Effects of Food Availability on Space and Refuge Use by a Neotropical Scatterhoarding Rodent

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ABSTRACT

Animals that rely on refuges for safety can theoretically increase their foraging area without simultaneously increasing predation risk and travel costs by using more refuges. The key prediction of this theory, a negative correlation between food abundance, home range size and the number of refuges used, has never been empirically tested. We determined how home range size and refuge use by the Central American agouti (*Dasyprocta punctata*) varied across a gradient of abundance of the agoutis' principal food source: seeds and fruits of the palm *Astrocaryum standleyanum*. We used both manual and automated radio telemetry to measure space use of 11 agoutis during 2 mo of the *Astrocaryum* fruiting season, and of another set of 10 agoutis during 6 mo in which the animals largely relied on cached *Astrocaryum* seeds. We found that agoutis living in areas of lower food density had larger home ranges, and that all individuals used multiple refuges. The number of refuges, however, was not correlated with home range size. Consequently, agoutis that had larger home ranges roamed farther from their refuges. These results suggest that agoutis increase their home range size in response to food scarcity at the cost of their safety.

Key words: *Astrocaryum standleyanum*; Central American agouti; *Dasyprocta punctata*; food limitation; home range; Panama; predation risk; radio telemetry.

MANY PREY SPECIES SPEND A LARGE PORTION OF THEIR TIME HIDING from predators in a central refuge, especially while sleeping. Central-place foraging theory predicts that these species concentrate their activity near the refuge because energy expenditure and predation risk increase with distance from the refuge (Covich 1976, Orians & Pearson 1979, Kotler *et al.* 1999). Patterns fitting this prediction have been documented in a variety of species including rabbits (*Oryctolagus cuniculus*; Banks *et al.* 1999), pikas (*Ochotona collaris*; Holmes 1991), marmots (*Marmota caudata*; Blumstein 1998) and baboons (*Papio cynocephalus*; Cowlishaw 1997). The concentration of herbivore activity around these refuges has important ecological implications in terms of the intensity of browsing and directionality of seed dispersal. For example, rabbits graze more heavily around their burrow (Bakker *et al.* 2005), and hoarding rodents often transport seeds toward central refugia (Smith & Reichman 1984).

Restricted movement around one central site limits foraging opportunities, which can be problematic especially when nearby food patches have been depleted or overall food availability is low (Covich 1976, Andersson 1978, Gilliam & Fraser 1987). In general, individuals living in habitats with low food density are

predicted to compensate by spending more time foraging and traveling over farther distances, and to have larger home ranges (Andersson 1978). Indeed, there is a well-established negative relationship between home range size and local food availability for a wide variety of species (Boutin 1990, Adams 2001). Such behavioral adaptations imply a trade-off between predation risk, travel costs and food acquisition: as an animal covers more area to feed, it travels farther away from the safety of the central refuge.

In theory, refuge-inhabiting animals can increase their foraging area without simultaneously increasing predation risk and travel costs by using additional refuges scattered throughout the home range (Covich 1976). This behavioral adaptation has been suggested for some species (*e.g.,* Chapman *et al.* 1989, Blumstein 1998). The key prediction of this theory, that the number of refuges used increases with home range size, has never been empirically tested.

We studied the effects of local food availability on space and refuge use by the Central American agouti (*Dasyprocta punctata*, henceforth 'agouti'), a Neotropical forest rodent that uses multiple refuges and has been reported to behave as a central-place forager (Smythe 1978, Aliaga-Rossel *et al.* 2008). Theory predicts that agoutis have more refuges in areas where lower food abundance forces them to forage across larger areas. We tested two hypotheses: (1) home range size in agoutis is negatively related to

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local food availability and (2) the number of refuges used by agoutis is positively related to the size of the home range and negatively related to food availability.

METHODS

Study area and species.—Fieldwork was conducted on Barro Colorado Island (BCI) (9°10′ N, 79°51′ W, Gatun Lake, Panama) between October 2008 and May 2010. Barro Colorado Island is a 15.6 km² island, covered with semi-deciduous moist tropical lowland forest of different successional stages. The climate is seasonal, with a 4-mo dry season from December to March. BCI has been protected from poaching since 1960 and has an almost complete mammal fauna (Wright *et al.* 1994).

The Central American agouti is a medium-sized (2–4 kg) frugivorous, diurnal, scatterhoarding rodent found from Mexico to Argentina (Smythe 1978, 1989). Agoutis are known to use multiple refuges within their home range, including burrows and dense vine tangles, to avoid predation (Smythe 1978). The ocelot (*Leopardus pardalis*) is the main predator of agoutis on BCI, and predation pressure is high (Moreno *et al.* 2006). The agouti's diet consists of fruit pulp and seeds from large-seeded plant species, supplemented with smaller fruits and seeds, animal matter and leaves (Smythe 1978, Smythe *et al.* 1982, Henry 1999). For significant parts of the year, the staple food for agoutis on BCI are the fruits and seeds of *Astrocaryum standleyanum* (Arecaceae, henceforth '*Astrocaryum*'), a widespread and often abundant species of arborescent palm (Smythe *et al.* 1982, Smythe 1989, Aliaga-Rossel *et al.* 2008, Gálvez *et al.* 2009, Lambert *et al.* 2009, Jansen *et al.* 2010). *Astrocaryum* produces up to eight infructescences that each contain up to 400 seeds, with each seed approximately 2 × 1.5 cm in size and covered by a stony endocarp, a fleshy mesocarp and a leathery exocarp (De Steven *et al.* 1987, Jansen *et al.* 2008). Fruits ripen from December onwards and are shed during the early wet season (March to early July) (De Steven *et al.* 1987, Smythe 1989). Agoutis on BCI intensively scatterhoard *Astrocaryum* seeds during the fruiting period and heavily rely on these cached seeds during the rest of the year, particularly from September onwards (Smythe 1978, 1989, Jansen *et al.* 2010). In contrast, fruits and seeds of other large-seeded tree species that agoutis on BCI are known to consume, including *Attalea butyracea* (Arecaceae), *Dipteryx oleifera* (Fabaceae) and *Gustavia superba* (Lecythidaceae) are important seasonally rather than throughout the year (Smythe *et al.* 1982, Forget 1992). Most seeds of *D. oleifera* and *G. superba*, for example, germinate within 2–3 mo and are thus less suitable as long-term food supplies (Clark & Clark 1984, Sork 1985).

Agouti trapping and radio telemetry.—Agoutis were captured in areas with contrasting abundance of *Astrocaryum* palms, using live traps (Tomahawk Live Trap co., Hazelhurst, Wisconsin, U.S. A.) baited with coconut or banana. Traps were checked twice daily; late in the morning and right after dusk, following peak agouti activity times. Captured animals were anesthetized with 0.8 mg/kg Telazol (Tilamine hydrocholoride + Zolazepam).

Adult individuals (>2.3 kg; Smythe 1978) were fitted with a VHF radio-collar (Advanced Telemetry Systems Inc., Isanti, Minnesota, U.S.A.). The trapping and radio-collaring procedures were approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute, and conducted under research permits authorized by the Barro Colorado Nature Monument.

We manually collected bearings for a first set of ten radio-collared agoutis during October 2008 to March 2009 using a hand-held receiver (AOR 8000; AOR ltd, Tokyo, Japan) and a Yagi directional antenna. Locations for each agouti were collected multiple times per week, between the hours of 0530 and 1830 h. We used an Automated Radio Telemetry System (ARTS) to collect bearings for a second set of 11 agoutis in 2010, which were living in the center of the island where the ARTS error margin was lowest (Crofoot *et al.* 2008). Technical descriptions of the ARTS can be found in Crofoot *et al.* (2008) and Kays *et al.* (2011). To improve coverage of the collared animals we supplemented the seven above-canopy tracking towers of the ARTS with two 3-m understory tracking towers. We used 2 wk of ARTS bearings data (22–28 April and 8–14 May), which coincided with the peak fruiting of *Astrocaryum*. These bearings were manually smoothed using the software PV-Wave (Visual Numerics, Houston, Texas, U.S.A.) to reduce background noise (*cf.* Crofoot *et al.* 2008). To calculate location fixes from both the 2008–2009 and the 2010 bearings, we used LOAS 4.0 (Ecological Software Solutions LLC, Hegymagas, Hungary). Nighttime data points were excluded. All location fixes were considered independent as intervals between consecutive points were >30 min, which is enough time for an animal to cross its entire home range (Aliaga-Rossel *et al.* 2008). The average number of location fixes per individual was 57.5 (SD = 12.1) for the manual tracking, and 62 (SD = 23) for the automated tracking, which was more than the minimum of 30 fixes per animal that are needed to obtain acceptable home range estimates (Seaman *et al.* 1999). We used the ABODE Home Range Tool (Laver 2005) in ArcGIS 9.3 (ESRI Environmental Systems Research Institute, Redlands, California, U.S.A.) to calculate 95 percent Fixed Kernel isopleths from these locations. We used Least Squares Cross Validation (LSCV) to select the smoothing parameter (Seaman & Powell 1996).

We located the refuges for nine individuals studied in 2010 by manual radio tracking during the night, when agoutis normally reside in their refuges; the remaining two individuals from 2010 could not be tracked due to rough topography. By tracking agouti refuges during the night, we were typically able to find refuges without causing any disturbance to the agouti. Initial attempts to track agoutis around noon, when they have a midday lull in activity, invariably caused the agoutis to flee. This indicated that agoutis were not in secure refuges at those times. We defined a refuge as a location where an animal could be tracked and would not run away upon being approached (up to 1–2 m), indicating that the animal felt safe. If possible, we located the refuge entrance (*e. g.,* burrow). All refuge locations were recorded with a GPS receiver (Garmin CS × 60; Garmin ltd, Olathe, Kansas, U.S.A.). Each

radio-collared agouti was systematically tracked once every 2–4 nights from early April to mid-May 2010, resulting in 10–17 tracking nights per individual. Animals were sometimes found outside of a refuge, resulting in a total of 7–15 nights that an agouti was found in a refuge. To correct for differences in sample size between individuals, we standardized the refuge number by dividing the number of refuges by the logarithm of the total number of nights in which the animal was found in a refuge. For each agouti, we also measured the distance from each location fix (collected by ARTS) to the nearest refuge of the individual, and calculated the median of those distances.

FOOD AVAILABILITY.—We used the abundance of trees and fruits of *Astrocaryum standleyanum* as measure of food availability, assuming that this resource was the key determinant of food abundance during our study period. The first set of ten agoutis was tracked during the period of annual food scarcity (October to March), when agoutis on BCI heavily rely on previously cached seeds of *Astrocaryum* for food (Smythe *et al.* 1982, Smythe 1989, Jansen *et al.* 2010, W. J. Emsens, pers. obs.). The second set of 11 agoutis was tracked during the fruiting peak of *Astrocaryum* (April to May), when fresh *Astrocaryum* pulp and seeds constitute a staple food for agoutis on BCI (Smythe *et al.* 1982, Smythe 1989).

Local food availability was quantified as the density of *Astrocaryum* fruits and trees in the environment of each individual, which was standardized as the area within a radius of 100 m around the home range centroids, henceforth 'core area'. The size of this core area (3.14 ha) approximates the average size of agouti home ranges on BCI. Density measured across a standardized core area is independent of home range size, unlike density measured across the entire home range. For all agoutis, we measured tree density by mapping all stems of reproductive *Astrocaryum* with a GPS receiver through systematic ground survey. For the agoutis in 2010, we also estimated fruit density by counting fruits on all mapped *Astrocaryum* trees using a pair of binoculars (as in Jansen *et al.* 2008) from February to early March 2010, shortly before fruits started to fall. Fruit density was highly correlated with tree density in the core areas of the 11 agoutis studied in 2010 (Fig. 1; Pearson's correlation: $r = 0.88$, $t = 5.59$, df = 9, $P < 0.001$), showing that tree density was a good proxy for fruit density (as in Jansen *et al.* 2008).

DATA ANALYSIS.—We used linear regression of home range size against local food availability for both sets of agoutis to test the hypothesis that home range size decreased with food availability. We used Pearson correlation tests to determine whether the standardized number of refuges was correlated with home range size and with food availability for the 2010 agoutis. Pearson correlation tests were also used to determine whether the agoutis' median distance to a refuge was correlated with home range size and food availability. All measures of food availability were log10-transformed prior to analyses to conform to assumptions of normality.

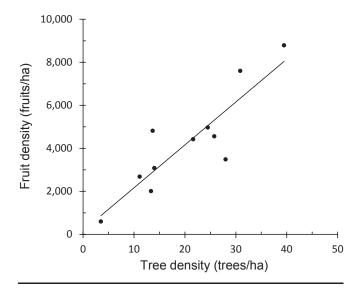All analyses were performed with R 2.13.0 (R Development Core Team 2011).

FIGURE 1. Relationship between tree density and fruit density of *Astrocaryum standleyanum* for 11 areas of 3.14 ha on BCI, Panama.

RESULTS

HOME RANGE SIZE.—Home range size (95% Kernel) ranged between 1.23 and 5.47 ha (mean = 2.71 ± 1.22 ha) among the ten agoutis manually tracked in 2008–2009 and between 0.74 and 6.12 ha (mean = 3.04 ± 1.43 ha) among the 11 agoutis automatically tracked in 2010. Home range size was not significantly different between the two sets of agoutis (Student's *t*-test: $t = 0.57$, $P = 0.578$) and did not differ between sexes in either 2008–2009 ($t = 0.62$, $P = 0.573$) or 2010 ($t = -0.46$, $P = 0.651$). For the agoutis studied in 2010, home range size decreased significantly with *Astrocaryum* fruit density in the core area (Fig. 2A; least-squares regression: $R^2 = 0.65$, $F = 16.57$, df = 1,9, $P = 0.003$). Home range size was also negatively related to *Astrocaryum* fruit density across the actual home ranges ($R^2 = 0.39$, $F = 5.69$, df = 1,9, $P = 0.04$). This relationship was robust, as we found a similar decrease in home range size with *Astrocaryum* tree density in the core area of the animals (Fig. 2B), both for the agoutis studied during the fruiting season in 2010 ($R^2 = 0.61$, $F = 13.93$, df = 1,9, $P = 0.005$) and for the agoutis studied after the fruiting season in 2008–2009 ($R^2 = 0.45$, $F = 6.47$, df = 1,8, $P = 0.035$).

REFUGE USE.—The nine agoutis from 2010 for which we obtained refuge data all used multiple (2–4) refuges interchangeably. The standardized number of refuges, corrected for differences in sampling effort, ranged between 1.7 and 4. The most commonly used refuge type (61%) was woody debris; either dense vine tangles or large, impenetrable piles of debris in tree-fall gaps. The second-most commonly used refuge type (26%) were subterranean burrows, located either out in the open or under a tree buttress. Agoutis also used hollow logs as refuges (13%). Some refuges in woody debris could have also included a burrow or hollow log, but it was impossible to determine this without destroying the vegetation.
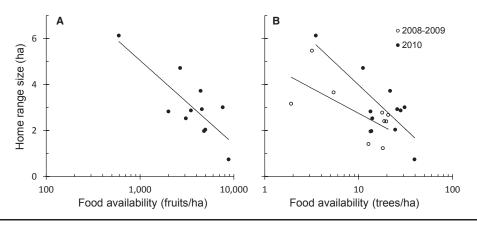
FIGURE 2. Relationship between local food availability and home range size for Central American agoutis (*Dasyprocta punctata*) on BCI, Panama. Home range size was measured as the 95 percent kernel of location fixes from radio tracking; food availability was measured as the density of *Astrocaryum* fruits (A) and trees (B) within 100 m from the home range centroids.

The number of refuges used was not correlated with home range size (Fig. 3A; Pearson's correlation: $r = 0.001$, $t = 0.003$, df = 7, $P = 0.998$) or with fruit density in the core area (Fig. 3B; $r = 0.13$, $t = 0.348$, df = 7, $P = 0.738$), which does not support the hypothesis that animals use more refuges as they have less food and larger home ranges. As a result, the median distance

between agouti locations during the day and the nearest refuge, which ranged between 34 and 87 m, was positively correlated with home range size (Fig. 3C; $r = 0.699$, $t = 2.588$, df = 7, $P = 0.036$), indicating that agoutis with larger home ranges foraged farther away from their nearest refuge. The correlation between the median distance to the nearest refuge and food avail-
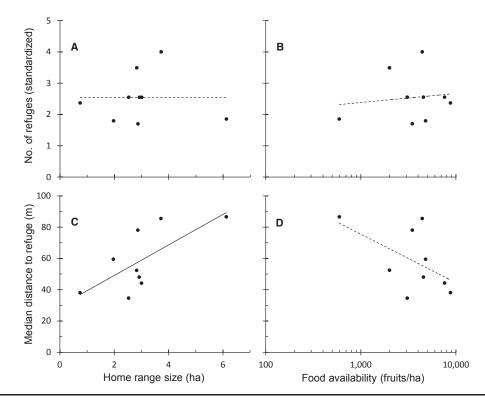

FIGURE 3. Refuge use and median distance to the nearest refuge in relation to home range size and local food availability for Central American agoutis (*Dasyprocta punctata*) on BCI, Panama. Home range size was measured as the 95 percent kernel of location fixes, food availability as the density of *Astrocaryum* fruits within 100 m from the home range centroids. Refuge use standardized for sampling effort was calculated as the total number of refuges recorded divided by the logarithm of the number of nights in which a refuge was found. The median distance to the nearest refuge was estimated with telemetry locations. Panels show the relationship of the number of refuges used by agoutis with (A) home range size and (B) food availability, and the relationship of the median distance of agoutis to the nearest refuge with (C) agouti home range size and (D) food availability. The solid line represents a significant relationship.

ability was negative, but non-significant (Fig. 3D; $r = -0.537$, $t = -1.686$, df = 7, $P = 0.197$).

Individuals were typically found in the same refuge for more than one consecutive tracking night before moving to another, but refuge-switching behavior was variable and unpredictable. For example, one female was found in the same refuge for eight consecutive tracking nights, was then found in a different refuge for only one tracking night, and then moved back to the initial refuge for another six tracking nights. In contrast, one male agouti was never found in the same refuge for more than three consecutive tracking nights and frequently switched between four different refuges. We found no evidence for simultaneous occupation of refuges by different agoutis, but two refuges were used by more than one radio-collared agouti on different nights.

DISCUSSION

We tested whether agoutis on Barro Colorado Island, Panama, used more refuges when they had larger home ranges. Increasing the number of refuges would theoretically allow these rodents to adopt larger home ranges without increasing predation risk and travel costs. We did find the predicted relationship of larger home ranges where food was less abundant, but found no relationship between the number of refuges and home range size. As a result, individuals with larger home ranges were generally found foraging farther from their nearest refuge.

We used the abundance of trees and fruits of a single tree species, *Astrocaryum standleyanum*, as a proxy for food availability. This tree is a very important food source to agoutis, but it is by no means the only food species. Despite this simplification, local densities of *Astrocaryum* trees and fruits explained home range size well. This finding is in agreement with Jorge and Peres (2005) who argued that agoutis, despite consuming a variety of seed and fruit species, might be highly dependent on one or a few large-seeded plant species. For example, agoutis in Northern Brazil largely relied on fresh and cached seeds of *Pouteria surumuensis* for at least seven continuous months (Silvius & Fragoso 2003), and agoutis in the Eastern Amazon largely relied on *Astrocaryum* sp. during the dry season and *Attalea* sp. during the wet season (Jorge 2000). Our results support the prediction that food abundance influences the area that animals use to obtain sufficient food (Andersson 1978). Similar patterns have been found in a variety of other vertebrate species (Boutin 1990, Adams 2001).

Nocturnal radio tracking showed that agoutis usually rest inside their refuges between dusk and dawn, when ocelots are most active and predation risk is highest (Lambert *et al.* 2009). Nevertheless, we found no support for the hypothesis that the use of multiple refuges is a strategy to minimize the distance to the nearest refuge in larger home ranges (Covich 1976, Chapman *et al.* 1989); agoutis with larger home ranges did not have more refuges. As a result, active agoutis with larger home ranges were generally found farther away from their nearest refuge, which is considered riskier behavior as it takes longer to retreat to cover when threatened (Covich 1976, Dill & Houtman 1989, Kotler *et al.* 1999). Also, agoutis living in large, food-poor territories

should spend more time foraging and traveling, which increases the risk of encountering predators.

Another factor that could affect predation risk is differences in the local activity of predators. Although all of our study animals are hunted by the same population of predators, there could be local differences in the intensity of predator activity. For example, if ocelots also respond to differences in agouti density, then ocelot activity might be higher in areas with greater agouti and *Astrocaryum* density. This possibility has been evaluated at our study site with remote camera deployments and it was found that ocelot activity did increase slightly with agouti density (J. W. Buis, & P.A. Jansen, pers. comm.). The ratio of agoutis to ocelots, however, increased with higher agouti density, which suggests that the relative predation risk to agoutis is still higher in areas with low food density, as there are fewer conspecifics to share the risk.

We see three non-exclusive possible explanations for the lack of correlation between home range size and the number of refuges used. First, it is possible that agoutis used additional refuges during the daytime. This, however, was never observed during our fieldwork. Our initial attempts to approach agoutis during their midday lull of activity invariably caused the agoutis to flee, indicating that agoutis were not in secure refuges at those times. Second, the number of refuges used may be determined solely by the availability of suitable refuge locations. If potential refuge locations are scarce or non-randomly distributed across the landscape, then there could be high competition for the best sites (*e.g.,* Schradin 2005). Third, it is possible that agoutis do not minimize their distance to a refuge while active. This would be in contrast, however, with the finding that core agouti activity is usually in the vicinity of agouti refuges (Aliaga-Rossel *et al.* 2008), and in contrast to the behavior of most refuge-inhabiting rodents (*e.g.,* Holmes 1991, Blumstein 1998).

In conclusion, this study demonstrates that agoutis had larger home ranges in areas where the density of their principal food source was lower. Individuals with larger home ranges, however, did not use more refuges, and as a result, they generally moved farther from the safety of their nearest refuge. These results suggest that agoutis increase their home range size in response to food scarcity at the cost of their safety.

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