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Foraging behavior and diet preference of Dasyprocta punctata

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ABRSTRACT

This study analyzed the foraging behaviors and diet preference of the agouties (*Dasyprocta punctata*) in Monteverde, Costa Rica. The Optimal Foraging Theory explains animal behaviors in terms of maximum efficiency; animals forage in a manner that is optimal to their fitness (Alcock 2005). *D. punctata* was expected to choose the fruit over seed because fruits would provide more energy for the time spent foraging and, therefore, maximize foraging efficiency. Also, *D. punctata* have been found to eat fruit when the supply is abundant (Smythe 1978). *Syzygium malaccense* was used to test whether entire fruits were preferred over naked seeds. A total of 154 seeds and fruits were made available during the experiment; 124 were removed, 59 seeds and 65 fruits (Fig. 3). No significant differences were found between seed or fruit preference ($X^2 = 0.290$, $p = 3.84$). Neither seeds nor fruits were eaten or cached at a significantly different rate ($t = 0.14$, $p = 2.1$). Differences found between the distances of the caches were not significant either ($t = 0.0008$, $p = 0.678$). No overall preference was found in the diet choice of *D. punctata*. Optimization may not be as straightforward as the amount of food consumed per unit time. *D. punctata* appeared to maximize their foraging efficiency by not being selective in food choice. Having an abundant food store provides year-round access to food, therefore alleviating environmental pressures.

RESUMEN

Este estudio analizó el comportamiento de forrajeo y la preferencia en la dieta de las guatusas (*Dasyprocta punctata*) en Monteverde, Costa Rica. La Teoría de Forrajeo Óptimo explica las conductas animales en términos de la eficiencia máxima; los animales se alimentan en de una manera que es óptima a sus adaptaciones evolutivas (Alcock 2005). Se predijo que *D. punctata* preferiría la fruta a la semilla porque la fruta proporcionaría más energía por el tiempo empleado alimentándose y, por lo tanto, produciría la máxima eficiencia de forrajeo. También se ha determinado que *D. punctata* se alimenta de fruta cuando el suministro es abundante (Symthe 1978). *Syzygium malaccense* se utilizó para probar si *D. punctata* preferiría frutas enteras a semillas desnudas. Se ofreció un total de 154 semillas y frutas y 124 fueron removidas (59 semillas y 65 frutas). No se encontraron diferencias significativas entre la preferencia por semillas o frutas ($X^2 = 0{,}290$, $p = 3{,}84$). Tampoco se encontraron diferencias significativas ni en las semillas ni en las frutas que fueron consumidas o enterradas ($t = 0{,}14$, $p = 2{,}1$). Las diferencias observadas entre las distancias de los depósitos tampoco fueron significativas ($t = 0{,}0008$, $p = 0{,}678$). Ninguna preferencia general se encontró en la elección de la dieta de *D. punctata*. Puede que la optimización no pueda ser medida tan directamente por medio de la cantidad de alimento consumido por unidad de tiempo. Aparentemente, *D. punctata* maximiza su eficiencia de forrajeo al no ser selectiva en la elección de alimento. La disponibilidad de depósitos abundantes de alimento garantiza el acceso a la comida durante todo el año, aliviando las presiones ambientales.

INTRODUCTION

Fruit availability in many tropical forests fluctuates greatly with the seasons (Sakai 2001). This inconsistency restricts animals and requires them to consume what is available at a given time within their range. Different from many rodents, agouties (*Dasyprocta spp*) do not greatly alter their feeding habits seasonally and remain frugivorous year round (Henry, 1999). *Dasyprocta*

do, however, switch from pulp-centered fruit to seed-centered diets in the wet and dry seasons respectively (Henry 1999). This response is a way for agouties to survive times of resource scarcity by eating the seeds they buried when fruit was abundant. This behavior, known as scatter-hoarding, is important to the dispersal and recruitment of many plants (Forget, Vander Wall, 2001). Many rodent species that are unable to store fat, such as *Dasyprocta*, also rely on scatter-hoarding to meet energetic requirements when resources are low (Henry 1999, Vander Wall 2001).

Animals are assumed to forage in a manner that is optimal to their fitness. The Optimal Foraging Theory explains animal behaviors in terms of maximum efficiency (Alcock 2005). Animals in search of food have decisions to make that will affect their efficiency and ultimately their fitness. Choices need to be made on where, how long, and what resources to forage (Alcock 2005). Factors outside an individual's control also affect how efficiently an animal is able to forage.

Foraging behavior may be influenced by factors such as predation, competition, reproduction, hunger, or seasonal variations in availability of resources. Few studies have been done that looked at the fluctuations of seed and pulp consumption in relation to seasonality. A study done in French Guiana (Henry, 1999) observed the diet of *Dasyprocta leporina* over the course of a year. Food types, quantities, and seasonal fluctuations were determined from the analysis of stomach contents. A significant correlation was found between *Dasyprocta* diet and tree seasonality. The abundance of fruit versus seed consumption was highly correlated with rainfall and tree fructification. Four times the amount of seeds was eaten in the dry season when fruit was scarce; likewise, their pulp consumption was five times greater during fruiting peaks.

Forget (2002) conducted a study on the seasonality of fruiting and food hoarding rodents and observed that rodents ate fruit during the wet season when resources were abundant and switched to seeds when fruit was unavailable during the dry season. In a similar study, *D. punctata* were observed to hoard much larger amounts of seeds during the wet season when fruit was abundant than during the dry season when fruit was scarce; when both were abundant, fruits seemed to be the favored resource (Smythe 1978).

The intent of this study was to examine the diet choice and caching behaviors of *D. punctata.* A field study experiment was conducted to test the preference of *D. punctata* between fruits and seeds of *S. malaccense.* Based on previous studies and the Optimal Foraging Theory, four main predictions were made: 1) agouties were expected to prefer fruit over seeds. Fruits would provide more energy for the time spent foraging and, therefore, maximize foraging efficiency. In addition, fruits were assumed to be preferred over seeds because agouties have been found to eat fruit when the supply was abundant. 2) More seeds will be cached because fruits will rot, are less efficient to handle due to their size, and may be easier for competitors to find. Also, if time is spent eating or removing the fruit from a seed it is expected to be more efficient to continue eating the seed rather than catching it. 3) Distance of cache from original position was expected to be greater for fruit than seeds; even though most fruits will be eaten, the ones that are cached will be moved further. Fruits can be considered a higher-value resource than a naked seed because of the initial energy investment to remove the pulp. It may be beneficial to cache the fruit resources at a greater distance to reduce the chances of competitors discovering the cache. Caches at a greater distance from host experience less predation because they are more spread out and less susceptible to density-dependent predation. High-valued seeds tend to get stored in more favorable conditions (Jansen el al. 2002). 4) Finally, it was expected that the majority of all samples would be eaten and few cached; although agouti's cache when

fruit is abundant, the fact that is was dry season meant resources were limited. It was assumed that the agouties were not satiated and, therefore, expected to consume all the food given to them.

MATERIALS AND METHODS

This experiment was conducted from April 21st until May 10th, 2006 near the Estación Biológica in Monteverde, Costa Rica (Fig. 1 and 2). The study was located in a clearing bordering lower montane forest at an elevation of 1530 m. This site was situated between two buildings and experienced frequent human activity along the edges. The area was chosen because agouties had been repeatedly seen foraging in this site. Previous studies on agouties have also been conducted there (Senf 2004).

Fruits from *Syzygium malaccense* were used as the test samples. The pulp was removed from half of the *S. malaccense* and the rest remained entire. In order to locate the samples once they were cached, each fruit and seed was tagged using one meter of fishing string and 12 cm of colored flagging tape. A hole was drilled through the top of each seed, strung with fishing line, and secured with three knots. White flagging tape was attached to the other end of the line to track the seeds. Green flagging tape was used to identify fruit seeds. Each flag was numbered in order to determine the fate of each individual seed or fruit. Fruits were tagged and numbered in the same fashion, making sure the hole was drilled through the top of the seeds within the fruits. Piles of ten fruit and ten seed samples were then placed next to each other within the experiment site. The piles were observed and replenished once daily to insure each pile always contained ten fruits and ten seeds. Each day the location of the seed pile was switched with the fruit pile in order to correct for any differences in pile locations.

After agouti visits, seeds and fruits were recorded as eaten, cached, remaining, lost, or rejected. Samples were considered eaten if the flag was found without any fruit or seed attached. Samples not located after removal by *D.* punctata were recorded as lost. Untouched fruits and seeds were recorded as remaining. Fruits were considered rejected if they remained untouched for six days or three consecutive agouti visits because they would rot. Seeds were rejected in the same manner to maintain consistency between fruit and seed samples. This ensured that the quality of the samples did not alter the data on seed and fruit preference. Finally, if a sample was found buried it was recorded as cached. The location of cached samples was determined by measuring the distance and angle from the original pile. This was done using a 60 m measuring tape and a compass. Figure 2 shows a map of the experiment site.

A Chi-squared test was used to determine the preference of the agouti between seeds and fruit. A t-test was used to see if there is a significant difference in the fate of seeds compared to fruits. Another t-test was used to test the significance in the difference between the distance from the original position to the caches for seeds and for fruits. All significance was determined at the 0.05 probability level.

RESULTS

Observations were made for 20 days during which agouties visited the test site 12 times. Initially, *D. punctata* were inconsistent in how often they foraged at the site but eventually began visiting daily. The samples remained for 2.4 days on average before being removed.

A total of 154 seeds and fruits were made available during the experiment and 124 were removed; 59 seeds and 65 fruits (Fig. 3 and Table 1). Two seeds and one fruit were rejected because they remained untouched for three visits or 6 days, whichever was longer. All seeds were located and eight fruits were lost. The majority of all samples were cached and not eaten; 101 samples were cached (Table 1).

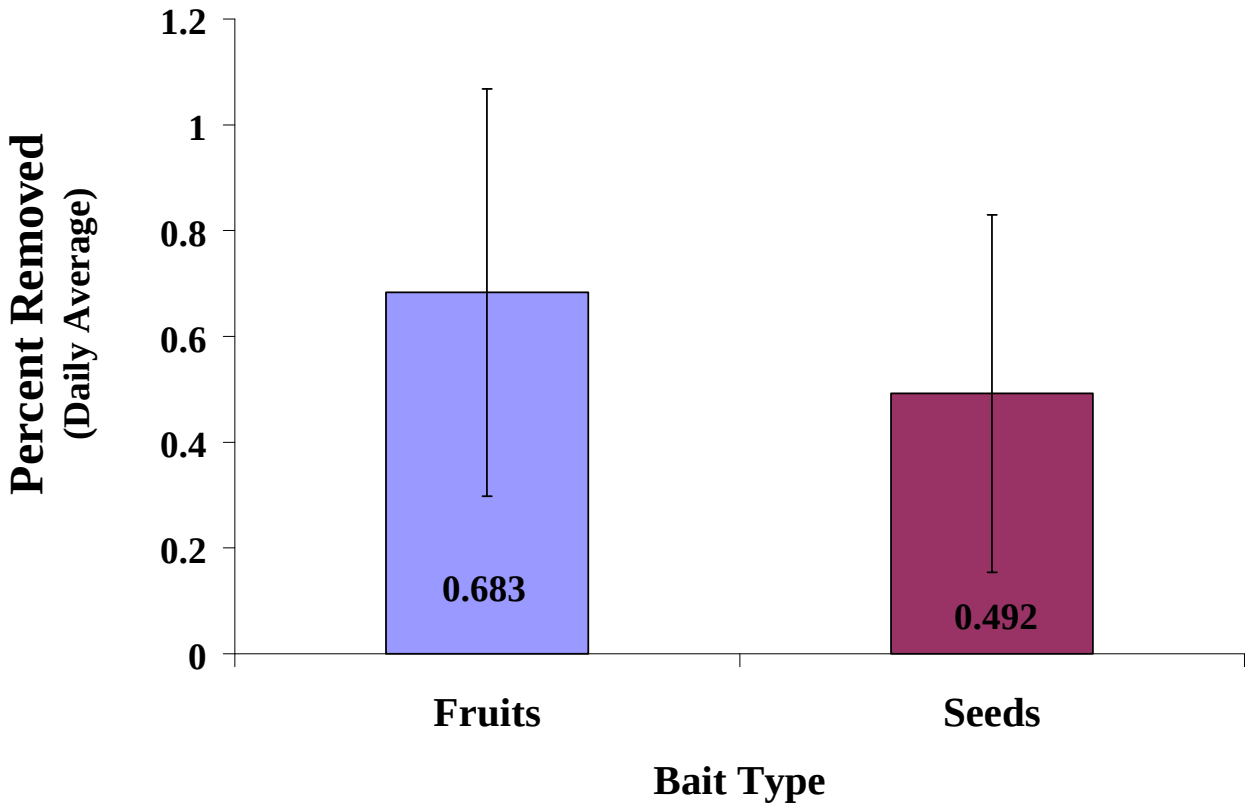

FIGURE 3. Average percent of samples either eaten or cached daily. The difference between the fruits and seeds was not significant. Error bars represent the standard deviation of the number removed for each bait type. Monteverde, Costa Rica. April-May 2006.

Though the samples were not entirely depleted daily, when given enough time, all samples were taken. More fruits than seeds were removed, but this difference was not significant ($X^2 = 0.290$, $p = 3.84$). *Dasyprocta punctata* did not significantly cache more fruits than seeds ($t = 0.96$, $p = 2.1$). During the first three days of data collection, *D. punctata* appeared to eat the fruit before caching but later began to cache without eating the fruit. Partially eaten fruit was observed in the experiment site near caches and around the original pile. Seeds cached were always naked, therefore, it can be reasoned that the *S. malaccense* pulp was not always consumed when the seeds were cached or eaten.

There was no significant difference between the distance the seeds and fruits were cached ($t = 0.0008$, $p = 0.678$). The average seed was cached 4.74 m from the host tree and the average

fruit was cached 8.81 m away. The farthest cached seed was 26.4 m and the farthest cached fruit was 23.75 m. Fruits were observed to be cached more consistently at a longer distance from the original pile than seeds. The majority of seeds were found within eight meters of the host tree (87%), while fewer fruits were observed within the same range (53%).

TABLE 1. Numbers of *Syzygium malaccense* taken from the experiment site. Cached seeds were samples found buried. Flags having nothing attached were considered eaten. Samples not located were classified as lost. Rejected samples were seeds or fruits which remained untouched for three consecutive agouti visits or six days, whichever was longer.

	Fruits	**Seeds**	**Total**
Cached	49	52	**101**
Eaten	16	7	**23**
Lost/Rejected	18	12	**30**
Total	**83**	**71**	**154**

DISCUSSION

The behaviors studied may be optimal for the fitness of the agouti even though the results do not support the conclusion that *D. punctata* choose fruits over seeds. *D. punctata* are not a density-dependent forager (Lanie 1998). Agouties are hoarding rodents and, therefore, would not limit themselves to the number of seeds they can carry away; the rodents take what is available. Coogan (2006) found similar results in that agouties did not show a preference between different seeds and they took all available resources. Sample of 20 *S. malaccense* and *Bactris gasipaes* seeds were set out for agouties, and both supplies were depleted daily. Hoarding behaviors may be observed year round in agouties as a way to always be prepared for unpredictable scarcity.

Time may also be a limiting factor when assessing the efficiency of optimal foraging behavior. Non-selectivity occurs because differences in the rate of energy gain between *S. malaccense* fruits and seeds may be too small for selectivity to be beneficial. A study on the relationship between sugar and water content of tropical fruits and their dispersers (Minikel 2000) found that mammalian dispersers show a preference for fruits with higher sugar content. Fruits with high water concentrations were found to have lower sugar concentrations. If *D. punctata* also prefer fruits with high sugar contents, the fruit of *S. malaccense* would not be preferred due to the high water content.

Optimum foraging success is often thought of as the maximum number of caloric intake per unit time (Alcock 2005); however, other factors need to be considered as well. Predators and competitors need to be taken into account when determining the most efficient foraging behaviors. *D. punctata* may have been influenced by the vulnerability of the open field. Caches were often found in the forest, along the forest edge, or under other trees and shrubs in the field. Very few caches were in the open. People walking through the site area may have prevented *D. punctata* from foraging in a normal manner.

The availability of food sources may not have been as limiting as originally thought. The dry season is often associated with fewer fruiting plant species but many plants do produce fruits just before the start of the wet season (Sakai 2001). These fruit producing individuals may have

been providing sufficient food for the test subjects. The agouties visiting the study site were also supplied with food from organic waste of the Estación and nearby houses which was thrown into the forest. Abundance of food sources may have satiated *D. punctata,* causing them to cache food for future consumption and, hence, removing all available samples. This may also explain why the agouties showed no preference between which resource was cached.

No overall preference was found in the diet choice of *D. punctata*. Optimization may not be as straightforward as the amount consumed per unit time. *D. punctata* appear to maximize their foraging efficiency by not being selective in their food choice. Having an abundant food store provides year-round access to food, therefore alleviating environmental pressures. Similar future studies could look at whether diet preference is affected by seasonality. Studies could also be carried out in more secluded sites in order to reduce the impacts of outside factors.

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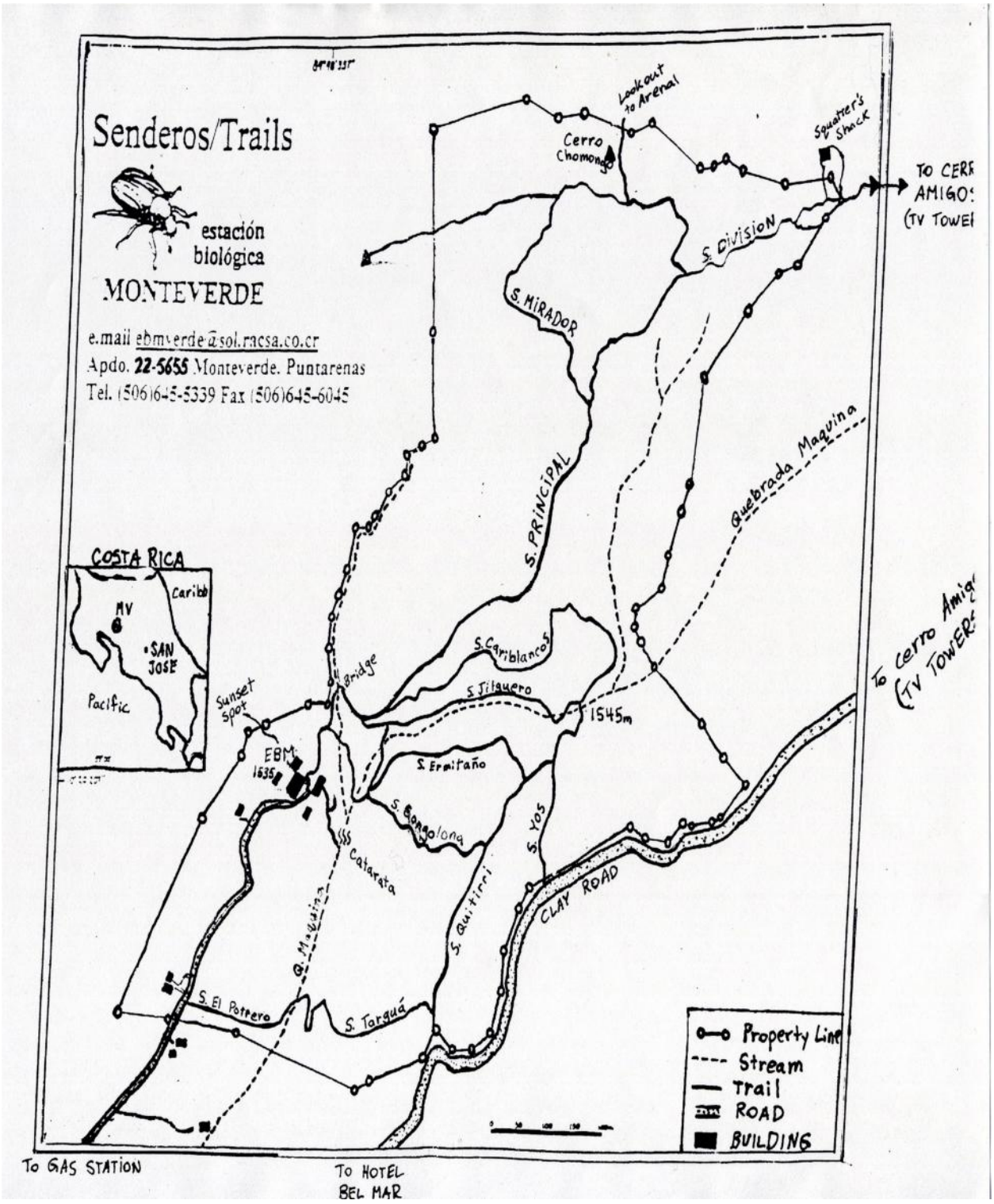
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(TV TOWEI
S. DIVISION
S. MIRADOR
S. PRINCIPAL
Quebrada Maquina
To cerro Amigo
(TV TOWERS
S. Caribblancos
S. Tilaguero
1545m
Sunset spot
bridge
EBM
1635
S. Ermitaño
S. Bongolona
S. Yos
Catarata
Q. Maquina
S. Quitirri
CLAY ROAD
S. El Potrero
S. Targuá
Property Line
Stream
Trail
ROAD
BUILDING
TO GAS STATION
TO HOTEL
BEL MAR

Figure 1. Map of study site at the Estación Biológica, Monteverde, Costa Rica. April-May 2006.

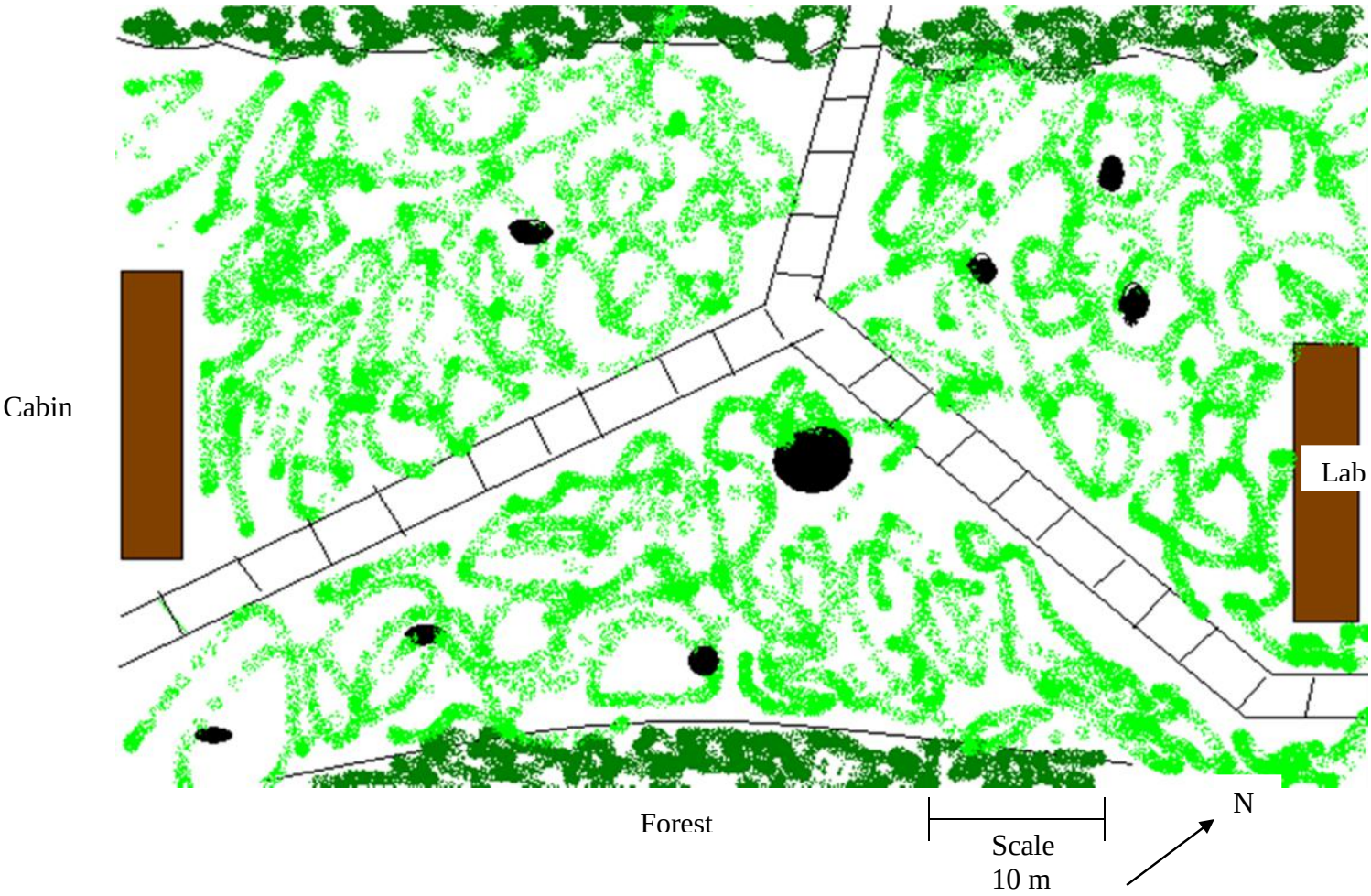

Figure 2. Map of experiment site, Estación Biológica, Monteverde, Costa Rica..