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Unpaved roads are not adequate surrogates of true transects for sampling agoutis

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Abstract: The distance sampling is one of the most widely used techniques for estimating abundance and density, particularly for mammals. Managers/researchers sometimes sample unpaved roads assuming that these do not violate important assumptions. However, relatively few studies have attempted to address this, simultaneously comparing behavior between roads and transects, a key issue as behavior can potentially affect detection. Here, we used distance sampling to compare abundance and behavior of agoutis between transects and unpaved roads. We sampled an isolated agouti population during two contrasting seasons. Road densities (347–432 agoutis/km² for dry and wet seasons, respectively) were statistically similar to those from transects (373–322 agoutis/km², respectively). However, road data had a different variance contribution, lower detection probability and poorer model fitting. We also found that agoutis move/interact and forage/feed differently on roads in comparison with transects and were more vigilant in transects than in roads during the first season we sampled (wet). Together, these findings indicated that (1) we detect agoutis differently on these two transect types and (2) road sampling more seriously violates the assumption of randomness of transects in relation to animals. We conclude that while avoiding roads is unfeasible given time and logistical limitations, researchers should be aware of the potential bias, making this clear when discussing and comparing their results.

Keywords: behavior; caviomorphs; distance sampling; population estimation; urban matrix.

Introduction

Estimates of population abundance are a basic step toward the establishment of a successful management and conservation strategy. Among the methods available for estimating abundance of tropical forest mammals of medium to large body sizes, line transect distance sampling is one of the most popular methods (Buckland et al. 1993, Barry and Welsh 2001). As every other method, the distance sampling has its own assumptions, which should be validated by the researcher if he/she intends to make valid inferences about density or abundance of the sampled population (Buckland et al. 1993). Some key classical assumptions of line transect distance sampling are (1) distance between animal and line transect is measured accurately and precisely; (2) animals are spotted on their original position when first detected by the observer; (3) all animals on the line transect are detected with certainty; and (4) transects are randomly positioned in relation to animals' distribution (Buckland et al. 1993). Currently, some degree of relaxation of these assumptions is possible. However, the quality of estimates will depend on the ability of the researcher to model the errors and/or bias introduced by the violation of those assumptions (Marques and Buckland 2003, Buckland et al. 2004, Borchers et al. 2010, Marques et al. 2012).

A recurrent violation of the aforementioned assumptions involves the use of roads as surrogates of true line transects. Some researchers may choose to sample animals using pre-existing trails or unpaved roads, due to lack of time, access restrictions or logistical limitations (Varman and Sukumar 1995, Ruelle et al. 2003, Ward et al. 2004, Butler et al. 2007). This argument implies that animal distributions in relation to roads fulfill the randomness assumption of distance sampling, something that has been confirmed for a rather small number of species (Venturato et al. 2009, Erxleben et al. 2011). This argument further implies that the behavioral repertoire of animals sampled along roads is not different from that of animals observed along true transects, an important factor as behavior can potentially affect detectability (Ramsey and Harrison 2004, Hounsoume et al. 2005, Smolensky and Fitzgerald 2010). If behaviors affecting detectability

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are not random in relation to roads, estimates will be compromised, despite any random geographic distribution of animals.

Besides the behavioral issue, sampling along roads and trails has other problems. Vegetation along their margins might be disturbed by edge effects, impairing the detectability of animals by the observer. Edge effect itself might cause problems, as some species are attracted to these disturbed places while others are repelled. We expected, therefore, that key population parameters (abundance and density) estimated from roads are different from randomly positioned transects. We further expected that the quality (precision) of the estimated parameters deteriorates when surveys are carried out along roads rather than on true transects (Varman and Sukumar 1995, Tomas et al. 2001, Marques et al. 2010).

The main objective of this paper is to test the hypothesis that the quality of density and abundance estimates from sampling black-rumped agoutis (*Dasyprocta prymnolopha* Wagler 1831) along true forest transects cut specifically for that purpose provides a more accurate estimate than those generated from using unpaved roads or pre-existing trails. Thus, we analyzed data from both seasons (dry and wet) and compared agoutis' density, abundance and behavior sampled from these two transect types.

Secondarily, we were also interested to assess the population size of our study subject as the black-rumped agouti is a Brazilian endemic (Paglia et al. 2012). Although this species is not threatened in Brazil, it is regionally endangered in the state of Minas Gerais (COPAM 2010). There are some studies reporting the effects of habitat fragmentation on agoutis (Jorge 2008, Jorge and Howe 2009) and others analyzing the density of agoutis in insular environments (Silvius and Frago 2003, Bovendorp and Galetti 2007, Aliaga-Rossel et al. 2008). However, none of these studies investigated how agoutis respond when they are isolated in forest fragments surrounded by an urban matrix. This information is very important for the establishment of effective management and conservation strategies for agoutis in general and for *D. prymnolopha* in particular.

Materials and methods

Study site

We carried out our study in the Natural History Museum and Botanic Garden (NHMBG), Belo Horizonte, Minas Gerais state, southeast of Brazil (Figure 1). Belo Horizonte

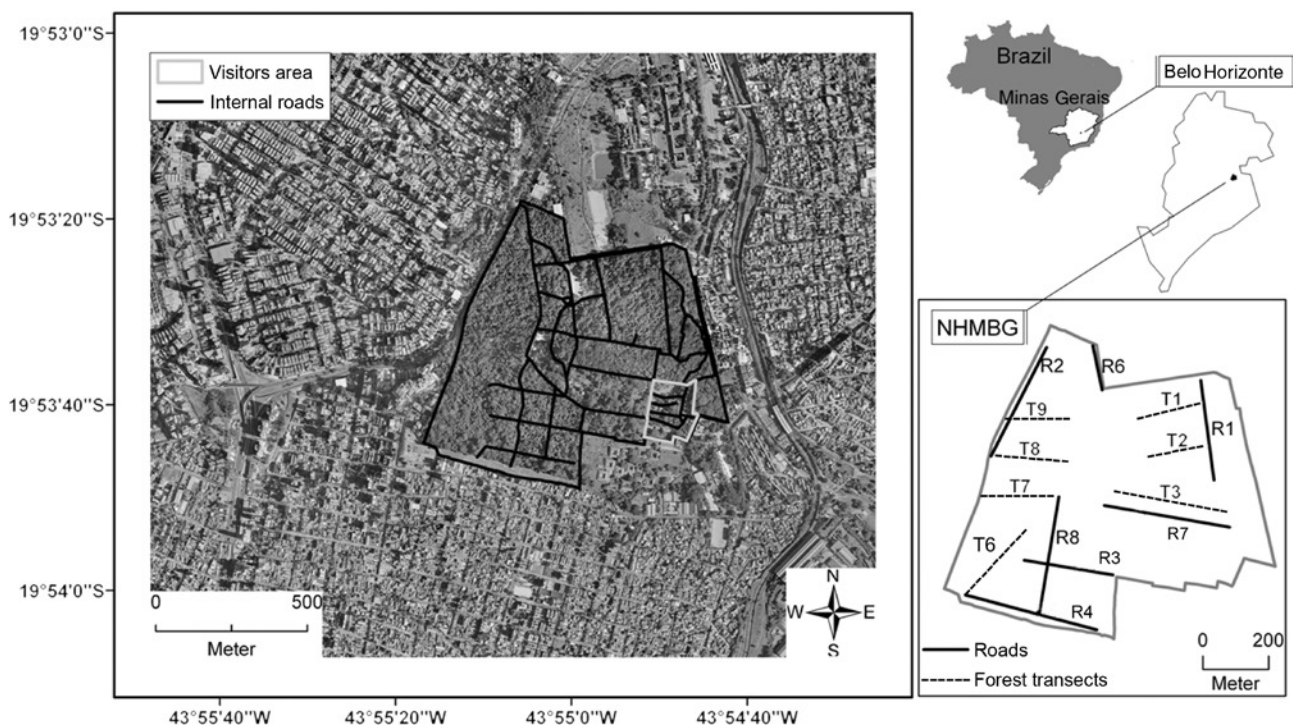


Figure 1: Location and limits of the study area, the Natural History Museum and Botanic Garden, and part of the surrounding urban matrix of Belo Horizonte city in southeastern Brazil. Forest transects and unpaved roads used for distance sampling (inset).

is a densely populated city (2.5 million inhabitants, 7167 people/km², according to the last official census in 2012) that occupies an area of 331 km². The NHMBG is one of the largest Belo Horizonte's isolated forests, with 60 ha. It is 2.2 km from the nearest limit between the urban matrix and the rural zone, and 5.5 km from the nearest forest fragment of similar or larger area. A hotter and wetter season lasts from October to March, and a cooler and drier season encompasses the months from April to September. In the last decade (2001–2010), the average annual precipitation during the dry and wet seasons was 190 mm and 1490 mm, respectively. Mean temperature for the same decade was 21.5°C and 24.1°C, during dry and wet seasons, respectively.

The NHMBG is crossed by an internal network of unpaved roads, which are used mainly by local staff. There are no data on traffic intensity, but based on what we experienced during sampling, together with the fact that sampled roads are restricted to internal staff, we infer that very few motor vehicles use some of these roads on a daily basis and at low speed (<30 km/h). In other words, the traffic frequency and speed do not seem to be unusual compared to unpaved roads traversing Atlantic forest remnants or protected areas located in the rural zone of southeastern Brazil, in general. There are also a spring and a small lake. The forest itself occupies an area of 57 ha and is a mosaic of exotic and native vegetation, in different successional stages (Faria et al. 2009, Felix 2009). This forest harbors 394 different angiosperm species, of which 43% are autochthonous to Brazil (Felix 2009). The fact that this region is located in a transition zone between Cerrado and Atlantic forest biomes is reflected in the composition and physiognomy of the study area flora (Felix 2009), which have elements of these two biomes. We sampled in this study, however, solely the closed canopy portions of this mosaic of vegetation and intentionally avoided portions where roads or transects could traverse open vegetation physiognomies (Supplemental Figure S1). It is equally important to mention that the distribution of transects and roads covered more or less similarly the local diversity of the closed forested formations. Given the relative small size of this fragment and the existence of internal “edges” (unpaved roads and open areas), the differences in forest structure and composition between the edge and the interior of this fragment are likely minor. In other words, the whole fragment would be more or less equally subjected to the disturbing effects of the edge proximity, as is expected for fragments of this size (Laurance and Yensen 1991). We are confident, therefore, that our comparison between transects and roads is not biased by differences in vegetation composition and physiognomy.

Study species

Agoutis (*Dasyprocta Illiger 1811*) are medium-sized, diurnal, Neotropical rodents (Smythe 1978). They are frugivorous and scatter-hoarders of seeds, which make them important seed dispersers (Peres et al. 1997, Asquith et al. 1999, Henry 1999, Dubost and Henry 2006, Galvez et al. 2009). Their diets include a broad variety of fruits and seeds (Henry 1999, Dubost and Henry 2006). Usually, a male-female pair shares a single area. Nevertheless, the pair bond may not be strong, as adults are usually solitary foragers (Smythe 1978). Reported home ranges of agoutis vary from 1 ha to 8.5 ha (Smythe 1978, Silvius and Fragoso 2003, Jorge and Peres 2005, Aliaga-Rossel et al. 2008). The geographic distribution of the black-rumped agouti encompasses the entire northeast region of Brazil and some states of both the northern and the southeastern regions (Ximenes 1999). This agouti is originally present in two biomes: Cerrado (Brazilian savanna) and Caatinga (xeric shrubland), both of which are poorly covered by protected areas. This species is not in the Brazilian Red list (Portaria No. 444, of December 17, 2014; available at <http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira>) and in the International Union for Conservation of Nature its conservation status is “Least Concern” (Catzeflis et al. 2008). However, in the red list of Minas Gerais, which encompasses the southernmost part of *Dasyprocta prymnolopha* distribution, this agouti is classified as “Vulnerable” (COPAM 2010). A single population of black-rumped agoutis lives in the area of the NHMBG. The occurrence of this species is poorly known in the state of Minas Gerais, which is in the southernmost part of the geographic distribution of *D. prymnolopha* (Bonvicino et al. 2008). However, given that this agouti species is not expected to occur in the region of Belo Horizonte, we infer that the study population is not native to this region. This population apparently resulted, therefore, from introduction of individuals that happened decades ago, most probably in the 1960s or even earlier, according to some staff we interviewed.

Line transect sampling

We used line transect distance sampling (Buckland et al. 1993, Barry and Welsh 2001) to estimate abundance of black-rumped agoutis in the NHMBG. We chose this methodology because this medium-sized mammal is not easily individualized, and its shyness makes live-trapping unfeasible (Smythe 1978, Jorge 2000).

Given that agoutis do not form cohesive groups (Smythe 1978), we always recorded distances for each

detected animal, even when two or more individuals were sighted close together. For each detected animal, we recorded the perpendicular distance from the transect line, group size, distance along transect and behavior at the sighting's time. We modeled detection rates from the perpendicular distance distribution to calculate the 'effective strip width' (ESW) using the program DISTANCE, version 6.0 (Thomas et al. 2010), which was then used to generate a population density estimate. We conducted the analyses under the engine of conventional distance sampling (CDS).

We compared estimates of abundance in two independent sets of "transects": one composed of true line transects (hereafter "transects") and the other of unpaved roads (hereafter "roads"). For the former, we cut with machetes seven transects (<1 m wide) inside the forest area of the NHMBG (Figure 1). The length of these transects varied from 230 to 450 m. Due to the small size of the study area, we opted for not distributing transects randomly. Instead, we spread them evenly throughout the forested area in order to have a representative sample of the forest types presented there. For the second set of transects, we used seven existing unpaved straight roads, varying in length from 128 to 432 m (Figure 1). These unpaved roads are much wider (2–5 m) than forest transects (<1 m wide). Fences enclose the area of the NHMBG, and walls are parallel to three sampled roads (R2, R4 and R6) located along the perimeter of the NHMBG (Figure 1, inset). For these three roads, we were able to sample only one side of the roads. Thus, when we input the lengths of R2, R4 and R6 roads in DISTANCE, we halved them (sampling effort = ½ total km walked), as recommended (Buckland et al. 1993). Each transect and road section were sampled seven and five times per season, respectively. Both transects and roads were randomly surveyed and we never sampled transects or roads that crossed each other in the same day. By doing this, we minimized the problem of counting the same individual twice during the same sampling section.

We conducted observations between 0600 h and 0900 h, which coincides with one of the peak activity times of agoutis (Smythe 1978). To better understand how seasonal changes in agoutis' behavior and vegetation structure impact the quality of abundance estimates, we sampled transects and roads during 5 months of the wet season (October 2010–February 2011) and again during 4 months of the dry season (May 2011–August 2011).

Agoutis' behavior

We recorded the behavior of agoutis at the sighting's moment to test whether it was different in forest transects

compared to roads, reasoning that this difference could potentially affect the quality of the density and abundance estimates. Following Smythe (1978), we considered five behavioral categories: resting, moving, foraging, feeding and interacting. When interacting, we also recorded whether the agoutis were acting agonistically (rushing, fighting) or not (courtship, mating, parental care) (Smythe 1978).

Distance analysis

We analyzed data collected from transects and roads separately. We manually grouped our distance data into intervals (Fewster et al. 2005), following recommendations from Buckland et al. (1993). We tried several different grouping intervals, from a minimum number of four up to 15 distance intervals. We also varied the cut-point distances, always trying to achieve the best model fitting (see below). We judged this "manual" grouping necessary because the software has limited possibilities of automatic grouping and roads are more similar to strips than to lines. Consequently, when we sighted agoutis exactly on the roads (anywhere along its width), we recorded the distance to the transect line as zero. We also ran a different analysis for each season, following the same protocol for both. In both seasons and in both transects and roads, we sighted ≥ 60 black-rumped agoutis, which is the suggested minimum to get statistically robust estimates in DISTANCE (Buckland et al. 1993). We had no evidence of having sampled the same agouti individual multiple times in a single sampling section. The distances we walked along transects and roads in both seasons were similar (Table 1; Mann-Whitney tests, dry season: $N_1=N_2=7$, $p=0.65$; wet season: $N_1=N_2=7$, $p=0.95$). Given these results, we assumed that our sampling effort was similar, both between transect types and between seasons.

In order to model the detection function, we analyzed the combination of two main key functions, hazard-rate and half-normal, with all the three expansion series available in DISTANCE. We first selected those combinations that converged and then we selected the best models through model fit [Akaike information criterion (AIC) and Chi-square distribution].

We selected O2 as the estimator of encounter rate variance ($ErVar$) because transects were systematically placed (Fewster et al. 2009). This estimator also enabled us to account for some heterogeneity of encounter rates (ERs) (n/L), since variance was no longer calculated using a general mean, but using similarities among transects.

We decided to group some DISTANCE output into three categories (model adjustment, precision and accuracy) in

Table 1: Line transect sampling effort during wet and dry seasons in the study area, the Natural History Museum and Botanic Garden at Belo Horizonte, Brazil.

Transect type	L (km)		n		n/L (n/km)	
	Wet	Dry	Wet	Dry	Wet	Dry
Transects	13.641	13.963	62	83	4.54	5.94
Unpaved roads	12.337	12.343	67	62	5.43	5.02
Total	25.978	26.306	129	145	4.97	5.51

L, Total distance traveled; n, number of agoutis sighted; n/L, rate of agoutis sighted per kilometer.

order to better understand how and why the quality of estimates (density and abundance) was different between roads and transects and also between seasons. We considered the following parameters for assessing quality of estimates:

- Model adjustment: AIC; p-value of the χ^2 test ($p-\chi^2$); number of necessary adjustment terms of the detection function model; constraints on shape function (strictly monotonically is better than relaxing this assumption. A monotonic detection function means that detection is always decreasing from the transect line; in other words, relaxing this assumption is an analytical alternative to deal with bad data).
- Precision: standard errors (SEs) and coefficient of variation (CV).
- Accuracy, which was assessed through three main parameters: detection probability (Pa), the largest sighting distance (w), and the variance components (ER, n/L and detection probability, Pa).

We did not pool seasonal data for a global estimate (dry+wet season) for two main reasons: (1) this might obscure important seasonal variation both in behavior and in detectability (see Results) and (2) 1 year is too long a period of sampling for assuming demographic closure in agoutis. The half-normal function best fitted our data for both roads and transects. Model fitting was, however, harder to achieve for road than for transect data (Supplemental Figure S2). We performed Z-tests adapted from a general formula for contrasting DISTANCE parameters (Buckland et al. 1993) to assess whether differences in density and abundance estimates between transect types within seasons, and between seasons within transect types were significant (adapted from Buckland et al. 1993).

In a similar way, we compared variation in behavior between transect types and between seasons using χ^2 tests (contingency tables). When the Chi-square was

significant ($p < 0.05$), we analyzed the Chi-square residuals to know exactly what behavior category was significantly different. In a first set of tests, given the low frequency of “interaction” and “feeding” behaviors (observed frequency < 5), we pooled these rare behaviors with “moving” (moving/interacting) and “foraging” (foraging/feeding) categories, respectively. By doing this, we guaranteed high power ($1-\beta$ -error probability > 0.80) of our Chi-square analyses, assuming a medium effect size (Cohen 1988). We calculated the achieved power using G*Power version 3.1.2, a free software (Faul et al. 2007). In a second set of χ^2 tests, we were interested to contrast the frequency of “vigilant” behavior of agoutis between transects and roads. For this, we assumed that agoutis are likely to be more alert or vigilant when either inactive (resting upright) or moving, and less vigilant and alert when feeding or foraging or interacting with other agoutis. There are no data on agoutis to back this assumption, but based on our experience and also on studies from other mammals, which report a negative association between feeding/foraging and being alert or vigilant (Lott and McCoy 1995, Duchesne et al. 2000), we guess that this relationship might also apply to agoutis. Based on this, we pooled resting and moving in a first class, as we assumed that agoutis tend to be more vigilant (or alert) when they are engaged in these two types of behaviors (“more vigilant” behaviors) than when they are feeding or foraging or interacting (“less vigilant behavior”). We used the freely available statistical software BioEstat version 5.3 (Ayres et al. 2007) to perform the Chi-square and residual analyses.

Results

Density estimates

Overall, we conducted 27.604 km of census walks along seven transects and 24.680 km along seven roads, resulting in 145 and 129 agouti sightings, respectively (Table 1). We detected agoutis at a higher rate on roads (median=7.29 sightings/km) than on transects (median=4.69 sightings/km) during the wet season (Mann-Whitney, $N_1=7$, $N_2=7$, $p=0.015$), but during the dry season, the ERs were similar (5.72 and 5.24 sightings/km on roads and transects, respectively; Mann-Whitney, $N_1=7$, $N_2=7$, $p=0.748$). We also observed differences in the sighting frequency distribution between transects and roads (Figure 2). Road sightings had a much higher frequency in the zero-distance class (median=0 m for both wet and dry seasons) than

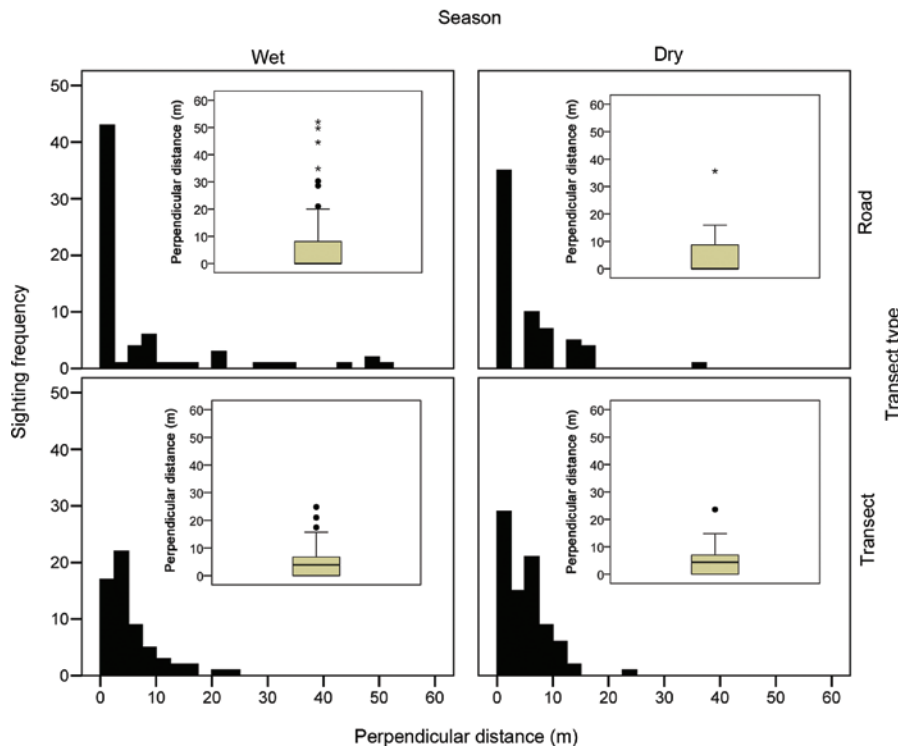


Figure 2: Sighting frequency distribution (histograms) and box plots (insets) of perpendicular distances of agoutis sighted from unpaved roads (top) and transects (down). Data from wet season are shown in the two figures on the left and from the dry season on the right.

Table 2: Main outputs of DISTANCE from sampling black-rumped agoutis along forest transects and unpaved roads.

Season	Transect type	NI	$p\text{-}\chi^2$	Pa	ER	w	ESW	CV	$ErVar$	$N (\pm SE)$	$D (\pm SE)$
Wet	Transect	5	0.49	0.28	4.5	24.8	6.9	10.98	17.9	193 (21.2)	321.9 (35.3)
	road	6	0.18	0.21	6.3	34.9	7.3	11.01	30.6	259 (28.5)	432.0 (47.5)
Dry	Transect	4	0.77	0.34	5.9	23.6	8.0	10.70	38.6	224 (23.9)	373.3 (39.9)
	road	7	0.21	0.25	6.2	35.6	8.9	13.95	60.2	208 (29.0)	347.1 (48.4)

NI, Number of grouping intervals; $p\text{-}\chi^2$, χ^2 test probability; Pa , detection probability (probability of sighting an agouti in the sampled area); ER, encounter rate (agoutis sighted/km); w , largest sighting distance (m); ESW, effective strip width (m); CV, coefficient of variation (%) of ESW; $ErVar$, percentage of total variance due to ER (%); N , estimated abundance (number of agoutis); D , estimated density (agoutis/km²).

transect sightings (median=3.3 and 4.4 m for wet and dry seasons, respectively). Road sightings were also sparser, with more observations at further distances from the transect line. Due to this, truncation of extreme values was imperative for road data in order to achieve acceptable model results.

The differing sighting distribution between roads and transects affected the estimation and the precision of key parameters. The probability of detecting agoutis in the sampled area (Pa) was, for example, 33% and 36% higher in transects than in roads during dry and wet seasons, respectively (Table 2). However, the average number of

agoutis sighted per kilometer (ER) was lower in transects, but solely during the wet season (Table 2; Supplemental Figure S3). The CV of the ER was at least twice higher for roads (82% and 57% for dry and wet seasons, respectively) than for transects (33% and 30% for dry and wet seasons, respectively; Figure 3S). For transect data, the major component of CV was the variance of the detection probability (Pa), in both seasons. Data from roads, however, had a different contribution of CV variance components: mostly ER in the dry season and mostly Pa during the wet season. These results indicate greater heterogeneity in ER along roads than on transects.

Table 3: Comparison of density and abundance estimates between transect types (within seasons) and between seasons (within transect types), using Z-tests.

Parameter	Season	Road		Transect		Road×transect	
		Estimate	SE	Estimate	SE	Z	p-Value
Density (agoutis/km ²)	Dry	347.11	48.42	373.30	39.96	-0.417	0.677
	Wet	432.00	47.55	321.90	35.34	1.858	0.063
Dry×wet							
Z			-1.251		0.963		
p			0.211		0.335		
Abundance (N)	Dry	208.00	29.02	224.00	23.98	-0.425	0.671
	Wet	259.00	28.51	193.00	21.19	1.858	0.063
Dry×wet							
Z			-1.254		0.969		
p			0.210		0.333		

SE, Standard error; Z, Z-test result; p, p-value (two tailed).

Notwithstanding these differences, seasonal abundances we estimated from roads (208–259 agoutis) were statistically similar to those estimated from transects (193–224 agoutis) (Table 3). Seasonal densities followed a similar pattern (Table 3).

Behavior

Behaviors of black-rumped agoutis are summarized in Figures 3–5. Within each season, the behavior pattern differed significantly when samples from road and transects are contrasted (wet season: $\chi^2=6.434$, $d.f.=2$, $p=0.040$; dry season: $\chi^2=7.582$, $d.f.=2$, $p=0.023$) (Figure 3). Analyzing the residuals of these Chi-squares, it becomes clear that during the wet season, agoutis sampled from roads showed a higher frequency of foraging/feeding ($p<0.05$) and a lower frequency of moving/interacting ($p<0.05$) than agoutis sampled from transects. During the dry season, agoutis sampled from roads rested less ($p<0.01$) than transect agoutis (Figure 3). Comparing seasons within transects and roads, we observed seasonal variation in behavior only for transect data ($\chi^2=10.062$, $d.f.=2$, $p=0.006$), which show that agoutis forage/feed more during the dry season ($p<0.05$) and move/interact much more in the wet season ($p<0.01$) (Figure 4). The behavior pattern observed from roads lacked seasonal differences ($\chi^2=1.572$, $d.f.=2$, $p=0.456$) (Figure 4).

Agoutis exhibited a higher frequency of more vigilant behaviors (resting/moving) than expected in transects than in roads, but only during the wet season ($\chi^2=7.852$, $d.f.=1$, $p=0.005$); during the dry season, the associations between two types of behaviors and

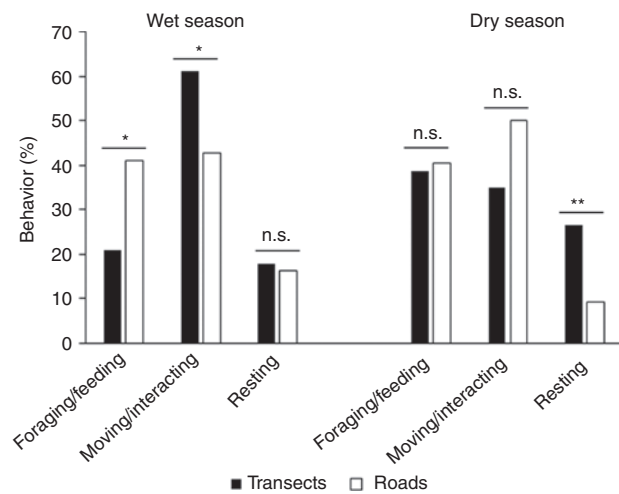


Figure 3: Behavioral comparison of black-rumped agouti (frequency expressed as %) contrasting transect types (forest transects×unpaved roads) during wet and dry seasons. Asterisks indicate behavioral categories where residuals of the Chi-square analyses were significant at $p<0.05$ (*) or $p<0.01$ (**). n.s., Non-significant residuals ($p>0.05$). See Materials and methods and Results for details.

transect types were not significant ($\chi^2=0.153$, $d.f.=1$, $p=0.696$) (Figure 5).

We observed an association between transects and seasons in the frequency of agoutis sighted in pairs (Fisher's test, 2×2 , $p=0.0006$): along transects, pairs were more frequent in the dry (12 pairs) than in the wet season (one pair); along roads, pairs were more frequent during the wet (11 pairs) than during the dry season (four pairs). A third (31%) of all agoutis seen in pairs during the dry season were interacting agonistically; for the wet season, this proportion dropped to 7%.

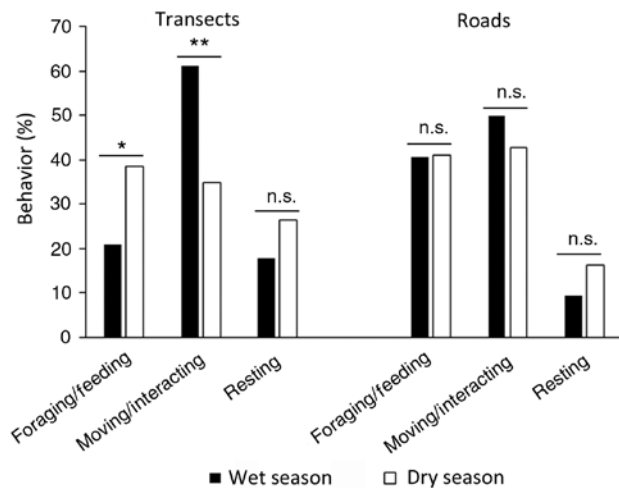


Figure 4: Behavioral comparison of the black-rumped agouti (frequency expressed as %) contrasting seasons (dry vs wet seasons) sampled from forest transects and unpaved roads.

Asterisks indicate behavioral categories where residuals of the Chi-square analyses were significant at $p < 0.05$ (*) or $p < 0.01$ (**). n.s., Non-significant residuals ($p > 0.05$). See Materials and methods and Results for details.

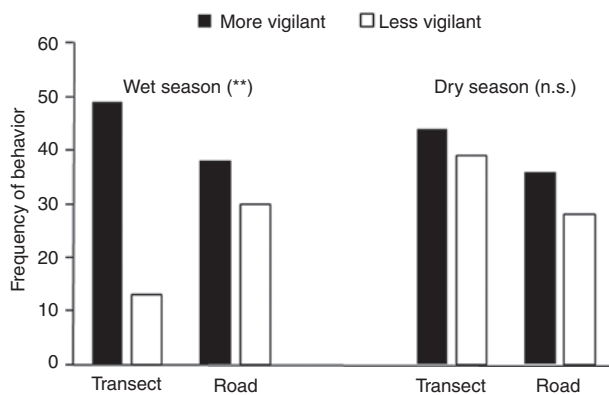


Figure 5: Frequency of more vigilant (resting/moving) and less vigilant behaviors (feeding/foraging/interaction) of agoutis sampled from forest transects and unpaved roads during the wet and dry seasons.

Asterisks indicate seasons where the χ^2 tests comparing frequency of more vigilant and less vigilant behaviors between transects and roads were significant at $p < 0.05$ (*) or $p < 0.01$ (**). n.s., Non-significant probabilities ($p > 0.05$). See Materials and methods and Results for details.

Discussion

Density estimation

Contrary to our expectations, density and abundance did not differ between transects and roads. We caution,

however, that estimates generated from road data were not similar to transect estimates regarding the estimation of important parameters and sources of bias. We based this assertion on three main lines of evidence. First, road data showed a different variance contribution. Perhaps due to a higher frequency of human visitors, agoutis used some roads, notably edge roads and roads used more frequently by park staff, much less than other roads. Consequently, the percentage of total variance due to ER was greater for roads than for forest transects (Table 2). However, given that transects were all cut at the same time and were used solely by observers during sampling, it is likely that agoutis reacted more similarly toward the human presence among transects than among roads. In other words, it is possible that a “novelty effect” (see below) is present and/or stronger in transects (all of them), while in roads, if this effect is indeed present, it is likely weaker and restricted to the roads less used by visitors. This means that variability among sampled roads was higher than among sampled transects and that it is harder to fulfill the assumption of randomness of transects in relation to the animals for road samples. It is important to emphasize, further, that we used only straight roads. Had we used curving, winding roads, as sometimes is the case, these problems would be exacerbated, particularly regarding the violation of transect randomness in relation to animals. Given that roads are mainly built for motor vehicles, they tend to go parallel rather than across natural gradients (for example along altitudinal isolines). Additionally, measuring perpendicular distances between an animal and a curved section of a winding road is problematic as the azimuth of the curved section is different from the azimuth of the road.

The second evidence for the difference between transects and roads was the discrepancy in ERs and detection probabilities. Road data resulted in a lower detection probability and poorer model fitting (lower $p\text{-}\chi^2$ values) (Table 2 and Figure 2; see also Supplemental Figures S2–S4). We mitigate considerably this bias analytically, trying several different combinations of distance classes, changing both the number of distance intervals and the cut-point distances, as recommended in circumstances of “problematic” data sets (Buckland et al. 1993). But even with these procedures to improve model fitting, the final models we get were always comparatively poorer than those from transect data, needing more adjustment terms or demanding relaxation of the important assumption of monotonicity in the detection function. Another cause of the high concentration of sightings close to zero distance resulted from the lack of obstructing vegetation. Thus, the detectability is relatively higher to a much longer distance in our frontal field of view in comparison with true

transects. This, in turn, caused another problem related to walking speeds. From the beginning, we tried to keep a constant walking speed for both roads and transects, but because roads lack obstacles, we ended up walking faster there (1.37 km/h against 0.61 km/h on transects, on average). Even though we walked faster in roads, the ER was higher, not lower, there in comparison with transects, although just during one season (wet season). A final additional source of bias resulted from the lateral view of roads being sometimes compromised by growth of edge vegetation. In our study area, this was particularly evident only along edge roads (R2, R4 and R6, Figure 1), which are more exposed to sunlight. Edge effects, including proliferation of sunlit vegetation, are relatively common along unpaved roads crisscrossing tropical forest remnants or along the perimeter of protected areas (Laurance et al. 2002). In other words, the distribution of sightings is more spread in transects than in roads. This helps to explain why sampling on roads resulted in a lower probability of detecting agoutis in the sampled area, even though roads returned a higher number of agoutis sighted per kilometer (higher ER).

In summary, along roads the gradient between forward detection probability and lateral detection probability is far from smooth (Figure 2), similar to what Hilário et al. (2012) observed while sampling marmosets from unpaved roads in a Brazilian Atlantic forest site. These distortions contributed to poorer modeling. Similarly, variation in the detectability and problems related to evasive movements were noticed by other researchers using road transects to estimate the abundance or density of other mammal species, such as foxes (Ruelle et al. 2003), pampas deer (Tomas et al. 2001) and primates (Hilário et al. 2012). It is clear then that data collected along roads did violate some important assumptions of the sampling method (Buckland et al. 1993), making it harder for us to get good modeling results from DISTANCE. Consequently, we had to use (or add more) adjustment terms during modeling, and we had to relax the monotonicity requirements in order to get any output at all from DISTANCE (Supplemental Figure S2).

Behavior

Besides the model fitting and precision issues remarked above, results from the behavior sampling showed convincingly that agoutis behave differently on roads when compared to transects. In the dry season, agoutis were observed resting less when sampled from roads, while in the wet season, they feed/forage more in roads when

compared to transects. Everything else being equal, observers can detect animals more easily when they are active (Little et al. 2014) rather than when they are inactive (resting, sleeping, etc.) and this is not different for agoutis. So if the agouti's activity level is different between transects and roads, then the corresponding detection efficiency is also different. In our case, this was particularly evident during the dry season (Figure 3). Without more detailed information on foraging behavior, and on food availability and distribution, it is difficult to ascertain why exactly agoutis are behaving differently in transects and roads.

Considering what is known about the ecology of agoutis in general, we suspect that food distribution and abundance might play a central role in their behavior. The soil of unpaved roads, for example, is comparatively more compacted (Lei 2004) and lacks the superficial layer of decaying leaves (personal observation). This is further aggravated if roads have open canopies as soil macrofauna and temperature are strongly correlated with canopy openness (Martius et al. 2004). It is likely, therefore, that the typical hoarding behavior of agoutis (Jorge and Howe 2009) might be impaired along the path of a road. Agoutis might find seeds there, but probably prefer to use adjacent areas, where the forest litter is present or less disturbed to bury seeds for future use. This difference can be further exacerbated if the vegetation along roads is impacted by edge effects, which can change not only the structure but also the plant species composition surviving on or near the edge (Laurance et al. 2002). Agoutis probably change other aspects of behavior as well when on roads due to higher visibility to other congeners and, possibly, higher exposure to visually oriented predators, including humans. Interestingly, we did detect variations in aggregation behavior between transects and sighted more agouti pairs in the wet season when we sampled them on roads, but saw more agouti pairs in the dry season when sampling along transects. As larger groups are easier to detect than smaller groups or single individuals (Royle 2008, Southwell and Low 2009), the number of agoutis sighted together can influence detectability and consequently blur seasonal comparisons if the transect type is not controlled for.

Another interesting result regards the frequency of vigilant behaviors, which were more frequent than expected in transects than on roads, but only during the wet season. During the dry season, the proportion of vigilant behaviors was similar between transects and roads. It is difficult to ascertain why, but perhaps, this is a consequence of agoutis moving comparatively more, and feeding/foraging comparatively less, on transects than on roads during the

wet season (Figure 3). Why, however, was the difference in vigilant behaviors not significant between transects and roads also during the dry season (Figure 5)? One hypothesis that we cannot discard might regard the “novelty” effect of sampling agoutis from transects. Agoutis are shy animals and even though they were long used to humans in our study area (a small fragment frequently visited by humans), they used to see humans normally near buildings and in the roads, but much less so in transects that we cut specifically for the purposes of this study. As we sampled the wet season before the dry (see Materials and methods), the reaction to humans in transects could have been more strong in the beginning of the study (wet season) than later (dry season). The variation we observed in ER corroborates this assertion, as this parameter was distinctly lower in transects sampled during the wet season (Supplemental Figure S4). This is an interesting hypothesis that surely deserves attention in further studies.

We observed further lack of synchrony between transects and roads regarding seasonal variation in behavior. Significant seasonal variation in foraging/feeding and in moving/interacting was detected only for agoutis sampled from transects (Figure 4). This seasonal variation is probably more meaningful biologically, as several studies carried out elsewhere suggest that agoutis do vary their behavior seasonally (Smythe 1978, Peres et al. 1997, Jorge and Peres 2005, Jorge and Howe 2009, Norris et al. 2010). Unfortunately, there are no data for black-rumped agoutis at other sites. During the wet season, agoutis use areas where they can find food of higher nutritional quality and areas where they can hoard seeds (Silvius and Fragoso 2003, Jorge and Peres 2005, Galvez et al. 2009). Although we do not have data on food distribution, our diet data on black-rumped (*V. S. Orsini*, unpubl. data) do support this. Additionally, during the dry season, black-rumped agoutis augmented foraging behavior, probably because they searched more intensely for hoarded seeds. Black-rumped agoutis also increased the frequency of agonistic behavior during the dry season, likely because they were “defending” areas where seeds are hoarded, as has been observed in other agouti species (Smythe 1978). This seasonality of behavior might indicate that the availability and distribution of feeding resources (mostly seeds and fruit) vary throughout the year. This translates into seasonal variation in the diet, as we noted for the study population (*V. S. Orsini*, unpubl. data) and other researchers observed for agoutis elsewhere (Dubost and Henry 2006). Seasonality in the production of fruit, flowers and other plant parts is a natural phenomenon and long known for the Atlantic forest in southeastern Brazil (Davis 1945, Jackson 1978). Sampling agoutis from roads, therefore,

buffered this natural seasonal variation in foraging behavior. To summarize, as behavior affects detection (Ramsey and Harrison 2004, Hounscome et al. 2005, Lukacs et al. 2010) and detection is a key issue in distance sampling (Buckland et al. 1993), behavioral variation, as observed here between roads and transects, surely compromises the comparison of estimates generated from these two transect types.

Overpopulation

With the exception of two studies carried out in small (~10 ha) urban parks where agoutis receive routine (F. Fernandez personal communication) or occasional supplementary feeding (Santos 2005), our density estimates of black-rumped agoutis in the NHMBG surpassed any published estimates thus far (Supplemental Table S1). Reported densities vary from 1 agouti/km² to 200 agoutis/km² (Cant 1977, Peres et al. 1997, Chiarello 2000, Silvius and Fragoso 2003, Tomas and Desbiez 2004, Jorge and Peres 2005, Bovendorp and Galetti 2007, Aliaga-Rossel et al. 2008, Jorge 2008), with the highest densities being found in islands (Bovendorp and Galetti 2007, Aliaga-Rossel et al. 2008). Why this is so is not known but, perhaps, results from the Island Syndrome (Adler 1996). This syndrome includes increased population densities and may be observed in some rodent populations that tend to be crowded in areas where food is abundant and where competitors and predators are not ecologically significant (Adler 1996, Lambert et al. 2003, Jorge 2008). These rodents can even endure in disturbed areas, if some forest characteristics are preserved. Crowding may be favored also by some characteristics of a given species, like feeding and reproductive flexibility and longevity (Adler 1998, Jorge 2008). Black-rumped agoutis living in the NHMBG fulfill all the aforementioned characteristics. Unfortunately, though, despite the aforementioned overpopulation density in urban areas, there are few other lines of evidence of Island Syndrome for other agoutis in urban areas to back our assertion. Nevertheless, this interesting finding deserves further investigation.

Conclusion

Although our estimates of density and abundance from roads were comparable to those from true transects, we caution that the quality of road estimates was inferior to that obtained from sampling true forest transects. We observed a clear stratification of detectability along roads, as roads lack vegetation along their path, but are sided by

forest. Further, agoutis had a behavioral composition significantly different from that observed along forest transects. Thus, detectability cannot be considered entirely similar between these two transect types. We should not recommend, therefore, using unpaved roads as adequate surrogates of transects for density or abundance estimation purposes, at least for our study animals. Even the use of more simple (and easier to be carried out) abundance indices, such as sighting frequency, might be compromised as ERs from roads are not comparable to transects, although we caution that the novelty effect might also be an issue. Thus, when avoiding roads is unfeasible given time and logistical limitations, researchers should be aware of the potential bias, making this clear when discussing and comparing their results. We remark, further, the importance of recording behavior data during distance sampling, as this information can help to interpret results. For instance, we demonstrated that black-rumped agoutis varied behavior seasonally, but only if observed from true forest transects. We further detect that vigilant behavior might be different between roads and transects, at least in the beginning of a study and/or during one season. Therefore, researchers should be careful when grouping sampling data from different transect types. Summing up all the evidence, we conclude that our data do validate our working hypothesis.

The overpopulation of agoutis in our study area is an important evidence of the ecological plasticity of *Dasyprocta* (Jorge 2008). It also points out that *Dasyprocta* may answer to urbanization in a similar way to true islands (Dickman and Doncaster 1989, Adler 1996, Lambert et al. 2003, Cavia et al. 2009). However, we still need more evidence as very few populations have been studied in urban fragments thus far in the Neotropics. Nevertheless, scientists should pay more attention to this, as urban fragments as well as zoo, botanic gardens and the like have an important conservation role in our ever-increasing urbanized World. Assessing how this genus responds to urbanization might be therefore strategically relevant to help its future protection.

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