



Original investigation

What bite marks can tell us: Use of on-fruit tooth impressions to study seed consumer identity and consumption patterns within a rodent assemblage

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ABSTRACT

Rodents have a highly specialized dentition, and incisor dimensions are very characteristic within each group. In this study we field-tested a rarely-used methodology – using marks left by rodent incisors in fruits and seeds to identify them. The width of the incisors marks made in Plasticine™ blocks using skulls from museum collections, were compared with the marks left on field-collected fruits and seeds. We confirmed the existence of allometric relationship between incisors width and body size. Furthermore larger and harder fruits showed larger bite marks compared with smaller and soft fruits/seeds, indicating the importance of fruit size and hardness in rodent food-plant selection. Based on tooth width measurements, the results also showed that smaller fruits/seeds are used by fewer rodent species, in comparison to fruits of larger size, these being more likely to be consumed and/or predated. Due to an overlap in body size between species, the method did not provide precise identifications of the rodent species consuming particular items, although it does reduce the likely suite of species responsible. However, when used in conjunction with the more commonly deployed tools, this method is highly viable due to easy use and low cost. Future studies using bite marks images and a greater range of morphological features could increase the precision of this technique.

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Introduction

Rodent assemblages are often species rich, ranging from 4 to 6 sympatric species in temperate areas to 15 or more in the tropics (Glanz, 1982). At sites in the tropics it is common for rodents to range in size across an order of magnitude (e.g. *Oligoryzomys microtis*, 14–23 g; Bonvicino et al., 2008; *Cuniculus paca*, 6–14 kg; Eisenberg and Redford, 2000). A specialized dentition allows these animals to feed on hard fruits and seeds, in addition to performing some non-food functions that require bite force, such as building dams, colony defense and breaking compacted soils for digging tunnels (Lessa, 1989b; Becerra et al., 2011). However, the prime use of incisors in food processing means both their shape and size are often highly characteristic for a given rodent species. Consequently, tooth size and shape are frequently considered key in the ecolog-

ical structuring of species assemblages (Moshe and Dayan., 2001). Incisor dimensions may distinguish sympatric congeners (Dayan and Simberloff, 1994), and is likely to scale allometrically with the body dimensions (Creighton, 1980; Creighton and Strauss, 1986). In addition, within a sympatric rodent assemblage, there may be consistent variations in incisors morphology between species of the same size class due to phylogeny or dietary specialization (Samuels, 2009). The variation in incisor dimensions within rodent assemblages opens the possibility of identifying species' presence and consumed items from bite marks on food remnants alone.

The identification of rodent species from bite marks is of potential value as a field technique since determining their diets has generally involved analysis of faecal pellets (Pulliam and Brand, 1975; Meserve, 1981), stomach contents (Taylor and Green, 1976; Barnett et al., 2000; Gebresilassie et al., 2004), or material obtained from stomach pumping (Kronfeld and Dayan, 1998). However, all three methods suffer from problems with comminution, so that the material analyzed consists of small particles that are easier to assign to a food type, but often hard to assign taxonomically to a genus or species (Hansson, 1970; Barnett and Dutton, 1995), espe-

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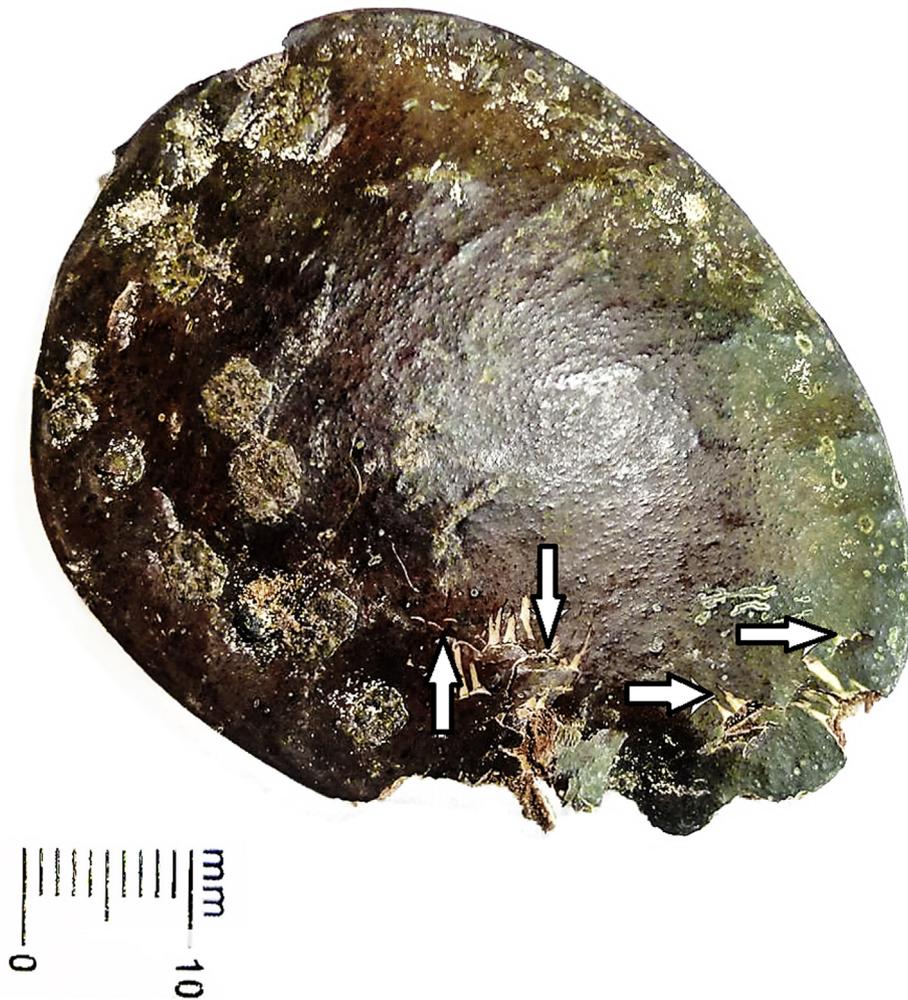


Fig. 1. The fruit of *Macrobium acacifolium* showing damage patterns typically caused by rodent bites. The arrows indicate marks left by the incisors that can be used for species identification.

cially when the ingested material is seed or fruit pulp (Barnett et al., 2000). This methodological shortfall is unfortunate since, in many ecosystems, rodents are one of the major seed and fruit predators and dispersers (Forget, 1993; Jansen et al., 2004; Sunyer et al., 2013; see Hulme, 1998 for review).

When rodents gnaw an object, the upper incisor is pressed against the object, leaving a pair of rounded hallmarks (Bang and Dahlstrom, 1974). There are variations in the way different species gnaw seeds/fruit and access their internal content, but the marks left by upper incisors are characteristic and also distinct from those left by the lower ones (Collinson and Hooker, 2000). Such bite marks on seeds and fruits (Fig. 1) leave a record that should allow which rodent species were visiting an area to be determined, and also permit the identification of which plant species the rodents were eating (e.g. Van Roosmalen, 1985; Cornejo and Janovec, 2010). Also, it offers a way to gain additional information on rodent species distribution, abundance, habitat use and natural history. Using bite marks is simple and non-invasive, compared to other identification methods, which may require cytogenetic and molecular techniques (Aniskin and Volobouev, 1999), in addition to the animal capture and handling. From a botanical perspective, this technique is also advantageous as it should also allow the nature and extent of seed predation by rodents to be quantified with some precision. This technique has already proved efficient for identification of foods eaten by adult pacas (*Agouti paca*), which incisors marks

are larger than 4 mm (Beck-King et al., 1999). To extend this application, we set out to test the viability of rodent bite marks as indicators of seed/fruit consumer species identity across an entire rodent assemblage.

Methods

Study site

The study was undertaken in terra firme (non-flooded) and igapó (seasonally flooded) forests (sensu Prance, 1979) in Jaú National Park (JNP), a 2,700,000-ha protected area in central Amazonian, Brazil. Major vegetation types at JNP include terra firme forest (70%) and igapó forest (12%) (Borges et al., 2004). The study site was located between Cachoeira do Jaú (01°53.21'S, 61°40.43'W) and Patuá village (01°53.16'S, 61°44.31'W) (Fig. 2).

Seeds were collected from the floor of unflooded igapó forest as part of a study of terrestrial seed feeding by the golden-backed uacari (*Cacajao ouakary*, Primates: see Barnett et al., 2012). Seeds were collected in 17 500 × 100 m areas centered on sites where terrestrial uacari feeding observations occurred. In each, the area was quartered by walking back and forth across the forest floor until the entire area had been subject to an acute visual search. All found seeds were visually examined for feeding damage and those that bore rodent bite marks (Fig. 3A) were bagged and identified later

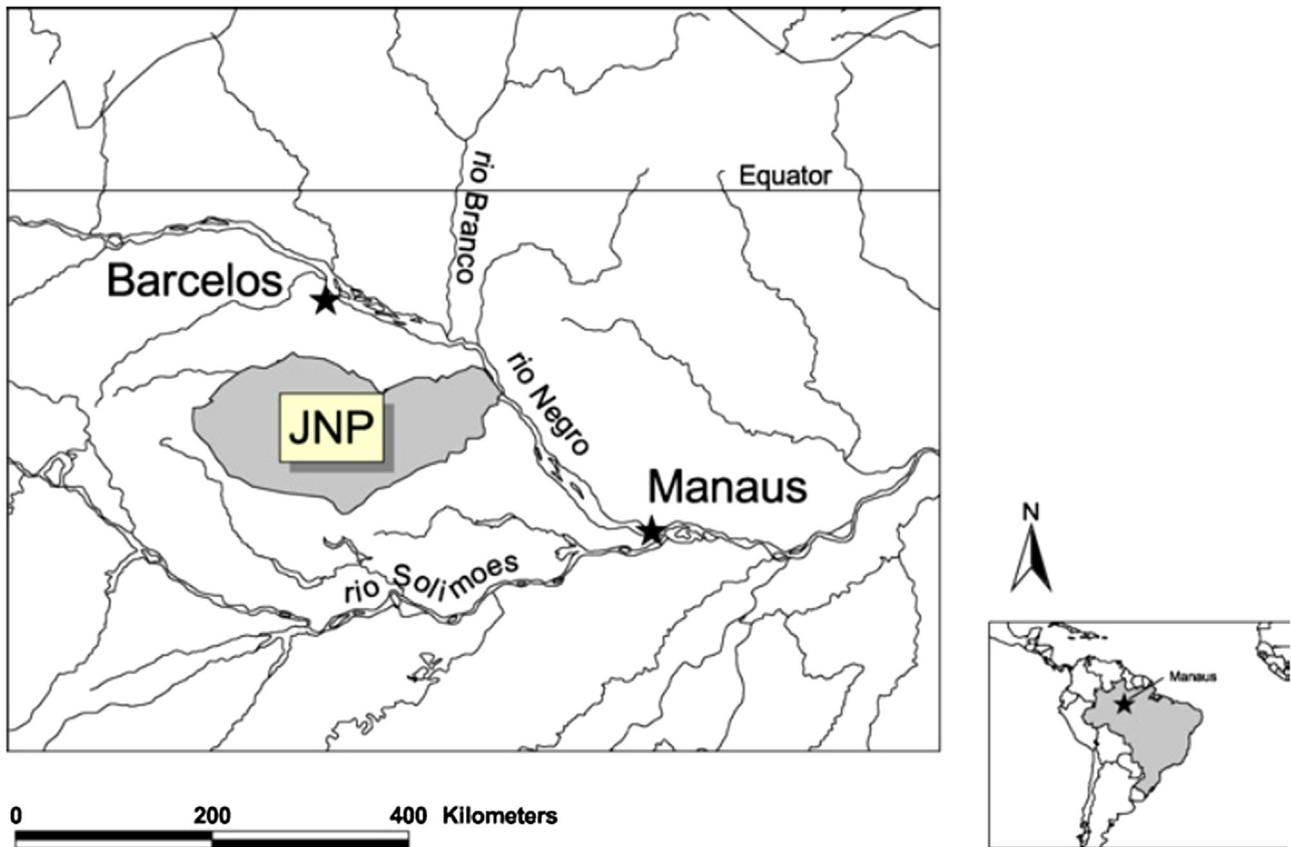


Fig. 2. Location of Jaú National Park, Brazil, in relation to Manaus and Rio Negro.

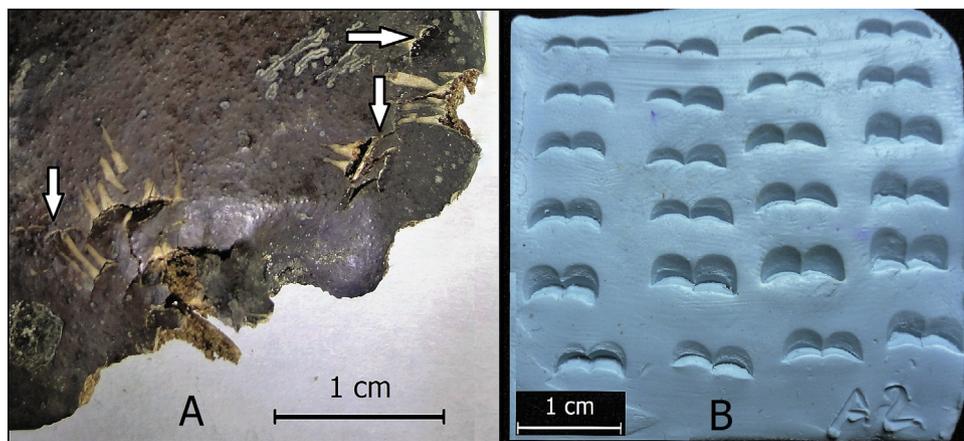


Fig. 3. (A) Bite marks in a *Macrobium acaciifolium* fruit. (B) Plasticine block with rodent upper incisive marks.

at a field lab. Hardness (penetrability) was measured with a FT 327 Facchini Fruit Firmness Tester (International Ripening Company, Norfolk, Va., USA), using the standard diameter bevelled penetrometer head, with the unit mounted in a Fridley Fruit Tester rig to maximize repeatability (see Fig. 3 in Barnett et al., 2015a).

All fruit/seeds that bore marks of having been recently bitten were measured. Old or rotting fruit/seeds were excluded. Only plant species for which we had more than four consumed fruits with bite records were used in subsequent analysis. Plant species were identified by comparison with a photographic database compiled for general studies of *Cacajao ouakary* diet (Barnett, 2010). The fruit length and width were measured to estimate the mean size of each fruit or seed. All fruits or seeds measurements were checked,

whenever possible, with previous studies allowing a more precise fruit/seed identification (Parolin et al., 2010; for a review). All fruits and seeds with tooth marks were classified as soft, when penetrometer values were <1 kg, and hard for values >2 kg. Values between these were classified as intermediate (Barnett et al., 2015a). The width of the mark was measured to the nearest 0.1 mm using SPI 2000 dial calipers (Swiss Precision Instruments, Garden Grove, CA, USA).

From IUCN shapefiles and the Small Mammals of South America (Patton et al., 2015), a list of rodent species was created for the JNP (see Table 1 in the Supplementary material). We used this list to create a database for comparison and identification of rodent species consuming the fruits and seeds. Upper incisors in skulls of already-

identified specimens from the mammal collections of the National Institute of Amazonian Research (INPA), the Zoology Museum of São Paulo University (USP) and the Natural History Museum, London (NHM) were pressed into 25 mm × 25 mm × 0.5 mm blocks of Plasticine (Mattel™) leaving an impression of the cutting edge width of the paired upper incisors (Fig. 3B). As Plasticine does not dry out (unlike Play-Dough and other alternatives), such blocks remain as a permanent reference collection of initial bite marks. When available, we used 4 juvenile and 4 adults of each species for measurements. However, not all species present in the collections had this number and range of individuals. Using the width measurement of each individual two upper incisors (from the marks made in Plasticine blocks), we calculated the average value per species.

The bite mark widths on the Plasticine blocks were compared with the bite marks widths left by rodents on seeds/fruits collected at Jaú. Part of the body length data for rodent species was obtained directly from specimens in the INPA collection (measurement information was available in the label), and the remainder was taken from the literature (Bonvicino et al., 2008; Patton et al., 2015). For the specimens without length measurements, we used data available in the literature. Where needed body length was calculated by subtracting tail length from total length.

Data analysis

We regressed tooth width against the body length to investigate whether the allometric relationship previously described for these two variables in rodents held for the subset of species that occurs in JNP. We used measurements from the museum-derived toothmarks in the Plasticine blocks and species body sizes obtained from the literature.

We used an Analysis of Covariance (ANCOVA) to investigate the relation between the mean width of incisor bite mark left by rodents in fruits/seeds at Jaú, and the mean sizes of fruits/seeds using fruit/seed hardness as a grouping factor. Both variables were \log_{10} transformed to meet model assumptions. Fruit sizes were estimated considering the surface area of an ellipse, and using the formula: $A = \pi \cdot a \cdot b$. Where A is the fruit/seed area, a is the fruit/seed length and b the fruit/seed width.

We cross-matched the upper incisor widths from the Plasticine blocks with the bites marks left in the fruits/seeds found at JNP to create a possible list of rodent species interacting with each plant species (see Table 2 in the Supplementary material). To accomplish this, we selected those rodent species in which incisors marks have the same width (± 0.01 cm) as the marks found on fruits. To investigate whether fruit/seed size has a role in rodent species diet selection, we used the total number of possible rodent species interacting with each plant species as an independent variable against the mean fruit/seed size in a generalized linear model with Poisson distribution. We used Poisson distribution in both models to account for residual variation from count data (number of possible rodent species interacting with each plant species). We also included the hardness of the fruit or seed as a covariate in the model. We compared the full model (fruit size and fruit/seed hardness) with a null model to test for model significance. We also reported the McFadden's pseudo r^2 as a measure of model fit (Long, 1997). All analyses were done in R environment (R Core Team, 2015).

Results

Of the 22 rodent species potentially present at JNP, two could not be found in the visited mammals collections (*Makalata macrura* and *Nectomys rattus*). *Hydrochoerus hydrochoeris* was not included in the current study since fruit and seeds do not form part of the diet of this species (Barreto and Quintara, 2013). A new *Makalata*

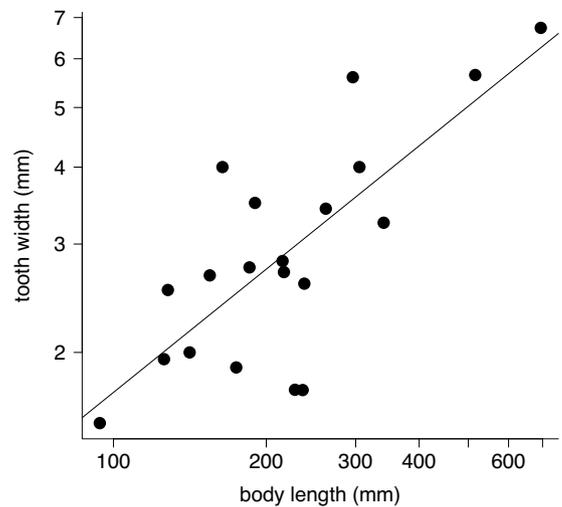


Fig. 4. Upper incisor widths and body sizes of rodents present in JNP (see Methods for details of data sources). Each point represents a species.

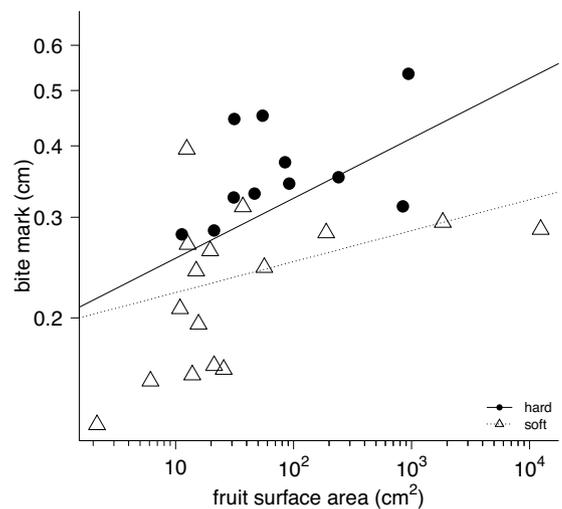


Fig. 5. Bite marks and fruit/seeds area of plant species sampled in JNP. Each point represents one plant species.

sp. from JNP, present in the INPA collections and in process of being described (Miranda CL, pers. comm.) was included in the analysis.

An allometric relation between tooth and body size holds for the assemblage of rodents from JNP (Fig. 4). Rodent body length can explain ~76% of tooth width variation for this subset of species ($r^2 = 0.76$; $F_{1,32} = 101.9$; $p < 0.001$).

Fruit size and hardness played an important role in rodent selection of diet plants (Fig. 5). Harder fruits/seeds possessed larger bite marks compared with soft ones (ANCOVA; $R^2 = 0.55$; $F_{2,30} = 18.92$; effect of fruit/seed size: $p = 0.002$; effect of fruit/seed hardness: $p < 0.001$). Therefore, given the allometric relationship between incisor size and body size for the rodent assemblages measured here (see Fig. 4), we conclude that larger rodent species tend to interact with larger and harder fruits (Fig. 5).

Some plant species, such as *Amanoa oblongifolia* (Phyllanthaceae), *Inga obidensis* (Fabaceae) and *Theobroma sylvestre* (Malvaceae), had bite marks ranging from 0.12 to 0.44 cm, which encompass the tooth width of 77% of all rodents present in the list of species for the JNP. Conversely, *Casearia* sp. (Salicaceae) and *Chrysophyllum sanguinolentum* (Sapotaceae) had bite marks ranging between 0.12 to 0.15 cm and 0.68 to 0.72 cm, encompassing the tooth width of only two rodent species: *Oecomys bicolor* and *Cunicu-*

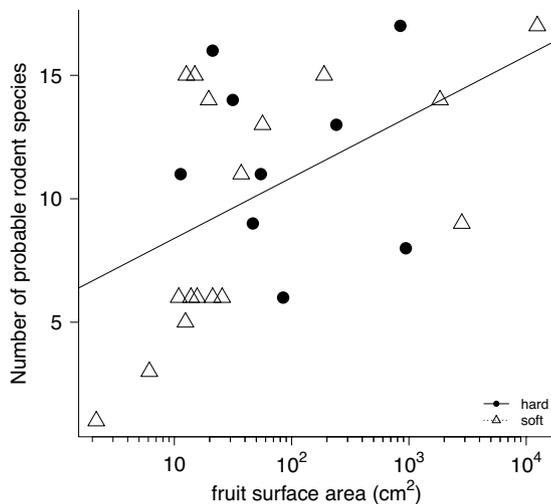


Fig. 6. Total number of possible rodent species (based on tooth width measurements) in relation to the mean fruit/seed size for plant species from JNP. Each point represents a plant species.

lus paca, respectively (see Table 3 of the Supplementary material for the complete list). Using the incisor tooth marks left on fruits/seeds, we obtained an average reduction of 46% in the set of possible rodents per plant species. At assemblage level (Fig. 6), fewer rodent species tend to interact with smaller fruit/seeds when compared with larger ones, and the fruit or seed hardness have no effect (pseudo $r^2 = 0.22$; $p = 0.001$).

Discussion

There was a clear relation between the body length and incisor width within the known rodent assemblage for JNP. Our results corroborate previous studies (Lessa and Patton, 1989a; Mora et al., 2003; Samuels, 2009; Vassallo et al., 2015), reinforcing evidence for the existence of this allometry in the rodents species present at JNP. As expected, we found an increase in the width of the incisor teeth, increasing in direct proportion to the size of the animal for almost all species (Fig. 4).

Based on the allometric relationship between incisor width and body size, it is possible to relate the animal's size with the mean volume of each fruit that was bitten by that species. The results show that larger species appear to be biting larger and harder seeds, while the small species choose the smaller and softer ones (Fig. 5). Previous work has shown that seed dispersers of different sizes respond to different seed traits, such as size or mass (Yi and Wang, 2015). Muñoz and Bonal (2008) found that seeds heavier than 70% of the rodent mean mass are not removed by the rodent species. Furthermore, it is known that the relation between the rodent mass and the seed mass is an important factor affecting seed predation (Galetti et al., 2015).

The higher nutritional reward gained from consuming larger seeds (Kerley and Erasmus, 1991) explains the patterns of seed consumption for the larger rodent species. However, for smaller species, manipulation of proportionately larger seeds is likely to be more physically difficult and costly in both terms of time and energy. Since seed size is frequently correlated to handling time, manipulation of larger fruits or seed by smaller rodent species likely decrease the efficiency of foraging (Stephens and Krebs, 1986; Kerley and Erasmus, 1991; Waite and Ydenberg, 1994). This may also influence vigilance, so increase predation risk (Lima, 1986).

Although it is known that the morphological characteristics of incisors (protrusion, incisors cross-sectional area, muscles of the jaw) in rodent groups have positive allometric relation with the

animal's mass/body size (Lessa and Patton, 1989a; Mora et al., 2003; Samuels, 2009), these are also directly correlated with the animal bite force (Becerra et al., 2011, 2012). Thus, the body size is related to the ability to eat hard items, with larger rodents being more easily able to consume items requiring greater bite force, as shown in our results (Fig. 5).

Our analysis did not achieve full separation of all species in the Jaú rodent assemblage purely on the basis of incisal width. This is, perhaps, not unsurprising, as there was also a concomitant overlap in body size between species (see Fig. 4), especially when juvenile individuals are included, as in the present study. Similarly Carvalho et al. (2015) demonstrated that using indirect method such footprints allow partial separation of felid species for identification. Despite this, our data suggests that some fruits may be consumed by several rodent species while other by just a small proportion of the overall rodent assemblage. Overall, larger seeds and fruits tend to be more often attacked by rodents than smaller ones, independent of their hardness (Fig. 6), evidence that the size of a seed/fruit influences the number of rodent species that will interact with it. There is also a considerable variation in the number of possible rodent species interacting with medium and larger fruit/seeds sizes. As discussed above, seed size is usually positively related to their overall energy content (Vander Wall, 1995; Castro et al., 2006), which explains the demand for these items by a greater number of species in the Jaú rodent assemblage. In our results, even for the hardest fruits, which may require more extensive handling, and hence enhances the risk of predation, energy reward appears to be the factor that best explains the result shown in Fig. 6. That seed size along may be used by rodents as a proxy for (anticipated) nutritive reward, is indicated by the study of Wang and Chen (2009) who found that, faced with seeds experimentally-manipulated to lack any energy content, rodents preferentially chose the largest ones available.

The methodology developed has some limitations; nevertheless this does not invalidate it as a simple useful tool that is, low-cost, non-invasive and easy to use under field conditions. Beck-King et al. (1999) found it is not possible to distinguish between subadult pacas (*Cuniculus paca*) and adult Central American agoutis (*Dasyprocta variegata*) using only bite marks; similarly, it was not possible to separate the marks left by young or subadult and adult animals in this study. However, the technique may still yield relevant information when the number of species occurring is reduced so that less overlap in the body length and incisors width values occurs (e.g. Beck-King 1999; Barnett et al., 2015b). Further precision may be possible with a more nuanced approach that includes such features as incisor tooth thickness (which is known to vary between congeners: Samuels, 2009), the curve of the teeth, the size of the space between them, and the presence of marks left by the grooves present (in some species) on the surface of the anterior enamel.

Conclusion

Using rodent bite marks on fruits and seeds clearly has ecological utility as it reveals at least which suite of species are attacking fruits and seeds, even if it does not always identify precisely which ones. The method is particularly relevant for studies that use bite marks to gain other ecological information, such as size-related foraging studies and data on the identity of plant species used by rodents. More generally, the seed size/rodent size ratios can help gain an understanding of the seed dispersal patterns, as well as which plant species are most consumed by rodents. It may be possible to improve the specificity of this technique by incorporating finer-scale features of inter-specific dental variation into the data set.

Conflict of interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2016.11.009>.

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