

Home-range use by the Central American agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama

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Abstract: This study investigates the movements and home range of the agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama. We captured and tracked 12 agoutis from January to December 2003. Home-range size (95% kernel) ranged from 1.56–2.45 ha (n = 6) for males and 1.34–1.97 ha (n = 5) for females. Agouti ranges overlapped and we estimated a density of approximately 100 agoutis km⁻². We compared agouti movement with the locations of refuges and food trees, and the results suggest that the agoutis are central-place foragers. Agoutis moved an average of 850 m d⁻¹ covering approximately 35% of their range daily. These movement data help us understand the potential impacts of agoutis as seed dispersers, predicting that *D. punctata* will encounter and hoard fallen fruit within 10–200 m (i.e. radius of home range) of its source, and move seeds towards refuges such as ground holes and dense vegetation around recent tree falls.

Key Words: agouti, *Dasyprocta punctata*, habitat use, home range, mammal density, predation risk, space use

INTRODUCTION

Dasyprocta punctata is one of the 11 species which comprise the genus *Dasyprocta*, common name agouti (Eisenberg 1989). Agoutis are medium-sized (3 kg) rodents that make up a high percentage of biomass in tropical forests, and are important not only as prey for a variety of predators including humans (Aliaga-Rossel 2004, Eisenberg & Thorington 1973, Terborgh *et al.* 2001), but also because of its role as a seed predator and disperser (Asquith *et al.* 1999, Hallwachs 1986, Henry 1999, Peres *et al.* 1997, Silvius 2002, Silvius & Fragoso 2003, Smythe 1978). Documenting the spatial scale at which frugivores move is important because it suggests how quickly fallen seeds may be found, and sets the distance that seeds could be dispersed. Knowledge of the movements of animals that feed at seasonally fluctuating fruiting patches is also of general interest because it allows for the quantification of the influence of food distribution on animal behaviour (Cowlshaw 1997, Ylonen *et al.* 2003).

Only a few studies have described the movement patterns for any members of genus *Dasyprocta*, typically with small sample sizes (*D. leporina*: 3–9 ha, n = 9 animals, Jorge & Perez 2005, Silvius 1999, Silvius & Fragoso 2003; 3.9 ha for a single *D. punctata*, Rodriguez & Vaughan 1985). However, there has been no description of habitat preferences or the intensity at which *Dasyprocta* uses space, which is likely to affect the frequency at which it encounters fallen seeds. The importance of small and medium-sized terrestrial rodents as seed depredators and dispersers is widely recognized. For example, studies on species of spiny rat (*Proechimys* spp.) and acouchy (*Myoprocta exilis*) have shown that their movements generate complex seed shadows that might affect forest structure (Adler & Kestell 1998, Adler & Levins 1994, Forget 1991, Jansen 2003).

We studied the spatial ecology of the Central American agouti (*D. punctata* Grey 1842) by radio-tracking nine animals and visually tracking three additional ear-tagged individuals on Barro Colorado Island, Panama. We describe their home-range size and intensity of space use, and relate these factors to food distribution and predation risk.

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METHODS

Study area

The study took place at the Smithsonian Tropical Research Institute on Barro Colorado Island (BCI, 9°9'N, 79°52'W), a 15.6-km² protected island in Panama, covered with tropical moist and semi-deciduous forest of several successional stages (Dietrich *et al.* 1996). Rainfall averages 2600 mm y⁻¹ with a seasonal dry period from January until early May. There is a strong fruiting seasonality with peaks during the rainy season and early dry season (Adler 1998, Foster 1996).

The January to December 2003 study period extended across the dry and rainy seasons. BCI has an intact community of interspecific competitors and predators of agoutis except for the absence of the white-lipped peccary (*Tayassu pecari*) and irregular presence of jaguar (*Panthera onca*). Agoutis are a regular prey item for ocelots (*Leopardus pardalis*) and puma (*Puma concolor*), both of which are common on BCI (Aliaga-Rossel *et al.* 2006, Moreno *et al.* 2006). We found no evidence that any agoutis were fed by humans during this study or in the recent past (i.e. there was no evidence of affinity for the research station dining hall). Breeding can occur at any time of the year, but the peak season is between late April and the middle of May (Aliaga-Rossel pers. obs., Smythe 1978).

Capture methods

Agoutis were captured and handled following SUNY-ESF IUCACC approved methodology. We used ten Tomahawk live traps from 7 January to 5 February and from 20 February to 20 March 2003 in different locations across approximately 1.5 km². Traps were baited with bananas (*Musa* sp.) and corn (*Zea mays*), camouflaged with vegetation, and left open for 12 h per day and checked every 3–4 h. One agouti was also successfully re-captured by using a Teleinject dart rifle.

Captured agoutis were anaesthetized with 0.8 mg kg⁻¹ of Telazol (Tilamine hydrochloride + Zolazepam) and were sedated within 5–10 min after injection. Captured animals were sexed, weighed, measured (Aliaga-Rossel 2004), and fitted with a Telonics radio-collar or ear tagged. After handling, animals were kept in traps and observed until they fully recovered from sedation before being released.

Radio-tracking

Individuals were located 1 d after capture using a standard ground-based triangulation method (Kenward 2001).

All radio-tracking was done on foot from mapped trails marked at 100-m intervals. Telemetry accuracy tests ($n = 5$), indicated that error was < 5 m. Daily data were taken for each agouti by triangulation, with less than 10-min lag time between taking subsequent bearings. For many of these radio-locations we confirmed fixes through visual observation of the animal. We minimized disturbance to the animal by spending little time in sight, and moving away promptly if the animal showed sign of stress.

Animals were tracked at least once per day, from approximately 07h00 to 12h00, and from 14h30 to 18h00. Some locations were also recorded at night (from 19h00 to 01h00). Structures used by agoutis such as burrows, gaps in the forest, and sleeping spots were also recorded and mapped using a Global Positioning System unit (GPS, Garmin 12XL). The habitat type for all the sightings was also noted. All sightings of ear-tagged agoutis were also recorded and used to determine their home-range areas.

Estimation of home range

We used the software programs ArcView GIS 3.3 (ESRI Environmental Systems Research Institute, Redlands, California, USA) and Animal Movement with the Home Range extensions to calculate agouti home ranges. The minimum convex polygon (MCP) has been the most commonly used approach for calculating animal home ranges, thus we estimated home-range areas using this approach to permit comparisons with existing published studies on agoutis (Jorge & Perez 2005, Silvius & Fragoso 2003). We also estimated the home range area with the Fixed-kernel method (Burgman & Fox 2003, Seaman & Powell 1996).

All fixes were used to determine home-range size at the 100% minimum convex polygon (MCP) level. We also estimated home-range size with a 95% MCP and fixed-kernel estimator using only locations separated by 30 min. These fixes were considered to be biologically independent as this was sufficient time for the agoutis to transverse their entire home range (Doncaster & MacDonald 1997). Using these independent data, we estimated the 95% (Fk95%) and 50% fixed-kernel isopleths (Fk50%) with least-square cross-validation (LSCV). Because this parameter varied among individuals we calculated the median (LSCV) for all individuals and used this single value in the final fixed-kernel analysis (Millsbaugh & Marzluff 2001, Seaman & Powell 1996). We used this Fk50% as the core area, representing areas receiving concentrated use by resident animals, where at least 50% of localizations occurred (Blundell *et al.* 2001, Samuel *et al.* 1985).

Movement patterns

On seven occasions, three agoutis (2 males and 1 female) were intensively tracked from 05h30 to 18h00 (more than 12 h of continuous data) with radio-locations determined every 30 min or less. These data were used to measure short-term movements and identify associations between agoutis and habitats. Distances travelled between locations derive from straight-line calculations between two points. These distances provide minimum estimates of how far animals travelled in a day, and helped determine the areas and features used most frequently. To estimate the area potentially searched per day by agoutis, we buffered each of these day paths with a 5-m strip. Given the lack of information on possible olfactory and visual perception in *Dasyprocta*; this is a conservative estimate of area of detection for this species (Aliaga-Rossel pers. obs, Smythe 1978).

Density

Assuming agoutis occupy all available habitats within the study site the density of adult agoutis in our study area was estimated based on home-range size and overlap (Fuller *et al.* 2001, Garant & Crête 1997).

Determinants of space use

We examined habitat selection by individual agoutis within their home ranges in relation to the location of important fruit trees, tree-fall gaps, and dens. We exhaustively searched all terrain of each agouti's 100% MCP area (in and around 25 m of the estimated border)

to map the location of three species of tree and the location of agouti refuges. These three tree species, *Astrocaryum standleyanum* L.H. Bailey, *Attalea butyracea* (Mutis ex L. f.) J.G.W. Boer (synonym: *Scheelea zonensis*), and *Dipteryx panamensis* (Pittier) Record & Mell, were used as models of food tree abundance and distribution because they are key food resources for agoutis at BCI and elsewhere (Smythe 1978, Smythe *et al.* 1996, Terborgh 1986). All features were georeferenced relative to fixed landmarks, or using a GPS. All trees that were large enough to produce fruit were mapped, although fruiting and non-fruiting individuals were not distinguished. We recorded the location of dens or refuges during early morning and late-evening tracking of collared agoutis.

We compared the density of fruit trees in 95% and 50% kernel home range to see if agoutis centred their home range on especially productive areas. We also noted the location of refuges related to these core areas. We analysed the data using t-tests and correlations with the software program STATISTICA.

RESULTS

Seven male and five female agoutis were trapped, anaesthetized and measured. Nine agoutis were fitted with radio-collars, and the rest were ear-tagged. One juvenile removed its radio-collar after 9 d. We did not statistically examine the home range for the juvenile because we collected too few fixes; however, we do report its home-range size (Table 1).

No agoutis were injured during capture and most showed no adverse effects from capture or collaring; one animal did get its front leg stuck under the collar but was able to remove it on its own without any other

Table 1. Home-range characteristics for 12 agoutis (*Dasyprocta punctata*). The sex of the agouti is indicated at the start of the individual code (F: female, M: male). Fixes were judged independent (indep) if separated by > 30 min. Home-ranges sizes (ha) based on the Minimum Convex Polygon (MCP 100%), 95% MCP, Fixed Kernel 95% (FK) method, and core area size (FK 50%). The juvenile agouti MJ-jo is not included in summary statistics due to its small data size (< 10 d of tracking). Food tree density is number of trees ha⁻¹ of 100% MCP. *Astroc* = *Astrocaryum standleyanum*, *Attalea* = *Attalea butyracea*, *Dipte* = *Dipteryx panamensis*.

Code for agouti	Tracking method	Time tracked (mo)	Fixes: all (indep)	100% MCP	95% MCP	95% FK	50% FK	<i>Astroc</i> density	<i>Attalea</i> density	<i>Dipte</i> density
F-Sm	Radio	<12	504 (305)	2.41	1.89	1.97	0.19	17.0	2.9	1.2
F-Mu	Radio	<1	42 (42)	1.63	1.21	1.42	0.16	9.8	0.6	3.1
F-Sh	Radio	<3	65 (65)	1.42	1.20	1.40	0.14	13.4	1.4	0.7
F-Ma	Visual	<12	117 (76)	1.86	1.51	1.78	0.11	5.9	2.2	1.1
F-Na	Visual	<3	81 (68)	0.99	0.91	1.35	0.24	16.2	4.0	7.1
M-Ca	Radio	<1	61 (60)	3.20	3.00	2.04	0.07	10.9	4.4	1.3
M-Si	Radio	<4	277 (182)	2.72	1.88	1.82	0.08	14.3	2.6	2.6
M-Ri	Radio	<6	315 (213)	3.23	2.01	1.75	0.08	19.5	4.3	1.2
M-Nn	Radio	<11	356 (240)	4.36	2.26	2.45	0.46	16.7	2.8	0.9
M-El	Radio	<7	272 (163)	2.02	1.42	1.56	0.16	13.9	2.5	3.0
M-Gf	Visual	4	67 (67)	2.56	2.03	1.50	0.11	19.1	2.3	1.6
MJ-Jo	Radio	<10 d	20 (20)	0.32	0.32	0.72	0.08	6.3	0	3.1
Average			225 (151)	2.54	1.84	1.81	0.18	13.7	2.4	1.8

consequences. The collar of male M-Nn captured in March stopped functioning between September and October; however, we continued to track this agouti using visual sightings, which was facilitated by his association with the radio-collared female F-Sm. Only two collared animals, a male (M-Elo) and a female (F-SM), were still alive at the end of the study (7 and 13 mo, respectively, after their captures), and an ear-tagged female (F-Ma) near the laboratory was still alive as of June 2007. A total of 2178 locations were recorded for all agoutis. Four of the radio-collared agoutis were killed by ocelots in the dry season (Aliaga-Rossel *et al.* 2006); thus seasonal comparisons of home ranges are made with data for only four agoutis, the first such comparison for this species.

Estimates of home range and core area

Home-range size for all agoutis using MCP (100% of locations, Figure 1) ranged from 0.99–4.36 ha (mean \pm SE = 2.56 ± 0.29 , $n = 11$); from 2.02–4.36 ha (mean \pm SE = 3.02 ± 0.33 , $n = 6$) for males, and 0.99–2.41 ha (mean \pm SE = 1.66 ± 0.23 , $n = 5$) for females (Table 1). Fixed-kernel range-size at 95% ranged from 1.56–2.45 ha (mean \pm SE = 1.86 ± 0.17 , $n = 6$) for males and 1.34–1.97 ha (mean \pm SE = 1.58 ± 0.13 , $n = 5$) for females. Male ranges were almost twice as large as female agouti home ranges (using MCP 100% contour line), but were only marginally statistically different using the fixed-kernel method set at the 95% level (t-test $t = 0.09$, $df = 9$, $P > 0.05$).

The greatest number of locations ($n = 504$) was for the female agouti F-Sm, with locations recorded from 30 January to 28 December 2003. This individual's home-range size of 2.40 ha (MCP), and 1.97 ha (Fk95%) was the largest of any female studied, however home-range size did not increase substantially after 1 mo of tracking.

All home ranges had one or two high-use areas, usually situated in the centre of the range. The fixed-kernel 50% estimate for the core areas ranged 0.07–0.46 ha (average = 0.165, SE = 0.033, $n = 11$) and included 17–47% of all fixes. Core areas always included main refuges of climber thickets as indicated by Samuel *et al.* (1985).

There was a high degree of overlap between agouti home ranges. This included overlap between marked (Figure 1) and unmarked individuals that were residents of the area. For radio-collared animals this overlap was 20% to 57% among females; and 37% to 91% for males. Adult males tolerated the presence of one or more females and juveniles (91% overlapped of an adult male range with a juvenile); although, they exhibited aggressive behaviour towards other adult males, that might prevent higher overlap.

Daily movement pattern

The mean daily movement distance by the agoutis followed throughout the day was 831 ± 215 m ($n = 7$), with 33.9% of their time being spent in their core areas. When individuals reached the edge of the home-range area they exhibited patrolling and marking behaviour. To estimate the area searched per day by an agouti we conservatively presumed that they could detect food within 5 m of their path, resulting in a single day average of 0.65 ha covered (0.40–0.85 ha).

Densities

Given an average male's home-range (100 MCP) size of 3.0 ha, and assuming an overlap between animals, we calculate that there are three adult agoutis per home range (a male and two females) (Figure 1). Using this information we calculate the adult density of agoutis in the study area at 100 km^{-2} (using fixed-kernel 95 a density of 161 km^{-2}).

Habitat selection

The palm *Astrocaryum standleyanum* was very common in the study area, averaging 13.7 ha^{-1} within agouti home ranges (Table 1). Thus, radio-tracked animals had access to a large number of *A. standleyanum* trees (average: 36, range: 16–73) within their home range but fewer *A. butyracea* or *D. panamensis* trees. The densities of *A. butyracea* trees did not vary across the different agouti home ranges (correlation between number of trees and territory area, $r^2 = 0.97$, $P < 0.001$), while the densities of *A. standleyanum* and *D. panamensis* were variable across agouti territories (correlation between number of trees and territory area, not significant).

Comparing the density of food tree species in the core home range area with the non-core home range area, there was no significant difference for *A. standleyanum* in the core area (16.4 ha^{-1} versus 9.4 ha^{-1} ; $t = 1.9$, $df = 11$, $P = 0.08$), and neither for the other two tree species (*D. panamensis* 2.1 ha^{-1} vs. 1.8 ha^{-1} , $t = -0.24$, $df = 11$, $P > 0.1$; *A. butyracea* 2.6 ha^{-1} versus 2.2 ha^{-1} , $t = -0.33$, $df = 11$, $P > 0.1$). All core areas contained an individual major sleeping and resting sites.

DISCUSSION

We observed significant overlap in home-range areas for neighbouring individuals. In contrast, Smythe (1978) who also worked at BCI, found that *Dasyprocta punctata* maintained areas of exclusive use, as did Silviu & Frago (2003) for the agouti *D. leporina* in Brazil. Note however that in the latter study the radio-tracked individuals were

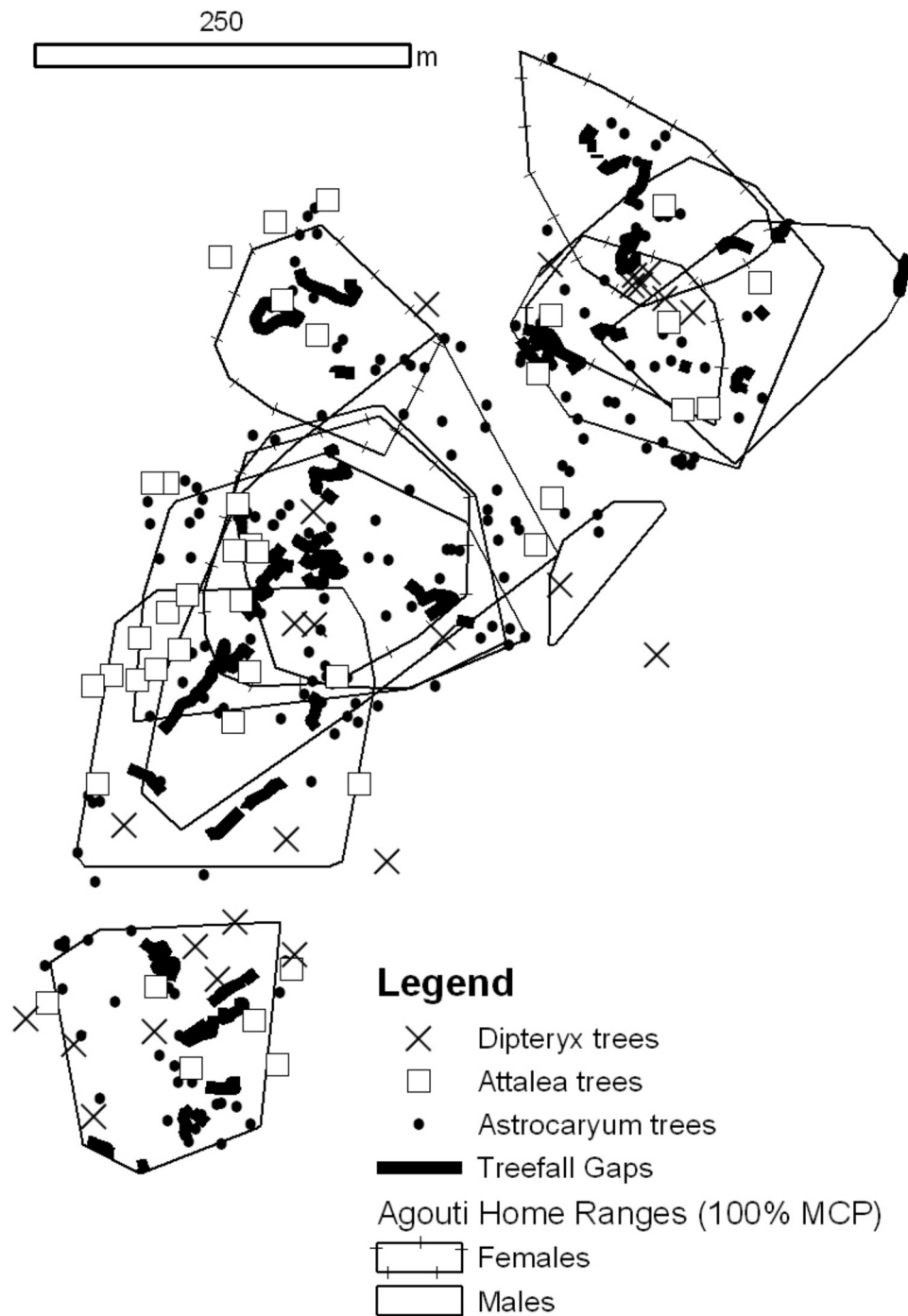


Figure 1. Home range (100% Minimum Convex Polygon) of the agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama, Central America.

captured in areas far from one another and so were unlikely to have overlapped.

Home-range size and density

The agouti ranges in our study were smaller (1–4 ha, MCP method) than reported for *D. leporina* in Brazil (3.5–9.0 ha, Jorge & Perez 2005, Silvius & Fragoso 2003), but

similar to the 3.9 ha reported for a single female *D. punctata* in Costa Rica (Rodriguez & Vaughan 1985). A previous study on BCI reported slightly smaller home ranges (1–1.5 ha) than we found (Smythe 1978), which might be expected as these were calculated from mark-resight data and not radio-telemetry fixes.

The differences in space use and density between our study and those of *D. leporina* could be due to differences

in body size, patterns of food availability, or predation. *Dasyprocta leporina* in Brazil is 30% larger (average 4.45 kg) than *D. punctata* (average 3.47 kg) (Aliaga-Rossel 2004, Eisenberg 1989, Silvius 1999, Smythe 1978, Smythe *et al.* 1996), which might at least partly explain their more extensive spatial use, independent of other ecological differences between the sites (Jetz *et al.* 2004). We do not believe that low predation risk on BCI explains these differences in home-range sizes, as studies at BCI of both *D. punctata* and local predators suggest intensive predation; for example, our agouti population experienced a 0.69 annual mortality from predation (Aliaga-Rossel 2004, Aliaga-Rossel *et al.* 2006). Furthermore, BCI agoutis made up 28.4% of puma diet and 22% of ocelot diet in the 4 y preceding this study (Moreno *et al.* 2006). Predators apparently regularly cross the 200-m distance between BCI and the National Parks on the mainland (IBID), eliminating any potential for an 'island effect' influencing our results (Moreno *et al.* 2006).

A higher abundance of food, or differences in the spatial distribution of food, may offer another explanation for the higher agouti density observed on BCI. Unfortunately, data are not available to compare across these studies. Although other competitors for food are present (*Agouti paca*, *Peccari tajacu*, *Sciurus granatensis*), one major food competitor, the white-lipped peccary (*Tayassu peccari*), is absent from BCI but present in the Brazilian sites where agouti space use has been studied (Fragoso 1999, Jorge & Perez 2005, Silvius & Fragoso 2003). Regardless of type of fruit crops produced or their amount, this difference in the potential competitor community may result in more available food at BCI, leading to smaller agouti home ranges and higher densities. Seasonality of food could also affect home-range size and sociality, with larger home ranges needed to adapt to highly seasonal food availability, and possibly allowing for more social activity (i.e. Resource Dispersion Hypothesis, Carr & Macdonald 1986, Johnson *et al.* 2002).

Likewise, our agouti density estimated from these home ranges (100 km⁻² using MCP, 161 km⁻² using Fk95) is higher than those reported from other areas (c. 40 ind km⁻² in Brazil, Jorge & Perez 2005, Silvius & Fragoso 2003; 5.2 ind km⁻² in Peru, Janson & Emmons 1990). Two previous estimates of agouti density on BCI calculated from mark-resight data (Smythe 1978) and transect surveys (Wright *et al.* 1994) found similar, although lower values (84 ind km⁻²) than our study. It is unclear if this relative density difference represents a steady increase in agouti density over time, three snapshots of a naturally fluctuating population, differences in methodology, or variation across sites within BCI.

Female agoutis on BCI used slightly smaller home ranges than males, a result also found by Silvius & Fragoso (2003) and suggested by Smythe (1978) for

BCI. However, Jorge & Perez (2005) reported no sexual differences in home-range size for *D. leporina*. Larger male ranges are common among many mammal species, particularly in polygamous species (Eisenberg 1989), where males seek to increase the number of potential mates they encounter. Our results on home-range overlap and size suggest that on BCI agoutis may exhibit a polygamous mating system, as suggested by Eisenberg (1989), rather than the strict monogamous system suggested by Smythe (1978). Furthermore, agoutis in areas of high home-range overlap tended to exhibit higher tolerance levels between home-range co-inhabitants, although every encounter observed between males resulted in aggressive behaviour and the chasing of the intruder out of the home area. Individuals with relatively large home-range areas may have greater difficulty detecting intruding animals, especially in complex forest environments with limited visibility. This would potentially decrease aggressive encounters between individuals and permit some overlap in home-range areas (Aliaga-Rossel 2004).

Determinants of space use

The use of space by *D. punctata* represents its adaptation to the pressures of finding food, avoiding predators, and reproducing. Because our study site was relatively uniform in habitat type, we focused on specific habitat features relative to these pressures by mapping all possible major food trees and potential anti-predator refuges (dens and tree-fall gaps). Smythe (1978) suggested that agoutis centre their home-ranges on important fruit trees, and our quantitative analysis found support for that in higher densities of one of their preferred foods, *A. standleyanum*, in core areas. In addition major sleeping and refuge sites were all located close to or within core areas, suggesting that agoutis are central-place foragers around the distribution of refuges. These refuges probably function primarily to avoid predation as suggested by Smythe (1978). The tree species included in our habitat analysis are key landscape elements for *D. punctata* as noted by Smythe *et al.* (1996) and Glanz *et al.* (1996).

Implications for seed movement

We found that an agouti searches roughly 35% of their total home range each day suggesting that agoutis probably encounter most fallen fruit in their home range within 1–3 d. Given their attachment to refuges, we predict that most cached seeds are moved towards their refuges (burrows in the ground and dense vegetation thickets; Aliaga-Rossel 2004). Given their 1–4 ha range size, the total distance that seeds are likely to be moved

before caching could be no greater than a home range diameter (140 m to 200 m) and most likely less than half of this.

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