included in all other analyses presented. Seeds cached far from the source had a lower probability of being relocated by us due to the searching strategy used, but we expect that the patterns, as observed, would probably not change drastically if all seeds would have been found in every plot.

Table 1. Numbers of seeds and some mean values for all plots. Between brackets is the number of data on which the means were based. The number of found seeds includes seeds that were left on the source and also seeds in categories not shown in the table. The number of robbed seeds is derived from data from the videotapes.

Plot	# total	# left	# found	# cached	# eaten	# broken[1]	# robbed	Mean weight (g)	Mean distance (m)	Mean Nnd[2] (m)	Mean direction[3]	Mean cache time (s)	Mean speed (m/s)[4]
1	49	1	41	40	0	0	0	22.5 (48)	12.1 (40)	4.46 (40)	No (40)	93 (9)	0.19 (9)
2	49	0	31	24	7	0	0	26.8 (48)	19.4 (22)	5.59 (22)	335 (22)	180 (20)	0.29 (19)
3	49	1	46	37	8	0	0	23.7 (49)	14.8 (37)	5.07 (37)	176 (37)	159 (27)	0.18 (25)
4	49	0	30	28	0	1	0	24.7 (49)	43.7 (28)	11.8 (28)	13 (28)	268 (3)	0.21 (2)
5	49	0	40	17	1	22	0	24.2 (49)	28.3 (17)	9.03 (17)	55 (17)	103 (14)	0.38 (11)
6	48	0	44	4	5	11	23	24.3 (48)	28.7 (4)	12.7 (4)	-	298 (4)	0.20 (4)
7	49	1	43	39	3	1	0	24.0 (49)	12.8 (39)	2.84 (39)	159 (39)	-	-
8	49	0	47	44	1	2	0	22.6 (49)	10.8 (44)	3.16 (44)	63 (44)	53 (25)	0.51 (25)
9	49	0	39	20	6	0	12	22.9 (49)	24.6 (20)	7.11 (20)	11 (20)	159 (15)	0.23 (13)
10	49	3	43	23	5	0	14	21.4 (49)	21.7 (23)	6.18 (23)	No (23)	192 (18)	0.24 (18)
11	49	0	41	34	7	0	0	25.0 (49)	39.5 (34)	8.31 (34)	66 (34)	236 (21)	0.28 (21)
all	538	6	445	310	43	37	49	23.8	21.4	5.98		156	0.29

[1] broken threads

[2] nearest neighbour distance

[3] No = uniform distributed around the 360º arc and therefore no mean dispersal direction

[4] Cache distance divided by cache time

I TESTING THE TWO MODELS

a) Cache sequence and distance

Separate analysis of the plots revealed that seeds taken later were cached further away for plot 1 and closer to the source for plot 5 (figure 1). However, all plots together showed that no significant linear relation exists between cache sequence and cache distance from the source (t-test, n = 10, p = 0.316). This is not supporting the predictions of the two models that the first seeds are cached close to the source and the later ones further away (ODM) or far and close to the source (TRM).

Acouchis cache both seeds taken early and seeds taken later close and further away from the source.
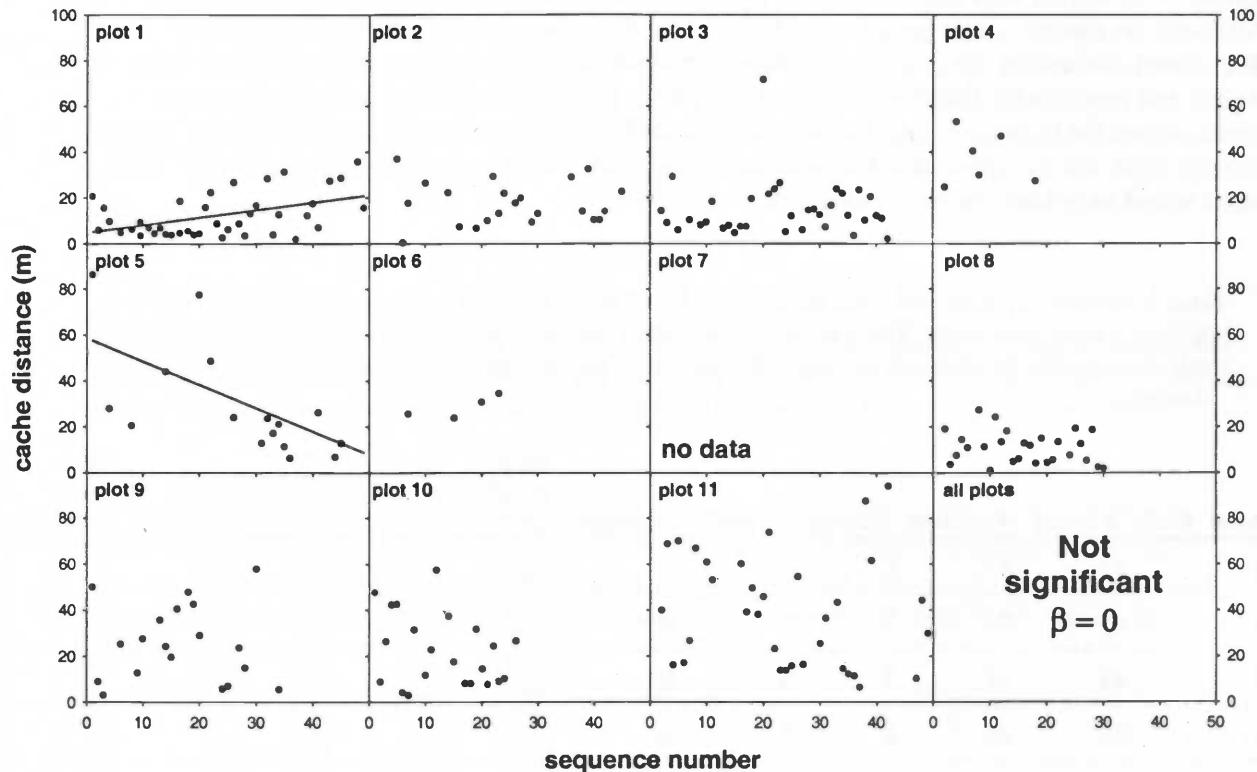

Figure 1. Correlation between sequence number and cache distance.
Two plots give a significant correlation, all plots together no significant correlation (t-test, n = 10, p = 0.316).
plot 1 : y = 4.797 + 0.314x, n = 40, p = 0.003, R^2 = 0.188
plot 5 : y = 58.683 − 1.108x, n = 16, p = 0.007, R^2 = 0.38

b) Nearest neighbour distance and distance

The nearest neighbour distance did increase with distance in 8 plots (figure 2), as well as across all plots together (t-test, n =11, p = 0.002).

This is in accordance with the prediction of the TRM that the density of seeds decreases with the cache distance but not for the ODM, which predicts a constant density.

Seeds cached far away from the source are cached further away from other seeds.

c) Mean weight and mean distance

No significant increase of the nearest neighbour distance with mean seed value could be found (lin. regr., n =11, p = 0.190).

We found an increase of the mean distance with the mean value of the seeds in a plot (figure 3), if plot 10 is ignored (lin. regr., n = 10, p = 0.044). At plot 10 the acouchy started caching with 35 seeds instead of 49.

This supports the prediction of the two models that the mean caching distance increases when the mean value of items in the source increases.

If the mean weight of seeds in the source is higher, seeds are cached at a higher mean distance from the source but not further away from each other.
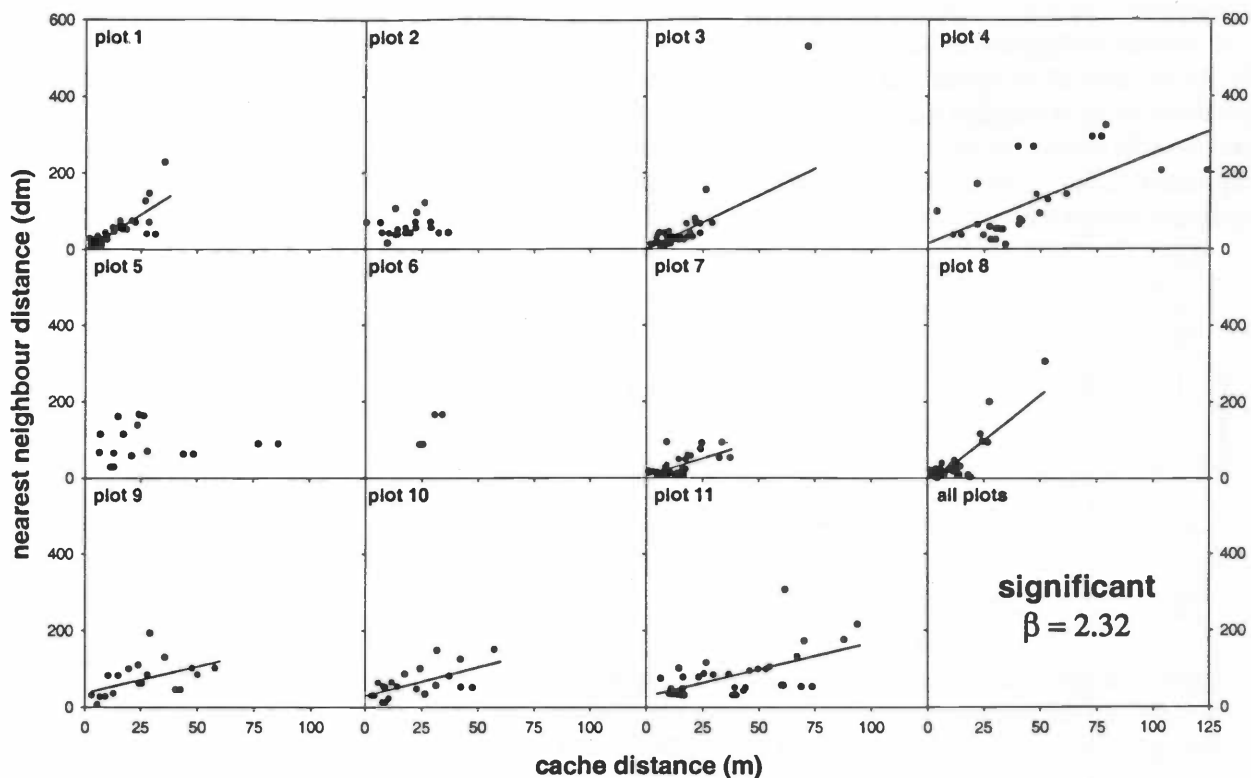
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Figure 2. Correlation between cache distance and nearest neighbour distance.
Eight plots gave a significant correlation, all plots together also significant (t-test, n = 11, p = 0.002, mean β = 2.32).
plot 1: y = 0.144 + 3.679x, n = 40, p < 0.001, R^2 = 0.628
plot 3: y = 0.089 + 2.818x, n = 37, p < 0.001, R^2 = 0.807
plot 4: y = 15.58 + 2.351x, n = 28, p < 0.001, R^2 = 0.405
plot 7: y = 5.120 + 1.825x, n = 39, p < 0.001, R^2 = 0.373
plot 8: y = -19.44 + 4.734x, n = 44, p < 0.001, R^2 = 0.664
plot 9: y = 37.15 + 1.379x, n = 20, p = 0.024, R^2 = 0.210
plot 10: y = 29.28 + 1.502x, n = 23, p = 0.002, R^2 = 0.346
plot 11: y = 13.807 + 1.405x, n = 34, p < 0.001, R^2 = 0.300
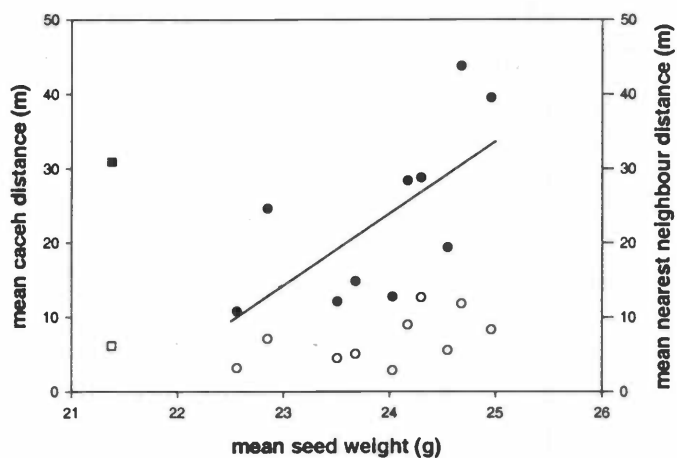
Figure 3. Relations between mean seed weight per plot (all seeds) and mean cache distance (black symbols) and mean nearest neighbour distance (open symbols).
Significant correlation for mean seed weight and mean cache distance if plot 10 (squares) is ignored (line, y = -208.12 + 9.67x, n = 10, p = 0.044, R^2 = 0.416). No significant correlation between mean seed weight and mean nearest neighbour distance (lin. regr., n = 10, p = 0.109)

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d) Uniform distribution around the 360° arc

The animals had cached the seeds uniformly around the 360° arc only in 2 plots (Raileigh-test, figure 6). An increase of the amount of variation around the mean dispersal directions of the other plots did not result in an increase in mean distance (lin. regr., n = 8, p = 0.687)(figure 4). The prediction of the two models, that the mean caching distance increases when only a part of the 360° arc is used, is not supported. Also, no significant correlation exists between mean nearest neighbour distance and variation around the mean dispersal direction (lin. regr., n = 8, p = 0.877).
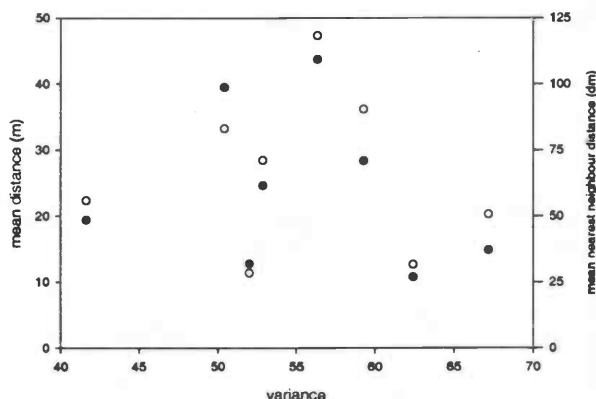

Figure 4. Relation between the variance around the mean dispersal angle (Raileigh-test) and the mean cache distance and mean nearest neighbour distance per plot. Only not uniformly distributed patterns were analysed. No significant correlation (lin. regr., n = 8, p = 0.687 and lin. regr., n = 8, p = 0.877, respectively).

e) Caching sequence and caching speed

Acouchis did not hide more quickly when there are still a lot of seeds left in the source. Neither by hiding the first seeds closer to the source (see a) nor by a higher initial speed (figure 5). A positive linear relation was found only for plot 8, but not for all plots together (t-test, n = 10, p = 0.858). Our hypothesis, that acouchis hide faster when there is still a large quantity of food in the source, is therefore not supported.
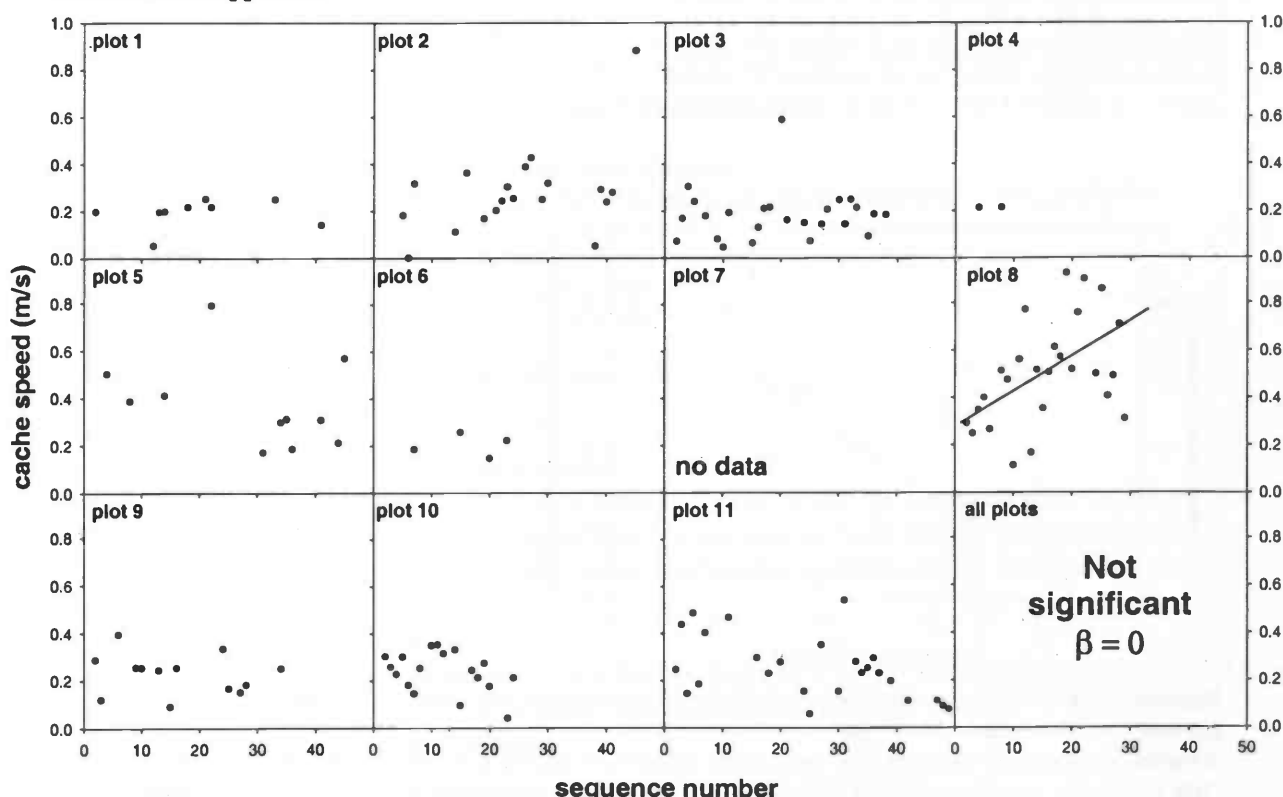
Figure 5. Relation between sequence number and caching speed.
Only one plot gave a significant relation (not with Spearman rank test). All plots together gave no significant correlation (t-test, n = 10, p = 0.858).
Plot 8: y = 0.277 + 0.015x, n = 25, p = 0.003, R^2 = 0.296

8
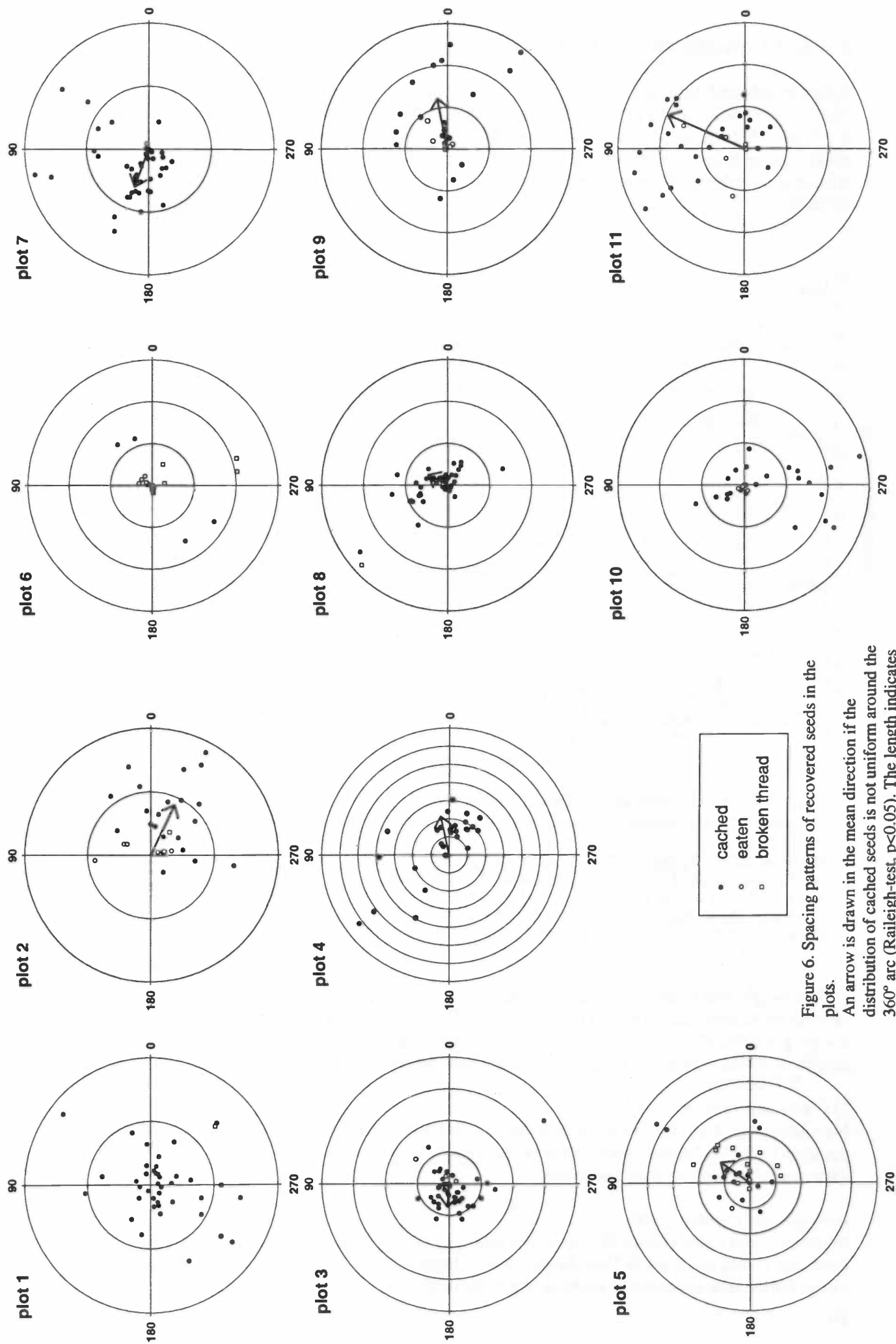
Figure 6. Spacing patterns of recovered seeds in the plots.

An arrow is drawn in the mean direction if the distribution of cached seeds is not uniform around the 360° arc (Raileigh-test, p<0.05). The length indicates the mean cache distance. Circles are drawn at 20 m intervals.

II SEED VALUE AND SPATIAL DISTRIBUTION.

f) Seed weight and distance

Heavier seeds were cached further from the source in 6 plots. This trend was significant across all plots (t-test, n = 11, p < 0.001)(figure 7). Seeds not found were significantly heavier than cached seeds we could relocate (t-test, n_1=304, n_2=92, $mean_1$=27.0, $mean_2$=23.2, p < 0.001). This indicates that the relation is probably even stronger because especially the seeds cached further have a lower chance to be relocated.
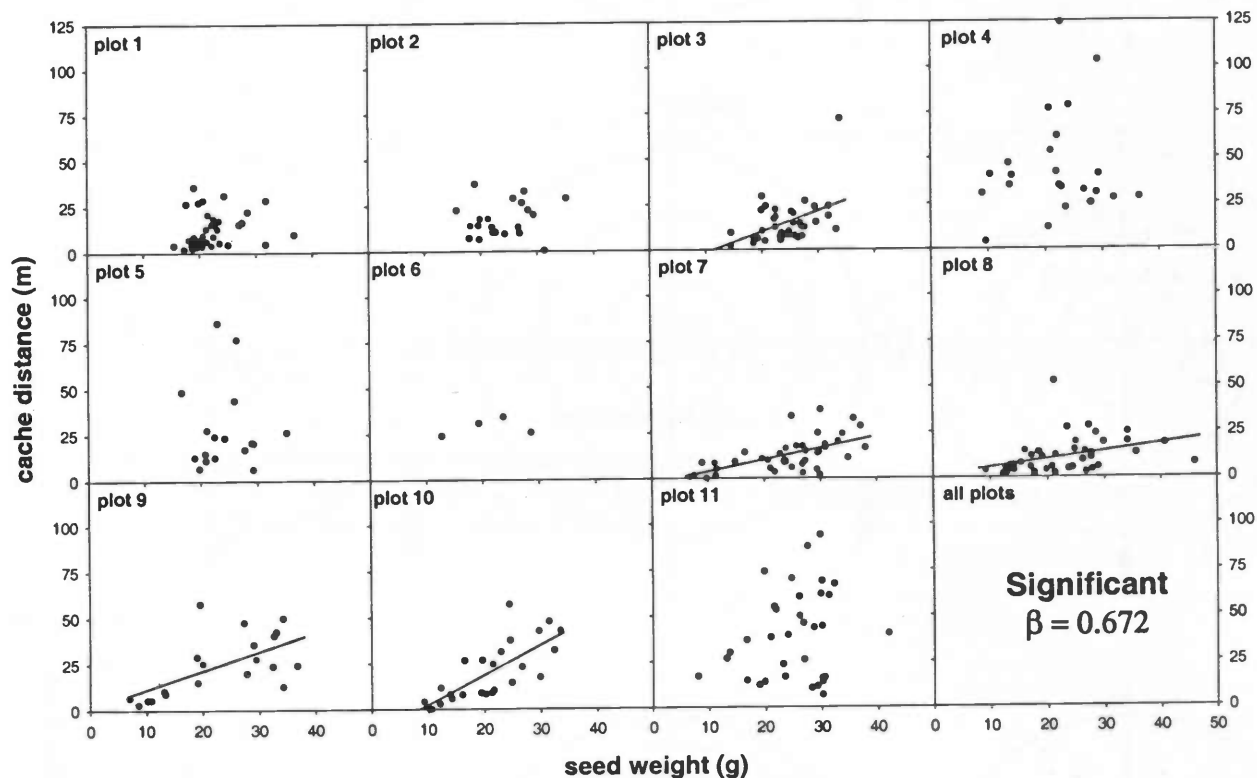

Figure 7. Relation between seed weight and cache distance.
Five plots show a significant correlation, all plots together also significant (t-test, n = 11, p < 0.001, β = 0.672).
plot 3: y = -12.96 + 1.139x, n = 37, p = 0.005, R^2 = 0.178
plot 7: y = -2.556 + 0.637x, n = 39, p < 0.001, R^2 = 0.323
plot 8: y = 1.142 + 0.431x, n = 44, p = 0.017, R^2 = 0.108
plot 9: y = 1.177 + 1.022x, n = 20, p = 0.004, R^2 = 0.336
plot 10: y = -13.95 + 0.752x, n = 24, p < 0.001, R^2 = 0.516

g) Seed weight and nearest neighbour distance

Heavier seeds were cached further from each other in 2 plots, as well as across all plots together (t-test, n = 11, p = 0.002)(figure 8). This is a logical outcome because we have already seen that nearest neighbour distance increases with distance (see b) and heavier seeds are cached further away (see f).

h) Cache sequence and weight

No relationship at all was found between these factors (t-test, n = 10, p = 0.992)(figure 9). Acouchis did not seem to choose between seeds in the plots. In most cases the acouchy took one of the seeds it encountered without hesitation or search.

i) Weight and caching speed

No relation was found (figure 10). No deviation from zero for ß was found for the plot-results combined (t-test, n=10, p = 0.750). Acouchis do not spent more time in hiding higher valued items except for the time necessary to cache at larger distances.

Figure 8. Relation between seed weight and nearest neighbour distance.
Two plots show a significant correlation, all plots together also significant (t-test, n = 11, p = 0.001, β = 1.25).
plot 7: y = 1.133 + 1.133x, n = 39, p = 0.026, R^2 = 0.103
plot 10: y = 1.328 + 2.793x, n = 23 p = 0.014, R^2 = 0.218

Figure 9. Relation between sequence number and seed weight.
No significant correlation (t-test, n = 10, p = 0.992).
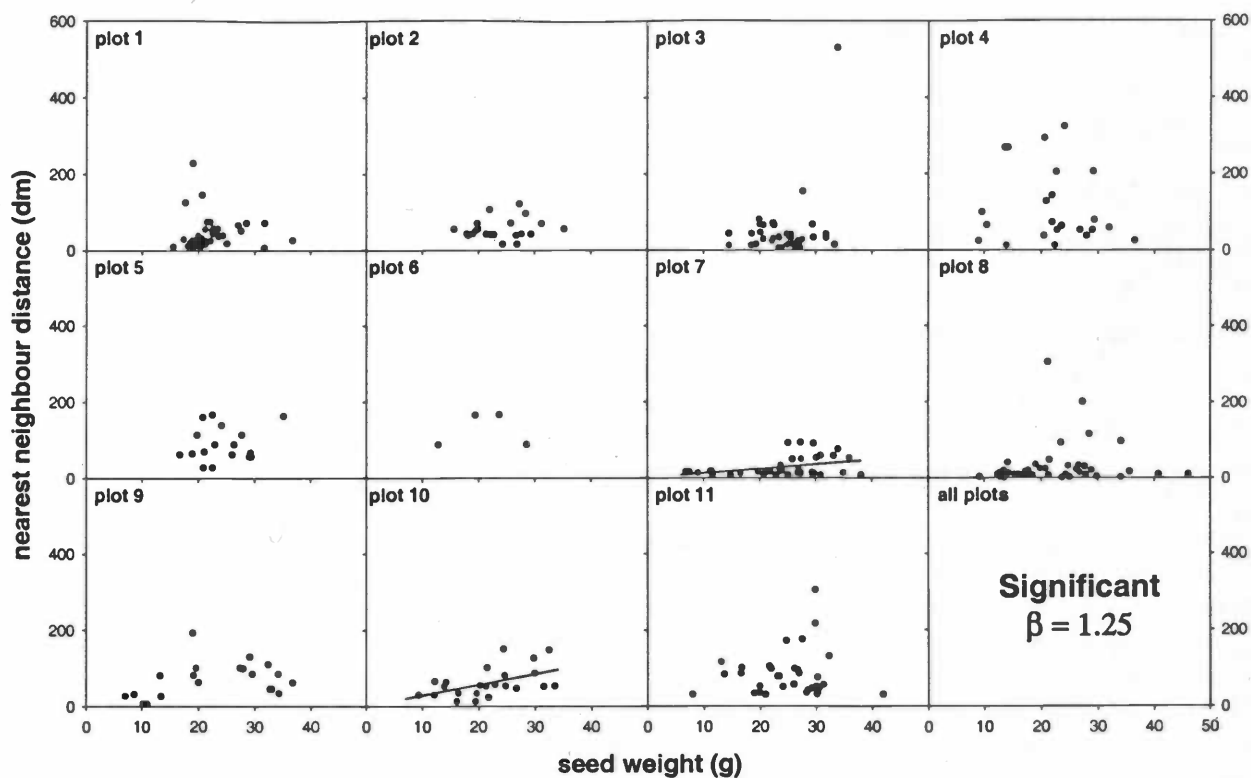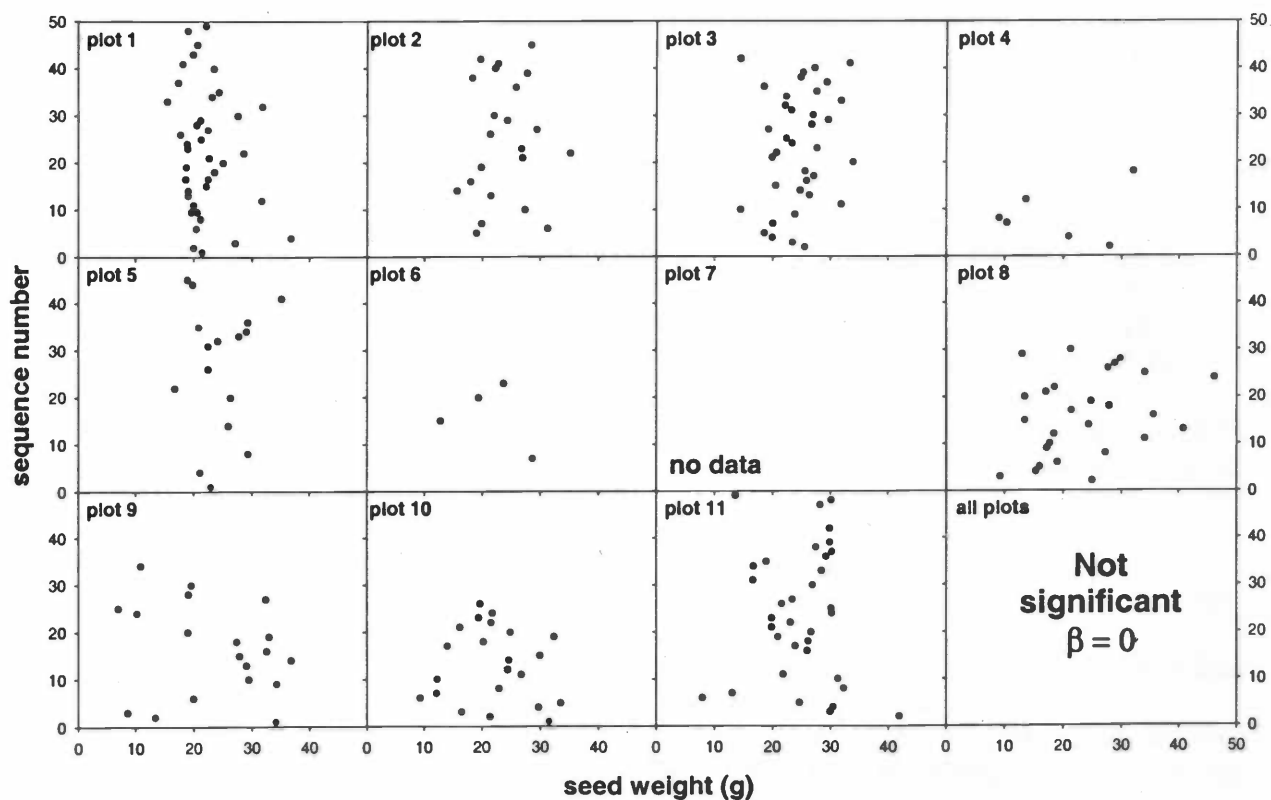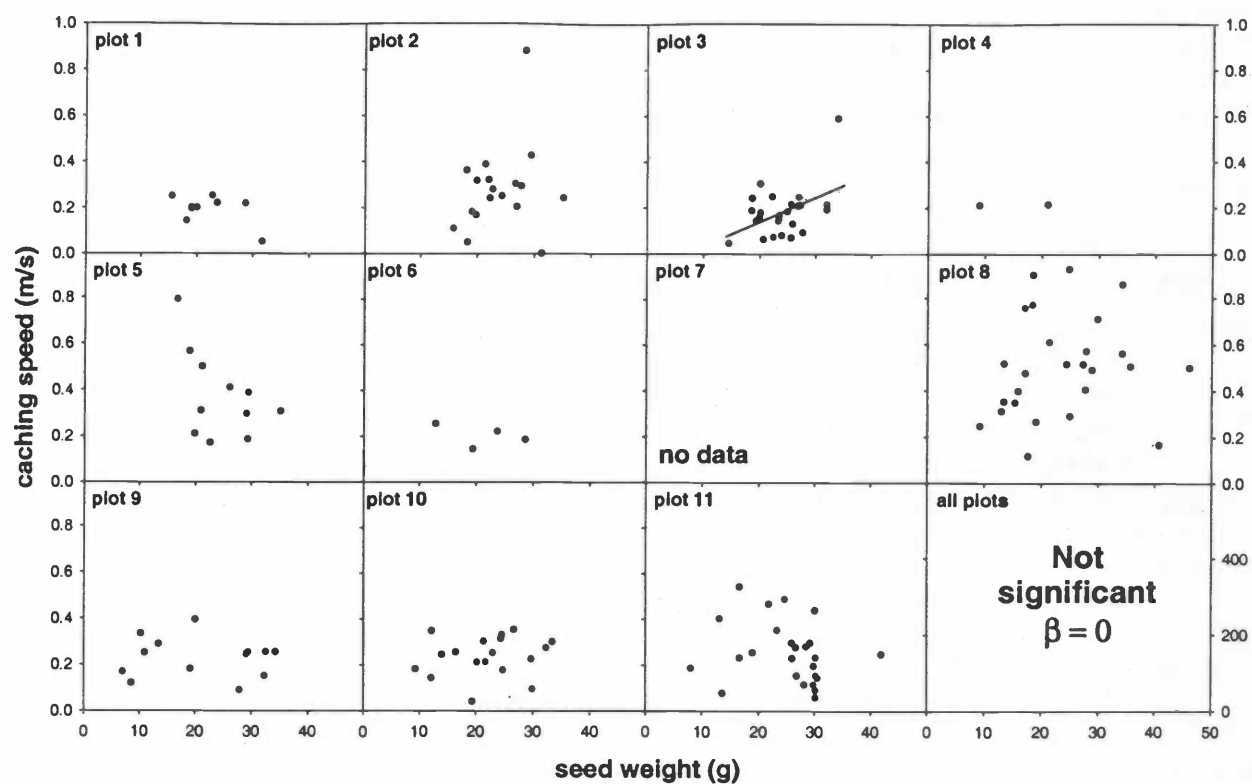
Figure 10. Relation between seed weight and caching speed.
One plot shows a significant correlation, all plots together not significant (t-test, n=10, p = 0.750).
Plot 3: y = -0.072 + 0.0106x, n = 27, p = 0.022, R^2 = 0.121

DISCUSSION: Explaining the observed scatterhoarding pattern

Both the Optimal Density Model (ODM) of Stapanian and Smith (1978) and the Time Restraint Model (TRM) of Clarkson et al. (1986) predict that earlier cached seeds will be buried closer to the source. Furthermore, the ODM predicts that subsequent caches are made at increasing distances from the source in contrast to the TRM, which predicts that subsequent items are cached far and close to the source. Jokinen and Suhonen (1995) found that willow tits did follow the predictions of the TRM but crested tits showed no difference in cache distance between early and late cached seeds. Marsh tits hid the first seeds even further away then the later cached seeds (Cowie et al., 1981; Sherry et al., 1982). Clarkson et al. (1986) found different patterns for black billed magpies, some confirming their own TRM others the ODM, however Stapanian and Smith (1978) found no correlation between caching sequence and distance for fox squirrels contrary to their predictions.
Our results correspond with neither of the two models. No correlation was found between distance and caching sequence. Early and later cached seeds were cached both nearby and far from the source.

We expected that animals cache more quickly when the proportion of seeds remaining at the source is still large. Experiments with ravens showed that individuals could improve caching speed when the chance of source robbery is higher due to the presence of conspecifics (Heinrich & Pepper, 1998). We found that acouchis do not cache the first cached seeds more quickly, neither by hiding them close to the source nor by increasing travel or burial speed. On most plots acouchis stopped visiting the plots for sometimes several hours, not indicating a great urge to prevent source robbery. This indicates that the caching behaviour of the acouchis is not affected by a time restraint due to source robbery. Only once a plot (what was left of it) was completely destroyed, so the risk of source robbery is probably relatively low although almost 10 percent of the seeds were lost to source robbery in our experiments.

The density of buried seeds is the most important factor affecting cache robbery in both models. The ODM states that the optimum cache density is the minimum density, at which a cache robber has no chance of finding a second seed by searching, after finding a first one. Therefore seeds should be buried at this density in the whole caching area. The TRM predicts that density will be higher near the source because the animal is not only avoiding high densities but also minimising the time spent in caching. Indeed, such a negative correlation between distance from the source and density was found in studies with marsh tits (Cowie et al., 1981). In this study we come to the same conclusions for the scatterhoarding behaviour of acouchis. The further away from the source a seed is buried, the further away also from its nearest neighbour, thus supporting the TRM.

Both models predict that higher valued items will be cached at greater distances to decrease density, because it is assumed that the area searched by a cache robber is dependent on the value of the item found first. The models hold only for cases where all seeds at the source have the same weight.
When a source consists of items with different values, predicting patterns will be very difficult. If the first cached seeds are heavy, the models predict that the mean nearest neighbour distance and the mean cache distance will increase for these seeds. This would, however, lead to an increase in the time and energy spent for caching seeds later on, because the models also predict that the first seeds are cached close to the source. If distances become too great for the first cached seeds, the overall time and energy spent could become too high for profitable caching.
To prevent this we can think of a different scenario. Heavy seeds could be buried far away from the source but this does not correspond with the prediction that the first seeds are cached close to the source, unless the last seeds cached are the heavy ones. But this would be illogical when an animal is working under a time restraint.
As we can see, the models cannot explain the pattern anymore because the amount of variation of item value will determine which scatterhoarding pattern is best for saving time and energy.
Experiments with tits and kangaroo rats showed that preferred food was carried further away and at a lower density (Jokinen & Suhonen, 1995; Lisa and Daly, 1998). These experiments compared patterns from plots with items of the same value.

Our experiment was designed with sources consisting of seeds with different values to imitate natural food sources. We tried to keep all factors constant in our experiment including variation and mean of

the weight of the seeds. Still, differences in mean value appeared and therefore we could compare mean seed weight with mean cache distance and mean nearest neighbour distances.

We found an increase in mean cache distance with mean seed weight, however no significant relation between mean seed weight and mean nearest neighbour distances exists. Although the results confirm the predictions of the two models, we can not draw proper conclusions about the models predictions because a different experimental design has to be used with sources with larger differences in mean seed weight.

The models predict that the seeds should be uniformly spread around the 360° arc where all directions around the source are evenly available for caching seeds. Most tits in the study of Jokinen and Suhonen (1995) cached uniformly, only a few had preferential directions. Squirrels did also cache uniformly around the 360° arc (Rice-Oxley, 1993). In other studies, red squirrels, tits and magpies did not cache uniformly (Cowie et al., 1981; Kraus, 1983; Clarkson et al., 1986; Hurly & Robertson, 1987). We found uniform distribution in only 2 plots indicating that the rest of the acouchis had preferential directions. We do not know if the other directions were no option for the animals to bury seeds but we did not observe large changes in the vegetation that could account for the patterns. A possibility we did not study, was the influence of the borders of the different territories of the acouchis on their caching patterns. Maybe acouchis prefer to hide seeds towards (the centre of) their territory to prevent disturbance by conspecifics. Magpies did cache in non-overlapping areas when one source was available for several individuals (Clarkson et al., 1986). We have, however, no information about the locations and borders of different acouchy territories.

Acouchis might hide seeds in places with specific qualities. It is often suggested that caches are located near trees and trunks to facilitate later recovery. Large objects are important navigation clues for a lot of animals (Papi, 1992).

Also the substrate in which a seed is hidden can be of importance. Seeds can be cached in clay or sand, litter and mould. Every substrate will leave different digging traces when a seed has been cached. Cache robbers could be attracted to such traces and therefore the acouchy might favour certain substrates. Litter leaves probably the least visible digging traces and digging in it is probably also less energy and time consuming. Palm trees with a cone of litter around could be more attractive for acouchis. Kiltie (1981) suggests that peccaries are therefore attracted to search for food around these trees. We collected data about the substrate and nearby clues of caches but this has not been analysed yet.

The structure of the forest floor vegetation could also influence the direction in which acouchis scatterhoard. In dense vegetation cache robbers are thought to have difficulties to penetrate, whereas open structures are easily accessible. Very dense vegetation, as occurring in treefall gaps, is likely to also hamper penetration by the acouchis themselves. The effects of differences in structure on the scatterhoarding pattern of acouchis remain to be investigated.

The models predict that the cache distances of the seeds will increase in order to avoid an increase in density if the seeds are not uniformly cached. We could not find an increase in distance with decreasing variation around the mean direction, nor a decrease in nearest neighbour distance. This indicates that the areas used were still large enough to contain all seeds we offered without a necessary decrease in nearest neighbour distance. Apparently, seeds are cached closer to each other than theoretically possible with an optimal configuration. This can mean that seeds are cached in clusters or in linear configurations. Maybe, suitable caching places are not distributed evenly in the forest.

Because in the two models it is assumed that the searching behaviour of cache robbers depends on the value of the item found first, we expect heavier seeds to be cached at lower densities and, since density is negatively correlated with distance, at larger distances. Acouchis did indeed behave according to these predictions indicating that the behaviour of the cache robbers is as expected. But the relations between weight and density and weight and distance are not simply linear. There is still a lot of variation not explained.

Heavy seeds seem to be buried at both large and small densities and distances from the source. Fitting non-linear models to the data could improve explanation of the large variance but, looking at the distribution of the data, unexplained variance will remain high.

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Furthermore the relation between weight and nearest neighbour distance is weaker than the relation between weight and cache distance. This indicates that the value of the seed effects mainly the cache distance, suggesting that the nearest neighbour distance is less important for the security of higher valued seeds. Density dependent cache robbery seems to be not as important for the scatterhoarding behaviour of acouchis as was expected.

Acouchis did not spent more time in hiding heavy seeds more effectively (e.g. deeper or better covered) from cache robbers, except for the time spent extra for increasing the cache distance, but we did not measure these factors directly.

A factor, which explains that cache robbery may not have been very important for the scatterhoarding behaviour of acouchis, is the observation that acouchis have short-lived caches. After three days and sometimes even after one day, most caches are retrieved and subsequently eaten or buried again at another place (Bartholomeus, Jansen & Elzinga, non-published data). The chance of overall cache robbery on the initial hoarding pattern is therefore probably quite small.

This behaviour is often called rapid sequestering. The idea behind it is that the acouchis cache seeds quickly to prevent source robbery and optimise the scatterhoarding pattern the following days by reburying them in a larger area. We already concluded that acouchis have not a great urge to cache the whole source quickly, so this behaviour probably serves other goals.

Our results agree with the two models for two hypotheses (table 2). The prediction that the mean cache distance increases with the mean seed value is however, as explained before, not tested properly. The conclusion that nearest neighbour distance increases with cache distance confirms the prediction of the TRM but not the one of the ODM. We conclude that neither a short-term time restraint (source robbery) nor density dependent cache robbery is very important for the scatterhoarding behaviour of acouchis.

Table 2. Predictions of the Optimum Density Model (Stapanian & Smith, 1978) and the Time Restraint Model (Clarkson et al., 1986) compared with the conclusions of our experiments and the new model.

ODM	TRM	Our experiments	New model
First items are cached close to the source, subsequent ones further away	First items are cached close to the source, subsequent ones further away and close to the source	Both first and subsequent items are cached further away and close to the source	Both first and subsequent items are cached further away and close to the source
Density is constant in caching area	Density is decreasing with distance from source	Density is decreasing with distance from the source	Density is decreasing with distance from the source
Mean nearest neighbour distance increases if mean item value is higher	The same as ODM	Mean nearest neighbour distance does not increase if mean item value increases, but see text	Mean nearest neighbour distance increases if mean item value is higher
When not whole 360° arc is used, mean cache distance increases	The same as ODM	Mean cache distance does not increase when not whole 360° arc is used	Mean cache distance does not increase when not whole 360° arc is used

As previously explained density dependent cache robbery and source robbery do not appear to be very important for the cache spacing pattern of acouchis in this study, although overall food availability seemed low due to low fruit productivity. We expected that *Carapa* fruit would be more attractive to other animals and that their searching behaviour was more intensive. No large differences in cache behaviour seem to exist if we compare this study with similar studies in years with more fruit productivity (Rutten, 1999). They found that heavier seeds are cached at larger distances and also that there is no relation between caching sequence and cache distance. Unfortunately they could not investigate nearest neighbour distances due to the limited searched area of 25 m from the source. Therefore, we have no direct or indirect evidence that the chance of robbery changes with the amount of fruit availability.

A very clear difference exists, however, between the amount of seeds that were left on the plots. In our study almost all seeds were removed by acouchis but in former studies with the same amount of seeds on the plot sometimes more than half was left (Rutten, 1999). This is in accordance with a model by Waite and Reeve (1992) that predicts that in a territory where an encounter rate of food sources is high (due to high availability), the animal should leave a food source before it is completely ready with caching.

Rutten (1999) shows, however, a result that indicates density dependent cache robbery could be important for scatterhoarding behaviour. *Licania alba* seeds from a source containing 25 seeds were cached further away than seeds from a similar source placed earlier on the same spot. This is a strong indication that the acouchy is preventing an increase in density by avoiding burying twice in the same area. A difference exists also between the caching distance of sources with 25 seeds and sources with 49 seeds. The seeds of the latter were cached further. We had one plot containing only 35 seeds (plot 10), due to source robbery by peccaries, but the mean cache distance did not seem to differ from the others and seems to be even higher than expected (figure 3). In the experiments of Rutten (1999) only 10 – 50 % of the seeds were relocated, which is quite low compared to 83 % in our experiment, but they only searched within 25 m from the source.

The data of the different plots show considerable differences. Caching speed is for example quite high for plot 8 (figure 5). Apparently, individuals behave quite differently from each other when scatterhoarding.
We can only speculate why these differences appear. Differences in vegetation around the plots could be a cause but we did not observe any large differences in vegetation structure, substrate or other factors. Maybe differences in sex, age or size can account for the differences in scatterhoarding behaviour but we know neither of these factors. The size of the territory or a difference in robbers threat could also cause different scatterhoarding behaviour in individuals.

NEW MODEL

How can we explain the spacing pattern if density dependent cache robbery and source robbery are not very important factors in cache spacing pattern of acouchis?
Acouchis could be spreading the caches to avoid other risks. These risks would be independent of cache density and would become smaller if the area of seed spreading is larger. We can think of several risks that can effect a certain area.

1. The first is the roaming behaviour of peccaries. We observed them mostly in groups of 5-25 individuals searching an area for food after which they leave and search somewhere else. Peccaries are probably cache robbers but they could be searching density independently or at least nearest neighbour distance of the *Carapa* seeds does not affect searching behaviour. It is possible that they search for a certain time-span in an area or the availability of other food items determines their behaviour. The chance of loosing a large amount of seeds to peccaries will become smaller by making the area over which the seeds are cached larger. Seeds with more value are therefore spread over a larger area just to decrease the chance of their discovery and not for a decrease in density.
2. Another factor that could be a risk is the presence of falling trees. Quite often trees fall in the tropical forest and create a large gap where several trees cover the ground. This will cause loss of caches by creating inaccessibility or destroying clues important for retrieval. 1.5% of the trees fall down, of which a third create a canopy gap of more than 4 m^2, in the research area in one year (Van der Meer & Bongers, 1996). Some of the falling trees will create gaps on the forest floor but the chance that a tree will fall on a caching area is quite small and it is very unlikely that behaviour to avoid this has developed in evolution.
3. The loss of a section of the territory to another individual can also be a possible factor. Territories have unstable borders, are overlapping and can be invaded by young individuals. Site fidelity over a year is only 27% (Dubost, 1988).

4. The above mentioned risks are independent of the source. Another factor, which could be area dependent, is insect and pathogen infestation of the seeds. Insects are attracted to high seed densities near the mother tree (Hammond & Brown, 1998). Spreading the seeds will decrease infestation chance. Although we saw some insect infestation in seeds not buried we did not observe insect attack of cached seeds. Burial seems to be enough to prevent insect infestation.

5. Increased spreading could also enlarge positive effects. By spreading, an increased part of the caches could become located in more attractive vegetation with a more suitable structure or substrate. This could be important when suitable cache locations are rare in the scatterhoarding area.

Both models mentioned before assume that the animal has knowledge of the amount of items present in the source. In the natural environment of the acouchy this is not very plausible. Firstly it does not know how many seeds will fall shortly after it discovers a source and secondly the seeds are scattered over several meters. Therefore the new model has to work for all possible numbers of seeds.

We propose a model, which minimises energy spent and minimises area-affecting risks (or maximises area-affecting positive effects).

This model can explain the spacing pattern even if we assume that:
1. the animal has no knowledge of the amount of seeds (or their values) in the source;
2. short-term source robbery is not an important factor; and,
3. density dependent cache robbery is not an important factor.

Every seed will be transported a random distance D coming from a probability distribution of distances. Our data suggest that the logarithm of D has a normal distribution with mean μ and standard deviation s (figure 11). A more thorough mathematical examination, which incorporates energy costs of caching and cache loss, should indicate whether this is the optimal distribution under the given circumstances.

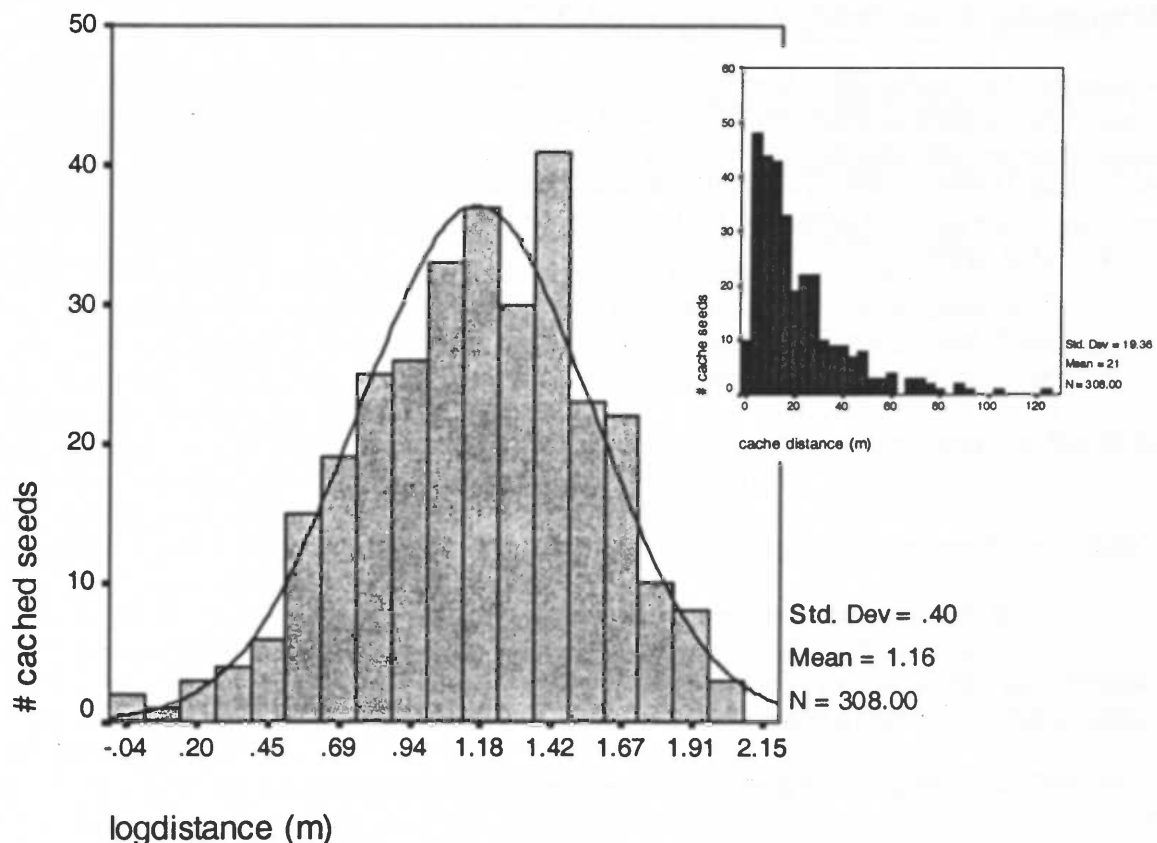
Figure 11. Distribution of cache distances.
The distribution of the log-distances is normal (plotted line; Kolmogorov-Smirnov-test, n = 308, p > 0.200).
The smaller figure, top right, is the distribution of cache distances without transformation.

The mean will increase with the value of the item. This will lead to higher mean distances for heavy seeds. Standard deviation will increase when the risk of cache loss increases. This will lead to higher overall distances when the chance of cache loss increases.

A difference in s will not greatly affect cache distances of seeds close to the source, because it is affecting the logarithm of the distances but larger distances will be influenced much more.

The distribution will not be influenced if a small minimum nearest neighbour distance does exist unless very large (unnatural) amounts of items would be offered. The animal will simply cache a small distance away from a previous cached seed that is encountered by chance.

Because of the range of possible distances a seed is cached from the source, the model can explain the large unexplained variance in the data.

We can make several predictions in addition to those in table 2 with this model:
1. The amount of items in the source does not influence the scatterhoarding pattern.
2. Previous caches will not greatly influence the distribution when suitable cache locations are not rare in the scatterhoarding area.
3. Cache distance is not dependent on cache sequence.
4. Mean cache distance increases when mean value of the items increases.
5. Cache distance is not influenced by the amount of the used 360° arc.
6. Heavier items are cached close and far away whereas lighter items are cached mostly close to the source.

The model we propose is very similar to a model for scatterhoarding patterns proposed by Hurly and Robertson (1987). They argue, referring to the optimal foraging theory (Krebs et al., 1983), that an animal is simply 'willing' to invest more time and energy for a more valuable seed to increase its security. It therefore will travel a larger distance and thus decreases density but not for the purpose itself of caching it at a smaller density. They also developed a model in which they state that animals travel a random distance but with an upper limit, which is proportional to the value of the item. However they do not mention the distribution of probabilities of the 'random' distance.

A more thorough mathematical investigation of the model is necessary to make clear if this model can explain spacing patterns effectively when source robbery and density dependent cache robbery are small. There are still some inconsistencies in the model, especially for predictions 1. and 2. with data from Rutten (1999). However, we think that these kinds of random models can explain the caching behaviour of the acouchis better than the two mentioned models of Stapanian and Smith (1978) and of Clarkson et al. (1986).

LITERATURE

Andersson, M. & J. Krebs 1978. On the evolution of hoarding behaviour. Animal Behaviour 26: 707-711.

Clarkson, K., Eden, S.F. Sutherland, W.J. and A.I. Houston 1986. Density dependence and magpie food hoarding. Journal of Animal Ecology 55: 111-121.

Cowie, R.J., J.R. Krebs and F.S. Sherry 1981. Food storing by marsh tits. Animal Behaviour 29: 1252-1259.

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.

Emmons, L.H. & F. Feer 1990. Neotropical rainforest mammals: a field guide. University of Chicago Press, Chicago/London.

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

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

Forget, P.M. 1994. Recruitment pattern of *Vouacapoua americana* (Caesalpiniaceae), a rodent-dispersed tree species in French Guyana. Biotropica 26: 408-419.

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

Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): The inheritors of guapinol (*Hymenaea courbaril*: leguminosae). In: Astradan, A & T.H. Fleming, Frugivores and seed dispersal.

Hammond, D.S. & V.K. Brown 1998. Disturbance, phenology and life-history characteristics: factors influencing distance/density dependant attack on tropical seeds and seedlings. In: Newbery, Brown and Prins (eds.) Population and community dynamics in the tropics, pp 51-78.

Heinrich, B. & J.W. Pepper 1998. Influence of competitors on caching behaviour of the common raven, *Corvus corax*. Animal behaviour 56: 1083-1090.

Hurly, T.A. & R.J. Robertson 1987. Scatterhoarding by territorial red squirrels: a test of the optimal density model. Canadian Journal of Zoology 65: 1247-1252.

Jokinen, S. & J. Suhonen 1995. Food caching by willow and crested tits: a test of scatterhoarding models. Ecology 76: 892-898.

Kiltie, R.A. 1981. Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. Biotropica 13: 141-145.

Klosinska, T. 1994. Winter strategies of small mammals. Wiadomosci Ekologiczne 40: 197-209.

Kraus, B. 1983. A test of the optimal-density model for seed scatterhoarding. Ecology 64: 608-610.

Krebs, J.R., Stephens, D.W. and W.J. Sutherland 1983. Perspectives in optimal foraging. In: Brush, A.H. & G.A. Clark (eds.). Perspectives in ornithology. Cambridge University Press, Cambridge.

Lisa, L. & M. Daly 1998. Effects of food preference on scatterhoarding by kangaroo rats, *Dipodomys merrioni*. Behaviour 135: 823-832.

Nillson, J.A., Kälander, H. and O. Persson 1993. A prudent hoarder: effect of long-term hoarding in the European nuthatch, *Sitta europea*. Behavioral Ecology 4: 369-373.

Papi, F. 1992. Homing mechanisms. Chapman & Hall, London.

Rice-Oxley, S.B. 1993. Caching behaviour of red squirrels, *Sciurus vulgaris* under conditions of high food availability. Mammal review 23: 93-100.

Rutten, A.L. 1999. Playing hide and seek: cache spacing decisions and cache robbery in the scatterhoarding Red acouchy (*Myoprocta exilis*). Students report, WAU, Wageningen.

Siepel, A.1998. Scatterhoarding by red acouchis (*Myoprocta acouchy*) in the Neotropics: an economic balance between the costs and benefits of seed choice and cache spacing patterns. Students report, WAU, Wageningen.

Sherry, P., Avery, M. And A. Stevens 1982. The spacing of stored food by marsh tits. Zeitschrift für Tierpsychologie. 58: 153-162.

Stapanian, M.A. & C.C. Smith 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. Ecology 59: 884-896.

Van der Meer, P.J. & F. Bongers 1996. Patterns of tree-fall and branch-fall in a tropical rain forest in French Guyana. Journal of Ecology 84: 19-29.

Vander Wall, S.B. 1990 Food hoarding in animals. University of Chicago press, Chicago/London.

Waite, T.A. 1990. Effects of caching supplement food on induced feather regeneration in wintering gray jays *Perisoreus canadensis*: a ptilochromology study. Ornis Scandinavica 11:122-128.

Waite, T.A. & J.D. Reeve 1992. Caching behaviour in the gray jay and the source-departure decision for rate-maximizing scatterhoarders. Behaviour 120: 51-68.

Wauters, L.A. & P. Casale 1996. Long-term scatterhoarding by Eurasian red squirrels (*Sciurus vulgaris*). Journal of Zoology 238: 195-207.

Wauters, L.A., Suhonen, J. and A.A. Dhondt 1995. Fitness consequences of hoarding behaviour in the Eurasian red squirrel. Proceedings of the Royal Society of London Series B Biological Sciences 262: 277-281.

Zar, J.H. 1996. Statistical analysis. Prentice Hall International, London.

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Appendix I

Recommendations for further research

Several predictions of the new model should be investigated because there is no or only incomplete data to test them.
1. The amount of items in the source does not influence the scatterhoarding pattern.
Data from Rutten (1999) indicates that there is a difference between the cache distance from a source of 25 seeds and 49 seeds. However she did only search for seeds within 25 meters of the source and she did not take into account the nearest neighbour distance. I suggest that a new experiment should be designed with sources containing 25 and 49 seeds. The searching strategy should be the same as ours to enable a large recovery rate.
2. Previous caches will not greatly influence the distribution when minimum nearest neighbour distance is small.
An earlier experiment described in Rutten (1999) showed that cache distance is bigger for seeds from a source of 25 seeds, placed at the same spot, after a similar source had been cached. The measurements were the same as in the previously mentioned experiment and therefore conclusions are based on quite low recovery rates. I suggest that the same experiment should be repeated with 49 seeds and a larger searching area. Replacement should not be done very shortly afterwards but with, for instance, one day in between (the day in which the seeds of the first source are searched for). Additionally more than two replacements could be done on the same spot. Disturbance of the area is necessary the day before the first source is placed to insure that disturbance by searching does not cause differences. Sources could be offered on spots several meters away from each other but within the previous caching area.
3. Mean cache distance increases when mean value of the items increases.
We found an increase of cache distance with mean seed weight. However, our experiment was not designed properly for testing this hypothesis. An experiment has to be set up with sources of different mean weight. The variance within a source should be the same.
4. Cache distance is not influenced by the amount of the used 360° arc.
An experiment could be done where an animal can leave the source only in a specific area within the 360° arc. This will be quite difficult to do in the tropical forest with acouchis but an experiment with scatterhoarding animals with a smaller caching area could be possible. I suggest an experimental set-up where the caching pattern of an individual, able to scatterhoard in all directions, is compared to the pattern of an animal, which can only leave the plot into certain directions.
5. Heavier items are cached close and far away whereas lighter items are cached mostly close to the source.
Our experiment consisted of sources with a normal distribution of seed weights. Experiments should be done where the source consists only of light and heavy seeds, to get a more clear view of the effect of seed weight on scatterhoarding behaviour.

Several other questions have arisen from this research.
1. What is the effect of the borders of the acouchy territories on the direction of the scatterhoarding pattern?
More knowledge is necessary in order to establish territory borders. Catching animals and marking them with dye could be helpful. It will also reveal if only one individual is scatterhoarding at a source. This is always assumed but it is not certain, especially because acouchis have often overlapping territories (Dubost, 1988). Data from radio tagged individuals could also be very helpful to reveal the home range.
2. Are caches of acouchis vulnerable to cache robbing?
Rutten (1999) did several experiments involving cache robbing but she did not know if acouchis or other animals robbed the artificial caches. We saw a group of white-lipped peccaries searching for food in an area where caches of an acouchy were located, but no cache was robbed. A permanent camera filming the spot of some (artificial) caches could show which animal is responsible for robbing. Marking seeds in artificial caches and searching the threads after robbing could show if the seeds are eaten (indicating peccaries?) or buried again (indicating acouchis or agoutis).

3. What is the searching behaviour of peccaries?

We do not know how peccaries are searching for food. Observing them and following a group could be useful and will give a clue of the searching strategies. Observing fruiting trees and non-fruiting trees with cameras during the day can also give some clues. It will reveal whether peccaries are attracted to certain places or that they just visit areas randomly. The same can be observed for acouchis in this way.

4. What is the effect of the vegetation on the location of caches?

Acouchis might cache on places with specific qualities. Substrate, vegetation structure and near by large objects could have an effect on the distribution pattern. We collected already data of these factors for the caches we retrieved but this has not been analysed yet. The natural distribution of substrate and objects should be known before comparing it to the cache distribution. Experiments could be done where sources are offered on plots with different vegetation structures. Maybe our own data could be used for this.