Population Density and Home Range Size of Red-Rumped Agoutis (Dasyprocta leporina) Within and Outside a Natural Brazil Nut Stand in Southeastern Amazonia

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ABSTRACT

This study examined whether the population density and home range size of red-rumped agoutis were affected by the spatial distribution of Brazil nut trees, at the Pinkaiti Research Station, in eastern Amazonia. Agouti densities in a Brazil nut grove were two-fold higher and home ranges were half the size than those outside it. This indicates that the large supply of Brazil nuts results in higher densities and smaller home ranges of agoutis in this seasonally dry Amazonian forest.

RESUMEN

Este estudio examinou a influência da distribuição espacial local de castanha-do-Pará na densidade populacional e a área de vida de cutias, na Estação de Pesquisas Pinkaiti, Amazônia Oriental. Densidade populacional de cutias dentro de um Castanhal foi o dobro e as áreas de vida metade daquelas observadas em área fora do Castanhal. Isto indica que a abundância local de castanha-do-Pará resulta em diferenças tanto na densidade quanto no tamanho da área de vida de cutias.

Key words: Agouti; Amazonia; Bertholletia excelsa; Brazil nut; Dasyprocta leporina; home range; population density.

PINPOINTING KEY DETERMINANTS OF SPECIES ABUNDANCE AND DISTRIBUTION has always been a central quest in ecology. Furthermore, this understanding is becoming increasingly relevant because of the rapid environmental changes in natural habitats all over the world. Agoutis (Dasyprocta sp.) are medium-sized (3–6 kg) terrestrial rodents, with a widespread distribution in Neotropical forests, from southern Mexico to northern Argentina (Nowak 1991). They feed primarily on seeds and fruit pulp available on the forest floor (Henry 1999), with a preference for large seeds, which they scatterhoard over their home ranges during periods of resource abundance to overcome periods of scarcity (Smythe 1978, Forget et al. 2001).

Despite their ubiquity, agoutis are notoriously difficult to capture and observe systematically, and studies on the relationship between the distribution of key resources and the spatio-temporal variation in agouti population abundance are unavailable. Here we examine the overall population density and home range sizes of the red-rumped agouti (Dasyprocta leporina) in an eastern Amazonian site, and compare with equivalent data from other regions. We also consider the local spatial and temporal variation in population density and home range size in areas with and without Brazil nut trees (Bertholletia excelsa). Brazil nut trees exhibit a highly clumped spatial distribution throughout Amazonian forests (Peres et al. 2003). Agoutis disperse the vast majority of Brazil nuts (Baider 2000), and appear to be indispensable for the persistence of natural Brazil nut stands. Yet the effect of this single resource type on the abundance of these ubiquitous, and fairly generalist frugivores, remains unclear. We therefore asked whether the local distribution of reproductive Brazil nut trees was a key determinant of the local density and home range size of agoutis.

The study was carried out at the Pinkaiti Research Station, a wildlife sanctuary located within the eastern portion of the Kayapó Indian Reserve in southeastern Brazilian Amazonia (7°46′14″S; 51°57′43″W), which has been affected by little anthropogenic disturbance. Elevation ranges from 200 to 450 m above sea level, and the climate is characterized by a clearly demarcated dry season from June to September. The average annual rainfall at Pinkaiti between 1996 and 2002 was 2180 mm, with monthly rainfall of ca 300 mm during the rainy season and usually less than 30 mm during the dry season.

The study was conducted between July 1997 and February 1999, at two sites 2 km apart. One site contained a sizeable cluster of nearly 200 Brazil nut trees ≥10 cm in diameter at breast height (DBH) (hereafter Castanhal). The mean density of adult Brazil nut trees (DBH ≥ 60 cm) at this site was approximately 2 trees/ha (Baider 2000). In contrast, the second site contained no adult Brazil nut trees (hereafter Non-Castanhal). Despite clear differences in the abundance of Brazil nut trees, the overall floristic composition of the two areas was fairly similar, as determined on the basis of 1411 trees ≥10 cm DBH sampled within 2.75 ha of forest plots (Salm 2004; Sorensen Similarity Index of 0.505). The overall forest structure was also comparable across the two sites. The
Castanhal forest was taller due to the higher abundance of large emergent trees, such as *B. excelsa*. Excluding Brazil nut trees, tree density at the Castanhal site is 594 ind/ha, and basal area is 24 m²/ha (Baidier 2000), compared to a tree density and basal area of 467 ind/ha and 27 m²/ha, respectively, at the Non-Castanhal site (Salm 2004). Therefore, we can safely assume that the most important difference in the agouti food supply across the two study areas resulted from the high levels of Brazil nut seed fall at the Castanhal, which was estimated to range between 39 and 101 kg/ha/yr on the basis of a 5-yr phenological study (Baidier 2000).

Agouti density estimates at the two study areas were based upon a repeated line-transect sweep census technique, modified from standard line-transect census, typically used in many tropical forest vertebrate studies (Peres 1999a). The line-transect method proved to be adequate in this study because agoutis are ubiquitous, and easily seen or heard. The sweep census method was adjusted from the standard line-transect census to provide potentially more accurate density estimates within a specified forest plot. To accomplish this, three to six observers simultaneously walked parallel transects of 700 m in length and 100 m apart, synchronizing the times of departure and arrival (by walking at a speed of 1 km/h). The censuses took place within the early morning (0600–0700 h) and late afternoon (1700–1800 h), both peak activity periods of agoutis. Upon each sighting or vocal detection event, the observer recorded the time, location along the transect, and estimated the perpendicular distance (PD) from the transect to the animal. The same observers took part in all of the censuses, to reduce any bias in PD estimates. Double sightings were never recorded because all detection events were restricted to animals within 30 m from any given transect.

The animals were captured in the Castanhal area using intensive searches assisted by hunting dogs and in the Non-Castanhal using a Tomahawk® live trap model 207 (Tomahawk Live Trap Co., Tomahawk, WI, USA; Jorge 2000). Captured animals were measured, weighed, fitted with a Télonics® radio-collar, model 125, (Télonics, Inc., Mesa, AZ) and released at the capture site approximately 24 h later. Radio-collared animals were monitored from 0530 to 2000 h because agoutis often operate at dawn and dusk under low light conditions (Smythe 1978). Animals were individually radio-located by either triangulation or direct observation within marked trail grids (50 × 50 m or 100 × 100 m). The time of day and the main activity pattern were also recorded.

Two females and one male (hereafter referred to as FC1, FC2, and MC, respectively) were captured within the Castanhal, whereas the third radio-tracked female (hereafter, FnC) occupied the Non-Castanhal area. The three focal agoutis at the Castanhal were followed for 3 mo (November 1997 to February 1998) providing 109 locations (FC1), 117 (FC2), and 114 (MC). FnC was followed from July 1997 to July 1998, providing 366 locations spread over 91 d of observation. To compare FnC’s home range area with that of individuals from the Castanhal area, we subsampled its positional data with a standardized procedure (110 locations, samples from November 1988 to February 1999 with the same daily and weekly distribution of locations).

To quantify the overall availability of mature fruits and seeds on the forest floor for terrestrial frugivore/granivores, such as agoutis, monthly census walks were conducted from April 1996 to March 1998 along a 5000 m transect with mean width of 1 m. Upon each encounter with a fresh fruit patch on the forest floor, we identified the source tree or woody liana, and measured its DBH. A rank value from one (small patches: 1–10 fruits) to four (large patches: > 50 fruits on the floor) was then assigned to describe the size of each discrete fruit patch, so that a monthly index of fruit availability (FA) could be derived as following: 

\[ FA = \sum (BA_i \times \text{rank}) / \text{total area} \] (Develey & Peres 2000), where \( BA_i \) is the basal area for each individual tree (\( BA_i = \pi r^2 \)). Monthly indices represent an average from the 24 consecutive months of fruit sampling (except for January, September, and December when the data available were restricted to a single year).

Population census data were analyzed separately by season and forest site, and in aggregate, by pooling all records within a season and site. Agouti densities were estimated with DISTANCE (version 3.5, Thomas et al. 1998). Home range size and shape were primarily estimated using the Harmonic Mean method (Dixon & Chapman 1980), which has the best performance in evaluating these parameters (Harris et al. 1990). We used 75 percent rather than 95 percent density curves (d.c.) because the former showed greater stability with small sample sizes, due to exclusion of rare locations in the most peripheral parts of the home ranges (Jorge 2000). The Minimum Convex Polygon method (Mohr 1947) was also used to allow comparisons with range size estimates from other studies. Home range sizes and shapes were estimated using HOME RANGE (Ackerman et al. 1990).

The overall mean density estimate for agoutis at Pinkaiti was 31 ind/km², which is substantially higher than that of other non-hunted Neotropical forests, including Tikal, Guatemala (8 ind/km²; Cant 1977), Cocha Cashu, Manu National Park, southern Peru (5 ind/km²; Janson & Emmons 1990), and two unflooded forests of central-western Brazilian Amazonia (Uruçu, 5 ind/km²; Peres 1999b; Lago Uauaquú, 8 ind/km²; Haugaasen & Peres 2005). The mean agouti density at Pinkaiti, however, is still nearly three-fold lower than that reported for Barro Colorado Island (BCI), Panama (84 ind/km²; Wright et al. 1994), and roughly equivalent to that in a semiprotected old secondary Panamanian forest where agoutis have been hunted by poachers (20–55 ind/km²: Wright et al. 1999). Thus, the population density of this ubiquitous Neotropical forest rodent appears to be highly variable over their geographic range.

Regional differences in granivore population densities could be related to the presence and abundance of specific large-seeded tree species, even in tropical forests containing hundreds of tree, woody liana, and epiphyte species (cf. Silvius & Fragoso 2003). However, other factors such as the co-occurrence of other terrestrial consumers of large seeds and the overall biomass of arboreal granivores and frugivores, which usually have access to seeds and fruits before their terrestrial counterparts, should also be considered.

Mean home range size (±SD) of the four radio-tracked agoutis at Pinkaiti was 3.4 ± 1.6 ha (75% HM) or 4.5 ± 1.3 (MCP) during a 3-mo sampling period. Regional comparisons of home range sizes are not as straightforward as those of population densities. There are only three ranging studies of natural agouti populations (Panama: Smythe 1978; Costa Rica: Rodriguez & Vaughan 1985; and Maracá Island, Brazil: Silvius & Fragoso 2003). Among these, only two used radiotelemetry. Home ranges of radio-collared agoutis at Pinkaiti are similar to those in Costa Rica (4 ha; one female radio-tracked for 2 mo) and Maracá Island, Brazil (3–8.5 ha; one male and four females radio-tracked for 2–9 mo), but slightly larger than those at BCI (1–2 ha for each pair, based on a capture-recapture study for several years).
The Pinkaiti region presents a marked dry season that clearly affects fruit availability within tree and liana crowns (Baider 2000) and reflects seasonal fluctuations in agouti density (Castanhal: 37 ind/km² during the dry season vs 17 ind/km² during the wet season; Non-Castanhal: 23 vs 9 ind/km²). In BCI, which also has a marked dry season, Smythe (1978) observed that females give birth at any time of the year, but that the probability of juvenile mortality was much higher during the period of food scarcity (70% vs. 5%). Smythe (1978) suggested that juvenile mortality may be due to higher rates of predation from male coatis (Nasua nasua), which shift from a more frugivorous to a more carnivorous diet when fruits become scarce. Coatis are unable to open the hard husks of Brazil nut fruits, thus they are expected to shift their diet at the Castanhal site as well as in areas where Brazil nuts are unavailable, and the predation rates should be equivalent within and outside the Castanhal.

With respect to range size variation, over an entire annual period, home range size for FnC ranged over 6.9 ± 0.4 ha (75% HM) or 9.2 ± 0.4 ha (MCP), but greatly varied over the months, becoming smaller and shifting the core area during the peak fruiting season (Fig. 1; Jorge 2000). Such variation showed a strong negative correlation with fruit availability of the previous month, when the month of May was excluded (Spearman correlation index r = –0.83; N = 8; P < 0.02). This correlation was also observed in another highly seasonal Amazonian forest where temporal shifts in intensively used areas and home range boundaries also occurred as a function of fruit availability (Silvius & Fragoso 2003). In this study, for instance, a fruiting Attalea palm near the range boundaries of FnC became the focus of its foraging activity during the peak of wet season (January-February). After the palm fruiting period was discontinued, FnC day ranges increased once again (Fig. 1), the core area shifted back to the usual site, and did not change over the rest of the year (Jorge 2000).

There were also considerable differences in densities across consecutive years within the Castanhal site. Densities were lower in 1998–1999 than in 1997–1998 during both seasons (dry season: 61 vs 37 ind/km²; wet season: 20 vs. 17 ind/km²; Table 1). Such a result is not easily explained by differences in Brazil nut production because in 1997 it was half of that in 1998 at this site (40 kg/ha vs 80 kg/ha: Baider 2000). One plausible explanation is a delayed effect, in that the agouti density decline observed in 1998–1999 may be a concomitant response to that in Brazil nut availability in 1997.

Finally, this study indicates that the local agouti density at Pinkaiti was context-dependent and apparently related to the distribution of Brazil nut trees. The density of agoutis within the large Brazil nut stand (Castanhal) was higher than that where Brazil nut trees were conspicuously absent. In both seasons of 1998–1999, the Castanhal site sustained almost twice as many agoutis per unit area than did the Non-Castanhal site (dry season: 37 vs 23 ind/km²; wet season: 14 vs 9 ind/km²; Table 1). Accordingly, the agoutis monitored at the Castanhal exhibited smaller home ranges than that of the female radio-tracked outside it, when considering the same period. Mean home range size for the Castanhal females ranged from 2.3 to 2.7 ha (75% HM) or from 3.1 to 4.5 ha (MCP), whereas the female outside the Castanhal (FnC) used an area approximately two-fold larger (75% HM: 5.8 ha; MPC: 6.4 ha). Since both forest sites are floristically and structurally similar, these differences are best attributed to the greater availability of large, palatable seeds on the forest floor at the Castanhal site, and may reflect

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**TABLE 1.** Sampling effort and density estimates of Dasyprocta leporina at Pinkaiti, Kayapó Reserve, Brazil, during dry and wet seasons at two sites, one with high density of and the other with no fruiting Brazil nut trees (Castanhal and Non-Castanhal). Sighting data were analyzed in aggregate by pooling both sites and both dry and wet season records, and separately, in six sampling blocks, using DISTANCE software 3.5.

<table>
<thead>
<tr>
<th>Site</th>
<th>Season</th>
<th>Month-Year</th>
<th>Sampling effort (m)</th>
<th>Individuals detected</th>
<th>Detection rate (inds. km⁻²)</th>
<th>Density ± SD (inds. km⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Castanhal</td>
<td>Dry</td>
<td>July/Aug-97</td>
<td>11,400</td>
<td>42</td>
<td>3.7</td>
<td>61 ± 9</td>
</tr>
<tr>
<td>Castanhal</td>
<td>Wet</td>
<td>Feb/May-98</td>
<td>15,000</td>
<td>18</td>
<td>1.2</td>
<td>20 ± 5</td>
</tr>
<tr>
<td>Castanhal</td>
<td>Dry</td>
<td>Jul/Aug-98</td>
<td>16,750</td>
<td>31</td>
<td>1.9</td>
<td>37 ± 7</td>
</tr>
<tr>
<td>Castanhal</td>
<td>Wet</td>
<td>February-99</td>
<td>9,375</td>
<td>7</td>
<td>0.7</td>
<td>17 ± 8</td>
</tr>
<tr>
<td>Non-Castanhal</td>
<td>Dry</td>
<td>Jul/Aug-98</td>
<td>19,625</td>
<td>27</td>
<td>1.4</td>
<td>23 ± 4</td>
</tr>
<tr>
<td>Non-Castanhal</td>
<td>Wet</td>
<td>February-99</td>
<td>11,300</td>
<td>5</td>
<td>0.4</td>
<td>9 ± 4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>83,450</td>
<td>130</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
the highly specialized seed-granivore interactions between *Bertholletia* and *Dasyprocta*, which have been observed since the time of the earliest naturalists in Amazonia (Huber 1910).

Agouti home ranges at the *Castanhal* contained an average of 2.3 fruiting Brazil nut trees ≥60 cm in DBH (range = 1–4; H.M. 75% d.c., Fig. 2). The annual crop per fertile tree at that site ranged from 103 to 270 fruits (1997–2000; Baider 2000), which is equivalent to an input of 39–101 kg of *B. excelsa* seeds ha⁻¹ (Baider 2000); mean seed per fruit = 17.5; mean unshelled seed weight = 13 g, and 1.65 fertile tree/ha) or 100–260 kg of *B. excelsa* seeds per agouti home range per year; 75 percent mean HM for the *Castanhal* animals = 2.5 ha). This is in striking contrast to the area lacking Brazil nut trees, which contained only a mixed assemblage of small, medium, and some large-seeded tree species.

Yet these interactions are neither necessarily reciprocal nor symmetrical in that most agouti populations occur well outside the natural geographic distribution of Brazil nut trees. This pattern was mirrored on a finer scale in this study in that Brazil nuts were almost certainly the top-ranking food species for agoutis occupying the *Castanhal* site, whereas this patchy resource was entirely unavailable for agoutis in most of the Pinkaiti study region, including the *Non-Castanhal* area.

In the absence of Brazil nuts, agouti populations most likely rely on other large-seeded species of varying degrees of palatability. In Maracá Island, Roraima, Brazil, agoutis rely mainly on two large-seeded species of Sapotaceae (*Pouteria surinamensis* and *Pradostia surinamensis*) and the palm *Attalea maripa* (Silvius & Fragoso 2003). At Pinkaiti, agoutis occupying areas lacking Brazil nut trees depended heavily on two arborescent palm species, feeding mainly on scatter-hoarded seeds of *Astrocaryum aculeatum* during the dry season and fresh fruits of *Attalea maripa* during the wet season (Jorge 2000). This suggests that, although often referred to as generalist seed predators, agoutis may actively search for certain species of large seeds, and from a bottom-up perspective agouti densities may be primarily regulated by the local abundance of large-seeded plants.

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