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SBMz · Sociedade Brasileira de Mastozoologia · SAREM

ARMADILLO (*DASYPUS* spp.) DENSITY THROUGH USE OF CAMERA TRAPPING AND BURROW DENSITY IN FRENCH GUIANA

Roxane Schaub[1,2], Léo Leclerc[1], Edith Guilloton[1], Jean-François Szpigel[3], Pierre Couppié[2,4], Rodolphe E. Gozlan[5], Luc Ackermann[6], Mariella Superina[7] & Benoit de Thoisy[8,9]

[1]CIC AG/Inserm 1424, Centre Hospitalier de Cayenne Andrée Rosemon, Cayenne, French Guiana. [Correspondence: Roxane Schaub <roxane.schaub@ch-cayenne.fr>].

[2]UMR Tropical Biome and Immuno-pathophysiology, Université de Guyane, Cayenne, French Guiana.

[3]Réserve Naturelle Régionale Trésor, Cayenne, French Guiana.

[4]Service de Dermatologie, Centre Hospitalier de Cayenne, Cayenne, French Guiana.

[5]ISEM, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France.

[6]ONF, Réserve Naturelle Nationale de La Trinité, Cayenne, French Guiana.

[7]IMBECU - CCT CONICET Mendoza – Universidad Nacional de Cuyo, Mendoza, Argentina.

[8]Laboratoire des Interactions Virus-Hôtes, Institut Pasteur de la Guyane, Cayenne, French Guiana.

[9]Kwata NGO, Cayenne, French Guiana.

ABSTRACT. Armadillo density estimates are important for species knowledge, but they are unknown in the Guiana Shield. We aimed at estimating *Dasypus* density through burrow density and camera trapping. We surveyed and trapped burrows in three protected sites in French Guiana, on strip transects covering 4.8 ha in each site, and estimated *Dasypus* density taking into account burrow measures and occupancy. Population densities ranged between 7.6 and 48.6 animals/km^2 for *Dasypus* sp. nov. and 10.3 and 34.7 animals/km^2 for *D. kappleri*. *Dasypus* density estimates through burrow survey and exclusive burrow entrance camera trapping is relatively low-cost, non-invasive and reliable.

RESUMEN. DENSIDAD DE LOS ARMADILLOS (*DASYPUS* spp.) MEDIANTE EL USO DE CÁMARAS TRAMPA Y DENSIDAD DE MADRIGUERAS EN LA GUAYANA FRANCESA. La densidad de armadillos es desconocida en el Escudo guayanés. Nuestro objetivo fue estimar la densidad de *Dasypus* a través de la densidad de madrigueras y mediante cámaras trampa. Identificamos y monitoreamos madrigueras en tres sitios en Guayana Francesa, en transectos cubriendo 4.8 ha por sitio. Estimamos la densidad poblacional de *Dasypus* teniendo en cuenta las medidas y la ocupación de las madrigueras. Las densidades poblacionales variaron entre 7.6 y 48.6 animales/km^2 para *Dasypus* sp. nov. y 10.3 y 34.7 animales/km^2 para *D. kappleri*. Estimar la densidad de *Dasypus* mediante las madrigueras y cámaras trampas es relativamente de bajo costo, no invasivo y confiable.

Key words: Camera trap, Cingulata, Guiana Shield, population indices.

Palabras clave: Cámaras trampa, Cingulata, Escudo guayanés, índices de población.

INTRODUCTION

Animal density estimates are important for species conservation, management and animal health, but difficult to obtain for nocturnal or cryptic animals, such as armadillos (Xenarthra: Cingulata) (Superina et al. 2014). While historical approaches to measuring animal density mainly used capture-recapture methods, track or direct observations surveys, camera trapping is expanding because it is relatively low-cost, non-invasive and suitable for many field conditions (Silveira et al. 2003). Camera trapping also provides information on behavior and interactions between species (Silveira et al. 2003). Camera trap surveys have provided good results for different Cingulata species (Aya-Cuero et al. 2017; Monteiro et al. 2019; Diniz & Bergallo 2020), including population density estimates and behavioral data (Aya-Cuero et al. 2017, 2021; Desbiez et al. 2020; Diniz & Bergallo 2020).

Armadillos are the main burrow diggers in the Neotropics. They use burrows daily for sheltering and sleeping, as well as for mating and litter raising. Except when foraging, they use several burrows alternately and spend most of their time underground (Loughry & McDonough 2013). Burrow entrance shape usually differs between armadillo species, with *Cabassous unicinctus* digging round holes (Carter & Encarnaçao 1983; Desbiez et al. 2018), *Priodontes maximus* inverted U holes, and *Dasypus* species inverted U or oval-shaped burrows (Platt et al. 2004; Trovati 2015). Measuring burrow density allows the study of armadillo use of different habitats and the drivers affecting habitat use (McDonough et al. 2000; Abba et al. 2015). However, data on armadillo densities or burrow densities are scarce, except for *Dasypus novemcinctus* in the southern United States of America (USA) (Loughry & McDonough 2013).

Differentiating burrows between armadillo species is not straightforward when several species cohabit (Arteaga & Venticinque 2010) and interspecies burrow sharing occurs, both with other animals and between different Cingulata species (Desbiez et al. 2018). Burrow counts alone do not allow extrapolation of burrowing animals density (Van Horne et al. 1997), but coupling them with burrow use would allow animal population indices extrapolations, such as species richness and demographic parameters (McDonough et al. 2000).

There are four armadillo species in French Guiana (FG): *Dasypus* sp. nov., long considered as *D. novemcinctus* but which is a distinct species exhibiting morphological (Billet et al. 2017; Hautier et al. 2017)

and genetic (Huchon et al. 1999; Gibb et al. 2016; Feijó et al. 2018, 2019) differences with individuals located outside the Guiana shield; *D. kappleri*; *C. unicinctus*; and *P. maximus* (Catzeflis & Thoisy 2012). Little is known about their ecology and behavior, particularly in the Guiana Shield.

The aims of our study were to assess the feasibility of estimating *Dasypus* species density by measuring burrow density and camera trapping at burrow entrances in FG, and to estimate social contact and burrow-sharing behaviors between armadillos.

MATERIALS AND METHODS

This study took place between October 2018 and June 2020 in three protected sites in FG: Trésor Nature Reserve (NR), Bagne des Annamites NR, and La Trinité NR (**Fig**. 1). In each site, we chose a path from which we could access an area of 50 hectares distributed on either side. Trésor NR has a continuous terra-firme forest, La Trinité a continuous terra-firme forest with limited flooded areas, and Annamites NR a continuous lowland forest with flooded areas. In each of the 50-ha areas, we censused 24 strip transects of 200 m each, separated by 50 m between transects on the same line and 100 m between transects on parallel lines (**Fig**. 2). Each transect was inspected over a width of 10 m, covering an area of 0.2 ha per transect and 4.8 ha per site.

The covered area was thoroughly inspected to identify all cavities, including under trunks and stumps. Each cavity was inspected by RS or LL to improve inter- and intra-site reproducibility. We retained only cavities that resembled burrows (i.e., a cavity dug by an animal—as opposed to collapses or log remains—based on entrance shape and inclination), had a minimum depth of 70 cm and a minimum height and width of 10 cm, corresponding respectively to the minimum measures of a burrow to possibly house *C. unicinctus*, the smallest armadillo species in FG. Each burrow was georeferenced and measured.

Camera traps (models HC-500, HC-550 and HP2X, Reconyx, Holmen, WI, USA; models SG560X and SG860C, HCO Scoutguard, Norcross, GA, USA; models STC-DS4K and 6XV4, Stealthcam, Irving, TX, USA; models MCG-13332 and MGC-13182, Moultrie, Birmingham, AL, USA; model BTC-8A, Browning, Morgan, UT, USA; model Trophy Cam HD E3, Bushnell, Cody Overland Park, KS, USA) were placed to target each burrow entrance or a selection of entrances, depending on trap availability. Cameras were set for 24-hour activity, maximum sensitivity and placed for six to 17 consecutive days.

The recordings were independently reviewed by RS, LL, and EG to check recording dates and times, species identification, sex determination, and behavior. Observations were deemed independent if separated by at least 30 min (Ouboter et al. 2021). *Dasypus* species were differentiated based on the following features that were easily distinguishable on our recordings: compared to *Dasypus* sp. nov., *D. kappleri* 1) is much larger; 2) has a much wider tail base; 3) has visible spurs on hind legs; and 4) has a light color of the cheeks contrasting with the darker cephalic shield, compared to the uniformly grey color of the head of *Dasypus* sp. nov., and a more robust muzzle (Aya-Cuero et al. 2019). All discordant determinations
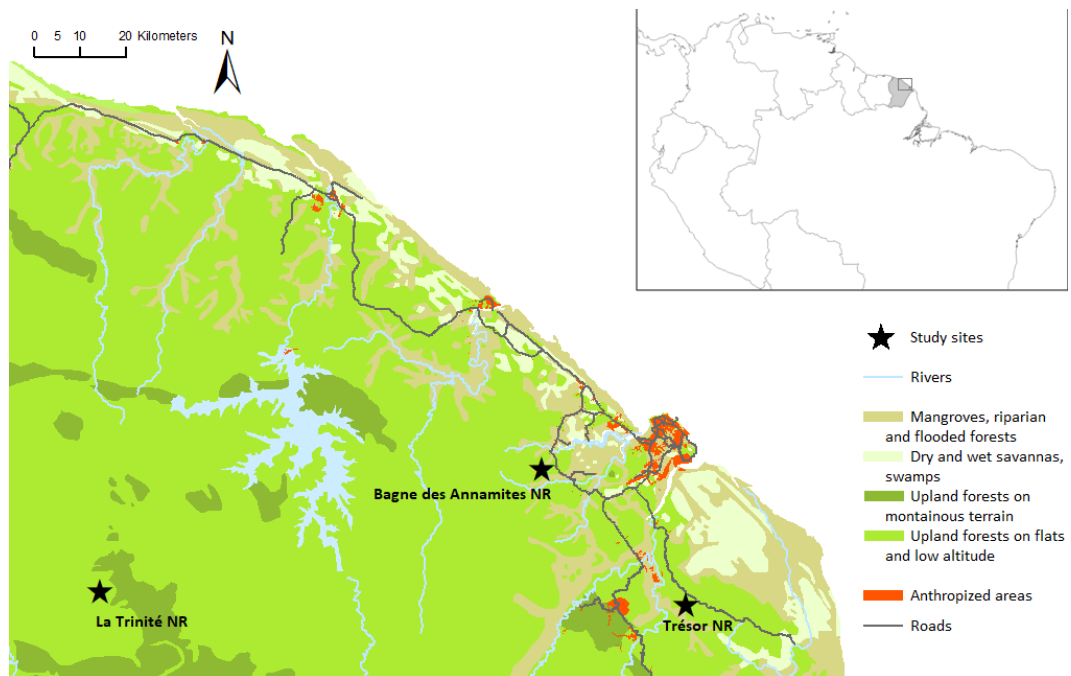
Fig. 1. Study sites location in French Guiana.

were reviewed by an armadillo expert (MS). The behavior of armadillos nearby a burrow entrance was defined as follows: 1) walking past or foraging without approaching the burrow entrance; 2) sniffing, foraging or mud bathing at the burrow entrance; 3) burrow use, namely entering the burrow completely.

Burrow density was calculated globally as the number of burrows divided by the surveyed area. Burrow densities were also calculated separately by site and by species, based on the number of burrows of each size as described below. Burrows were ranked by size according to the measures of the entrance. As we had no previous data on armadillo burrow entrance dimensions in the Guiana Shield, we used our observations to determine the minimal threshold for these dimensions for each species. They were defined as follows: threshold between size 1 and 2 defined by the smallest dimensions (height and width) where a *Dasypus* sp. nov. entered a burrow, and threshold between size 2 and 3 defined by the smallest dimensions where a *D. kappleri* entered a burrow (see **Table 1** for threshold values). Across all sites, the minimum sizes of a burrow entrance were 13 cm height and 19 cm width for *Dasypus* sp. nov., and 20 cm height and 21 cm width for *D. kappleri*.

We refined our estimates of burrow densities, and hence species, by considering the compatibility of each species with burrow entrance measurements. In the USA, the low variation in burrow size suggests that juveniles do not dig burrows but rather use existing ones (McDonough et al. 2000). Furthermore, although there may be overlapping in burrow entrance dimensions used by different armadillo species (Arteaga & Venticinque 2010), this should be limited as the overlap in size between species is limited (Richard-

Hansen et al. 1999). We did not use maximum thresholds for burrow size, as armadillos can use burrows much larger than their body size (Aya-Cuero et al. 2017), which we also observed.

Burrow occupancy was calculated by species by dividing the number of records of an armadillo entering a burrow by the number of trap-days on burrows consistent with the size of the species. Finally, for each species, armadillo population density per km² was estimated by multiplying burrow density by burrow occupancy. Both estimates were provided with their range. For the latter, burrow occupancy was calculated based on a narrow definition, i.e., an observation of an armadillo spending the entire day in the burrow (entering at the end of the night and exiting at the beginning of the next night); and on a broad definition, i.e., any observation of an armadillo entering a burrow entirely, no matter if it remained in the burrow all day or not.

Direct armadillo contact was defined as recording more than one individual at the same time. We defined indirect armadillo contact as recording at least two armadillos, each having a sniffing, foraging or mud bathing behavior nearby the same burrow entrance at any time. We also distinguished contacts when they occurred between individuals that we could positively identify as different (different species or sex or a distinguishing sign such as noticeable size difference, scars or carapace pattern).

RESULTS

We found 230 burrow entrances on a total surveyed area of 14.35 ha. Overall burrow density was 16.0 burrows/ha, with similar densities across the sites.
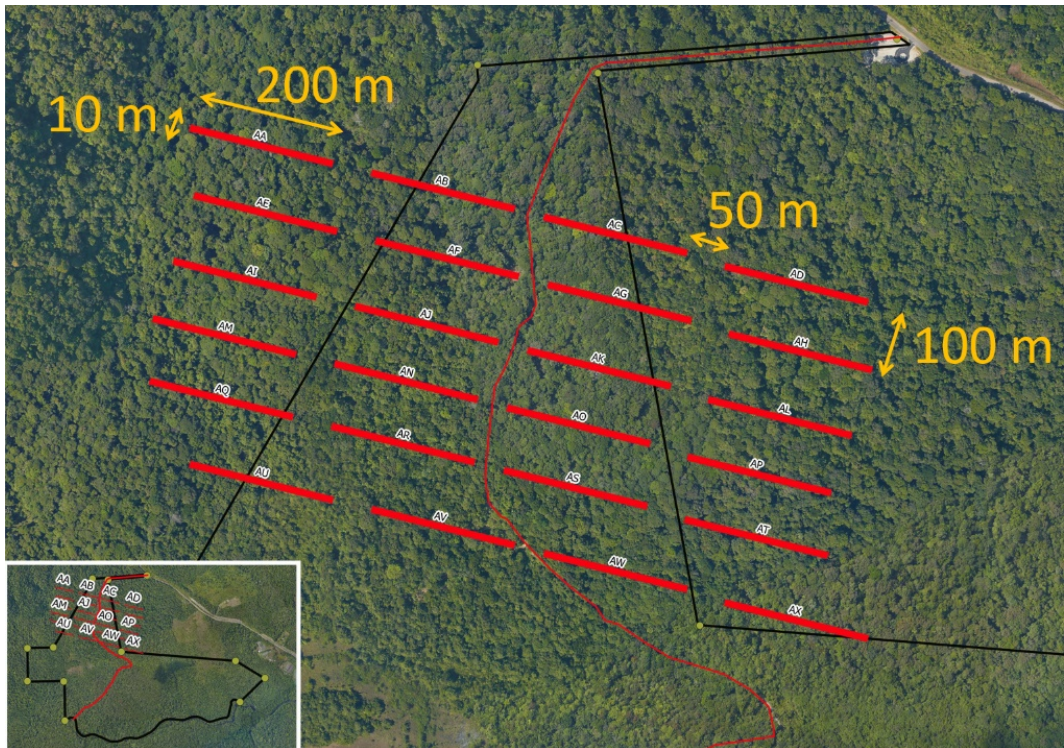
Fig. 2. Example of transect dispatch in Bagne des Annamites NR.

Burrow entrance measures were higher in La Trinité compared to Trésor and Annamites NR. We recorded a total of 1 087 trap-days on 126 burrow entrances, and at least one *Dasypus* was recorded on 66 (52.4%) of the trapped burrows. Detailed data per site are described in **Table** 1.

In Trésor NR, there were five records of *Dasypus* sp. nov. and 14 of *D. kappleri*. In Annamites NR, all 54 *Dasypus* recordings were identified as *Dasypus* sp. nov. In La Trinité NR, there were 21 records of *Dasypus* sp. nov., 42 of *D. kappleri*, three of an unidentified *Dasypus* and four of *P. maximus*. No *C. unicinctus* were recorded at any of our study sites. Most *Dasypus* interacted with the burrow entrance, with 41.0% approaching the burrow entrance and sniffing the ground, and some even foraging or mud bathing in the entrance, while 21.6% entered the burrow.

There were more small burrows (height <13 cm or width <19 cm) in Annamites NR compared to the other two sites and more large burrows (height ≥20 cm or width ≥21 cm) in La Trinité NR than at the other two sites. Burrow density for each *Dasypus* species was calculated after eliminating

burrow entrances that were too small to let pass an adult, i.e., the smallest burrows for *Dasypus* sp. nov. (i.e., 44 size class 1 burrows eliminated, **Table** 1) and all but the larger burrows for *D. kappleri* (i.e., 143 size class 1 and 2 burrows, **Table** 1). The *Dasypus* sp. nov. burrow density was slightly higher in La Trinité. *Dasypus kappleri* burrow density was twice as high in La Trinité NR as in Trésor NR.

Dasypus sp. nov. burrow occupancy rates were between two and six-fold higher in Annamites NR compared to La Trinité NR. *Dasypus kappleri* burrow occupancy rates were similar in Trésor and La Trinité NR. *Dasypus* sp. nov. density estimates were between 1.5 and 4.5-fold higher in Annamites NR compared to La Trinité NR. *Dasypus kappleri* density estimates were slightly higher in La Trinité NR compared to Trésor NR.

We did not record any direct contact between armadillos. We could not determine whether several individuals shared burrows simultaneously as we could not identify most armadillos individually. However, indirect contact between armadillos did occur through the successive use of a burrow (sniffing, foraging, digging, occupying). Out of 22

Table 1

Area surveyed, number, size and density of burrow entrances, number of trap days and *Dasypus* records by type of behavior nearby the burrow, per site and per species.

LOCATION	Trésor	Annamites	La Trinité
Surveyed area (ha)	4.75	4.80	4.80
Burrow entrances (N)	70	74	86
Successfully trapped (N)	37	25	64
With at least one *Dasypus* record (N (%))	13 (35.1)	16 (64.0)	37 (57.8)
Total trap days (N)	263	351	473
Burrow density (per ha)	14.75	15.42	17.9
Burrow entrance size (cm; median [IQR])			
Height	18 [15-23]	16.5 [15-19]	22 [18-25]
Width	25 [20-30]	20 [18-23]	25.5 [20-31]
D. sp. nov. recordings per type of behavior nearby the burrow (N (%))			
Walked past	3 (60.0)	23 (42.6)	8 (38.1)
Sniffing/foraging in entrance	2 (40.0)	19 (35.2)	10 (47.6)
Entering/leaving the burrow	0	12 (22.2)	3 (14.3)
Of which staying the whole day∗	0	3 (5.6)	2 (9.5)
D. kappleri recordings per type of behavior nearby the burrow (N (%))			
Walked past	3 (21.4)	0	13 (31.0)
Sniffing/foraging in entrance	7 (50.0)	0	19 (45.2)
Entering/leaving the burrow	4 (28.6)	0	10 (23.8)
Of which staying the whole day∗	3 (21.4)	0	3 (7.1)
Burrow entrance size class (cm; N (%))			
1: height <13 or width <19	11 (15.7)	20 (27.0)	13 (15.1)
2: height [13-20[or width [19-21[	32 (45.7)	43 (58.1)	24 (27.9)
3: height ≥20 or width ≥21	27 (38.6)	11 (14.9)	49 (57.0)
Trap days by burrow size class (N)			
Compatible with *D.* sp. nov. (burrow size 2 or 3)	230	282	421
Compatible with *D. kappleri* (burrow size 3)	127	77	296
Burrow occupancy per trap day (range; %)			
Compatible with *D.* sp. nov. (burrow size 2 or 3)	0	[1.1 - 4.3]	[0.5 - 0.7]
Compatible with *D. kappleri* (burrow size 3)	[2.4 - 3.1]	0	[1.0 - 3.4]
Burrow density by species (per ha)			
Compatible with *D.* sp. nov. (burrow size 2 or 3)	12.4	11.3	15.2
Compatible with *D. kappleri* (burrow size 3)	5.7	0	10.2
Dasypus density estimate (range; per km²)			
D. sp. nov.	0	[12.4 - 48.6]	[7.6 - 10.6]
D. kappleri	[13.7 - 17.7]	0	[10.3 - 34.7]

ha: hectare; N: number; IQR: interquartile range; D.: *Dasypus*; ∗: only occurrences of armadillos that stayed in the burrow for a whole day (with recordings of the armadillo entering the burrow late at night and leaving the burrow early at night the same day)

burrow entrances with indirect interactions between armadillos, at least eight occurred between two individuals that we were able to differentiate with certainty, with five of these indirect interactions taking place the same night.

DISCUSSION

This is the first study of armadillo burrow density, burrow use and population density in French Guiana and in the Guiana Shield. Overall gross burrow density of 16.0 burrows/ha was consistent between the three study sites and close to the 13.5 burrows/ha density found in central Amazonia (Arteaga & Venticinque 2010), and consistent with burrow densities ranging from 5.8 in savanna to 27.0 burrows/ha in pine forest in Belize (Platt et al. 2004).

Our estimates of *Dasypus* sp. nov. density ranges of 7.6–10.6 animals/km² in La Trinité NR and 12.4–48.6 animals/km² in Annamites NR are much higher than previous estimates of 3 *Dasypus* sp. nov./km² in FG, extrapolated from 188 *Dasypus* sp. nov. live rescue captures on 62.5 km² (catch area on the islands, which corresponds to half of the total catch area of 125 km²) during impoundment of a hydroelectric dam (Vié 1999). As armadillos are able to cross water bodies (Loughry & McDonough 2013), individuals could have escaped rising waters before rescue teams captured them, which may explain the low estimates in that study. To our knowledge, the only other *Dasypus* population estimate is from Amapá, a Brazilian state bordering FG, were the authors considered the smallest *Dasypus* species recorded on their camera traps to be *D. novemcinctus*, with an estimated density of 0.08 animals/km² (Michalski et al. 2015). However, the study location within the Guiana shield ecosystem suggests that

those animals would probably be *Dasypus* sp. nov. (Billet et al. 2017; Hautier et al. 2017). On the other hand, our estimates are close to those found for *D. novemcinctus* in the Brazilian Atlantic forest by direct animal observations, with 6 *D. novemcinctus*/km^2 (Ferreguetti et al. 2016); in Costa Rica with 9.4 *D. novemcinctus*/km^2 (Timock & Vaughan 2002); in Pará (southeastern Amazonia, Brazil) with 21.8 *D. novemcinctus*/km^2 (Peres & Nascimento 2006); and in the USA, where *D. novemcinctus* densities range from 10 to 37.5 animals/km^2 estimated by techniques such as capture-recapture and direct observations (Loughry & McDonough 2013).

Our estimates of *D. kappleri* density range of 10.3–34.7 animals/km^2 in La Trinité NR and 13.7–17.7 animals/km^2 in Trésor NR are also much higher than previous estimates of 1 individual/km^2 in FG, extrapolated from 63 *D. kappleri* live rescue captures on 62.5 km^2 during the dam impoundment (Vié 1999), and of 0.32 individuals/km^2 in Amapá (Michalski et al. 2015). Outside the Guiana Shield, *D. kappleri* density estimates are also much lower, with 0.16 individuals/km^2 in the Peruvian Amazonian forest estimated via camera-trapping (Mena et al. 2016) and eight individuals/km^2 in Pará, estimated through hunting surveys (Peres & Nascimento 2006). The difference in *Dasypus* sp. nov. and *D. kappleri* density observed between Trésor and La Trinité NR may be explained by the presence of tourism in Trésor NR (about 4 000 visitors per year use the trail that cross our study area), as opposed to La Trinité NR which is a scientific station that receives only a few researchers a few days per year. Indeed, in similar ecosystems *D. kappleri* is less abundant and *D. novemcinctus* is slightly more abundant in protected environment with tourism compared with a contiguous protected environment without tourism (Rocha et al. 2012).

Overall, our density estimates are considerably higher than those of other studies attempting to assess population parameters by direct daytime observations or by capture, or targeting several terrestrial vertebrates at once by camera trapping. In our study, except one observation, all *Dasypus* sp. nov. were recorded at night. *Dasypus novemcinctus* is predominantly nocturnal (Loughry & McDonough 2013) and *D. kappleri* is a strictly nocturnal species (Wilson & Mittermeier 2018), which may explain the extremely low estimates in studies that did not use camera traps or were done during day time.

Dasypus novemcinctus build above-ground nests in poorly-drained savannas in Belize (Platt & Rainwater 2003) and in Florida (Layne & Waggener

1984), as do *D. sabanicola* in Venezuela (Pacheco & Naranjo 1978). To our knowledge there are no observations of above-ground nests of *Dasypus* elsewhere. We therefore hypothesize that in non-flooded forest habitats, armadillos almost systematically shelter in a burrow. Hence, by camera-trapping all burrow entrances, we should have recorded all armadillos in the area.

Our study also provides preliminary data on armadillo behavior in FG. Firstly, we found evidence of intra- and inter-species territory sharing as we have numerous records with different individuals of these two species on the same camera traps. We did not record any direct interaction between armadillos, confirming that *Dasypus* sp. nov. and *D. kappleri* are mainly solitary, as is *D. novemcinctus* (Loughry & McDonough 2013). We observed, however, that most armadillos inspected the entrance of burrows they encountered during their movements. This is not surprising, as both *D. novemcinctus* (McBee & Baker 1982) and *D. kappleri* (Fleck & Voss 2016) are known to follow established foraging trails, which also lead to burrows.

We chose the strip transects method, like other authors (Platt et al. 2004; Arteaga & Venticinque 2008; Trovati 2015), rather than the plot method (McDonough et al. 2000; Arteaga & Venticinque 2010), because it is easier to implement in a dense Neotropical forest compared to open or less dense areas, such as the southern USA or the Brazilian Cerrado. Furthermore, accurate estimation of interaction between individuals is hampered by difficulties in distinguishing individuals. This is due to the poor quality of the images and mud frequently masking potential distinctive signs. Despite these difficulties, we were able to distinguish several individuals based on size and external markings, and there may have been more indirect interactions than reported here. We were also able to distinguish the two *Dasypus* species to obtain separate density estimates.

Unfortunately, because of few trap days in Trésor NR, we were unable to correctly estimate burrow occupancy for *Dasypus* sp. nov. in that area, as we recorded none entering a burrow. Approximately three to five weeks of camera trapping are required to obtain a satisfactory estimate of species richness (Kays et al. 2020); so it is likely that in Trésor NR the traps were not deployed long enough to capture the desired behavior.

Furthermore, we might have overestimated the upper value of the density ranges as all armadillos entering a burrow were counted for the burrow

occupation rates estimation, even if the animals left the burrow after a short time. Nonetheless, with the lower value of the density ranges which retained only armadillos staying the whole day in the burrow, we would rather risk a slight underestimation due to the possibility of a trap trigger failure that we have rarely observed. However, we obtained density estimates of the same order of magnitude across sites, i.e., between 7.6 and 13.7 animals/km^2 depending on the species and the site. Densities may also have been overestimated because we could not individually identify all animals. To reduce this bias, we calculated our estimates based on trap days. This allowed us to avoid counting the same individual twice in a day and averaging occupancy rates over a given period.

Lastly, we did not sample our study sites according to altitude or declination. Some authors corrected their crude burrow density estimate of 13.6 burrows/ha for these two topographic parameters and found that corrected mean burrow densities were 21.05 and 18.7 burrows/ha, across declination and elevation contour classes, respectively (Arteaga & Venticinque 2008). Sampling study sites taking these parameters into account, or adjusting estimates with those parameters, may yield more refined results.

Here we propose a new approach to armadillo density estimation through exclusive burrow entrance camera trapping. This method provides more reliable results than non-burrow camera trapping, requires less field work than direct observations and is less invasive and less expensive than the gold standard of capture-recapture methods.

We dedicate this article to the late François Catzeflis, who dedicated since 1994 most of his work to mammalogy in French Guiana.

ACKNOWLEDGMENTS

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