#### Mastozoología Neotropical, 24(1):163-175, Mendoza, 2017

Versión impresa ISSN 0327-9383 Versión on-line ISSN 1666-0536 Copyright ©SAREM, 2017 http://www.sarem.org.ar http://www.sbmz.com.br

Artículo



# THE GIANT ARMADILLO (*Priodontes maximus*) IN THE ARGENTINE CHACO

Verónica A. Quiroga<sup>1</sup>, Yamil E. Di Blanco<sup>1</sup>, Andrew Noss<sup>2</sup>, Agustín J. Paviolo<sup>1</sup>, and Mario S. Di Bitetti<sup>1</sup>

- <sup>1</sup> Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Facultad de Ciencias Forestales (UNaM) y Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA). Bertoni 85; CP: 3370; Puerto Iguazú, Misiones, Argentina. [Correspondence: Verónica Andrea Quiroga <veroquiroga@gmail.com>]
- <sup>2</sup> Department of Geography, University of Florida, 1405 NW 38th St., Gainesville, Florida, USA.

ABSTRACT. The giant armadillo (*Priodontes maximus*) is a difficult species to study because of low population densities, combined with nocturnal and fossorial habits. No systematic population studies have been undertaken to date in Argentina. Our objectives were to evaluate the species' presence, relative abundance, and temporal activity patterns across five locations with different levels of human disturbance and legal protection in the Argentine Chaco. Between June 2006 and January 2014, we completed 10 surveys, using camera trap and/or track plots, searches for burrows and tracks, and observations by local people and park rangers. We used camera trap records to determine presence, relative abundance (records/100 camera days) and activity patterns. We only recorded the species at three locations: Copo National Park, Aborigen Reserve and La Fidelidad Resource Reserve. At the Aborigen Reserve we documented burrows and tracks but obtained no photographs. At Copo and La Fidelidad we estimated relative abundance at 0.08 and 0.40 records per 100 camera days, respectively. We did not record giant armadillos near the edges of La Fidelidad, nor in the two locations with greater human disturbance. Camera trap records indicate that giant armadillos in the Argentine Chaco are strongly nocturnal. The population status of giant armadillos in Argentina is a matter of concern. With few or no records at other study locations, La Fidelidad may harbor one of the few relict populations of giant armadillos in the Argentine Chaco.

RESUMEN. El tatú carreta (*Priodontes maximus*) en el Chaco argentino. El tatú carreta (*Priodontes maximus*) es una especie difícil de estudiar debido a sus hábitos nocturnos y fosoriales y a sus bajas densidades poblacionales. En Argentina no hay estudios poblacionales sistemáticos realizados previamente. Nuestro objetivo fue determinar la presencia, abundancia relativa y patrones de actividad temporal en cinco sitios con distinto grado de intervención humana y categoría de protección legal en el Chaco argentino. Entre junio de 2006 y enero de 2014 realizamos 10 muestreos utilizando cámaras-trampa, colocación de huelleros, recorridos de búsqueda de cuevas y rastros e información de pobladores locales y guardaparques. Utilizamos datos de cámaras-trampa para determinar la presencia, abundancia relativa (registros/100 días cámara) y patrones de actividad. La especie fue registrada solamente en tres sitios: el Parque Nacional Copo, la Reserva Aborigen y la Reserva de Recursos La Fidelidad. En la Reserva Aborigen registramos cuevas y huellas, pero no obtuvimos fotografías. En Copo y en La Fidelidad estimamos la abundancia relativa en 0.08 y 0.40 registros cada 100 días-cámara respectivamente. No registramos tatúes ni en los bordes de La Fidelidad, ni en los dos sitios con mayor grado de disturbio humano. Los registros fotográficos indican que el tatú carreta es marcadamente nocturno en el Chaco Argentino. La situación poblacional del tatú carreta en Argentina es preocupante. Los escasos o nulos registros obtenidos

en las otras áreas sugieren que La Fidelidad podría conservar uno de los pocos relictos poblacionales de tatú carreta en el Chaco Argentino.

Key words: Camera traps. Conservation. El Impenetrable National Park. Relative abundance.

Palabras clave: Abundancia relativa. Cámaras trampa. Conservación. Parque Nacional El Impenetrable.

# INTRODUCTION

The giant armadillo (Priodontes maximus) is the world's largest armadillo and one of eight species of armadillos in the Argentine semi-arid Chaco. The IUCN/SSC classifies the species as Vulnerable with a declining population (Anacleto et al., 2014). In Argentina it is classified as Endangered (the Mammal Red List, Superina and Abba, 2012 and Resolution No 1030/2004 of the National Wildlife Service); and in Chaco Province it has been declared a Provincial Natural Monument (Ley Nº 4306). Hunting and habitat loss are the two principal factors blamed for its range-wide population decline (Peres, 2001; Porini, 2001; Aguiar and da Fonseca, 2008; Tarifa, 2009; Superina and Abba 2012). Although its meat may not be generally consumed in the Argentine Chaco, because of its large size and unique appearance it is captured for the pet trade, private collections, and as a trophy (Altrichter, 2006).

The giant armadillo is a difficult species to observe, and its presence is most often revealed by the large burrows it digs for itself for refuge (Carter and Encarnação, 1983; Arteaga and Venticinque, 2007 and 2010; Ceresoli and Fernández Duque, 2012). Although diurnal activity has been reported (Leite Pitman, 2004), its nocturnal and fossorial habits, combined with its usually low population density, make it difficult to study (Nowak, 1991; Redford, 1994; Anacleto, 1997; Noss et al., 2004; Aguiar and Da Fonseca, 2008; Cuéllar, 2008; Meritt, 2008; Silveira et al., 2009; Blake et al., 2012). Research on this species has been undertaken in the Amazon, Cerrado, Pantanal and Bolivian Chaco (Carter, 1985; Noss et al., 2004; Silveira et al., 2009; Desbiez and Kluyber, 2013), but is limited to a couple of general studies in the Argentine Chaco (Abba et al., 2012; Porini, 2001; Torres and Jayat, 2010), with no systematic population evaluations. Historically the species was distributed throughout the Argentine Chaco, with greater abundance in the semiarid subregion, but less than 3% of this subregion is formally protected (Torres and Jayat, 2010). Therefore, across most of its range in Argentina, essentially no information is available on how the species is responding to human disturbance and what the role of protected areas may be for its conservation. Our objectives were to evaluate the presence, relative abundance, and temporal activity patterns of giant armadillos across five locations that vary in the extent of human disturbance and in degree of protection in the central semiarid Argentine Chaco.

# STUDY AREA

The Gran Chaco is the second most extensive forest ecoregion in the Americas after the Amazon, and is the largest sub-tropical dry forest in the world (Morello and Adámoli, 1974; Morello et al., 2009). Sixty percent of the Chaco (675000 km²) is in Argentina and approximately 270 000 km<sup>2</sup> are semi-arid Chaco forests, including the hottest region of South America with maximum temperatures attaining 47 °C in summer (Prohaska, 1959), while dropping several degrees below freezing in winter. The Argentine semi-arid Chaco comprises dry forest plains with a marked seasonal climate, a median annual temperature of 24 °C, and annual precipitation of 400-800 mm, falling mostly in October-April (Caziani et al., 2003). The central area of the Argentine Chaco is known as "El Impenetrable" (The Impenetrable forest) not only because of the dense vegetation, but also because its semi-arid climate and the almost total lack of surface water makes human life very difficult (Morello and Adámoli, 1974). The two dominant tree species are Schinopsis lorentzii and Aspidosperma quebracho-blanco, accompanied by Ziziphus mistol, Prosopis nigra, Bulnesia sarmientoi and a dense understory dominated by Capparis spp., Acacia spp. and Celtis spp., among others (Morello and Adámoli, 1974; Caziani et al., 2003). The characteristics of the region support an extensive cattle ranching system, combined with heavy hunting of wildlife both by local residents of widely dispersed ranch outposts and by hunters from nearby towns (Baxendale and Buzai, 2009).

We surveyed five locations across the semiarid Chaco of northern Argentina, in the provinces of Santiago del Estero, Chaco, and Formosa. The locations were 40-160 km apart from each other and presented different degrees of human disturbance (Quiroga and Boaglio, 2006; 2007; Quiroga, 2013) (Fig. 1).

1) Copo National Park (1118 km²) is located in north-eastern Santiago del Estero Province, and has the highest legal protection level for Argentine natural areas. Our survey covered approximately the northern 30% of the park (367 km²). Several small settlements lie near the park, and one is 3 km inside the park. Compared to the other locations, the relative livestock density is medium to low. Lacking roads and trails, the interior of the park is inaccessible to livestock and to hunters, such that hunting pressure in the park is very low. The inaccessibility also restricted our survey

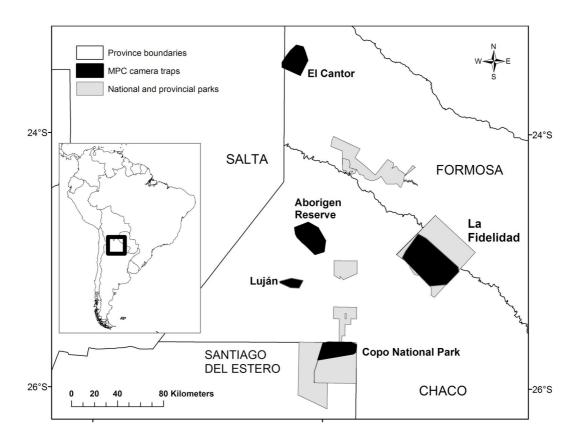


Fig. 1: The five camera trap survey locations in the Argentine semi-arid Chaco. MCP: minimum convex polygon that includes all the camera traps stations.

design, limiting our camera layout to the park boundaries and to four foot-paths that extend 5-15 km inside the park.

- 2) Aborigen Reserve (2500 km<sup>2</sup>) is located in northern Chaco Province. Our survey in the center of the Reserve covered 372 km<sup>2</sup>, about 20% of its area. Notwithstanding its name, no indigenous people occupy this Reserve. In addition, it is not included in Argentina's protected area network. The density of settlers in the Reserve is moderate (0.8 ranch outposts/100 km<sup>2</sup>). The relative livestock density is also moderate, and is complemented by an indeterminate number of feral donkeys (Equus africanus). The Reserve is bounded to the east by Fuerte Esperanza Park, a provincial protected area but with little effective protection. Three unpaved roads crossing the Reserve provide access to hunters both local and from nearby towns.
- 3) El Cantor is the name of a ranch outpost in northwestern Formosa Province. Our survey, centered on El Cantor, covered 363 km² of private ranchlands, to the boundary of Salta Province. The area is not legally protected, human population density is relatively high (1.3 ranch outposts/100 km²), the livestock burden is one of the highest for the locations we surveyed, and the road network provides easy access for local hunters.
- 4) La Fidelidad Provincial Resource Reserve (1500 km², recently upgraded to El Impenetrable National Park) lies between the Bermejo and Bermejito rivers, in Chaco Province. Our survey covered over 75% of the former Reserve (1156 km²), both interior and edges, and portions of the banks of both rivers. No people inhabit La Fidelidad, and the livestock burden is very low, limited to animals straying from ranch outposts outside the Reserve, but also feral donkeys and some horses (Equus equus). Historically a private property, public access to internal roads and trails remains prohibited, so hunting pressure is very low, and the conservation status is good.
- 5) Luján is the name of another ranch outpost, on Picada 8 which cuts across the center of El Impenetrable forest, in Chaco Province. Our survey centered on Luján covered 110 km² of private ranchlands. This area is one of the first settled and most densely populated portions

of El Impenetrable (3.5 ranch outposts/100 km²), with a high livestock burden and high hunting pressure compared to the other locations. Numerous roads and trails cross the area, connecting ranch outposts with each other and to nearby towns.

# **METHODS**

Between June 2006 and January 2014, we carried out 10 surveys across the five locations described above, using combinations of the methods detailed in **Table 1**. Our principal method was systematic camera trap surveys, but we also used track plots, searched for burrows and tracks, and compiled anecdotal information from local people.

# Camera traps

The systematic camera trap surveys were conducted as part of a study on jaguar, puma and their prey in the region (Quiroga et al., 2014 and unpublished data). Previous studies suggest that giant armadillos use unpaved roads and footpaths as movement corridors, as do the big cats, especially in Chacoan forest and environments disturbed by humans (Noss et al., 2004; Vynne et al., 2011). At each camera trap station we set either a single camera or a pair of cameras facing each other across a footpath or unpaved road. Cameras were active 24 h a day and the survey period varied by location (Table 2). Other authors have successfully used this type of survey design with giant armadillos (Noss et al., 2004; Silveira et al., 2009; Zimbres et al., 2013). We used the photo records to confirm the presence of the species, estimate relative abundance, and to describe activity patterns.

# Relative abundance

We calculated the number of giant armadillo records/100 camera days, as is widely reported in the camera trap literature (Silveira et al., 2003; Zimbres et al., 2013). In Bolivian Chaco forests, Noss et al. (2004) found that this relative abundance index for giant armadillos is consistent with density estimations from capture-recapture methods. We considered photographic records to be independent when separated by at least one hour.

# **Activity patterns**

We recorded the time of activity of the species by the hour printed on the camera trap photographs. As above, consecutive camera trap photos at a single station were considered independent records

Table 1

Methods and survey periods for giant armadillo presence and abundance at five locations in the Argentine semi-arid Chaco (n/s: not systematic).

Location	Surveys	Methods
El Cantor	June 2010	- Searches for tracks and burrows (n/s)
	June to September 2010	<ul> <li>Camera traps</li> <li>Searches for tracks and burrows (279 km in 20 trails from 0.8 to 8 km long)</li> </ul>
Aborigen Reserve	June to October 2006	- Track plots (June: n=75; October: n=90) - Searches for tracks and burrows (n/s)
	September/October 2007	- Camera traps.
	June to September 2008	<ul> <li>Camera traps.</li> <li>Searches for tracks and burrows (251 km in 12 trails from 1 to 8.5 km long).</li> </ul>
Copo National Park	July 2009	- Searches for tracks and burrows (n/s)
	September to November 2009	<ul> <li>Camera traps.</li> <li>Searches for tracks and burrows (344 km in 14 trails from 1 to 13 km long)</li> </ul>
Luján	October 2006	- Track plots (n=90) - Searches for tracks and burrows (n/s)
	October 2007	- Camera traps.
La Fidelidad Provincial Reserve	February 2013 to January 2014	<ul><li>Camera traps.</li><li>Searches for tracks and burrows (n/s)</li></ul>

if they were at least one hour apart. We used nonparametric kernel density functions to describe giant armadillo activity patterns based on independent photo records (Worton, 1989). More specifically, we used the modal.region() function in R (R Core Team, 2013) circular package (Agostinelli and Lund, 2013) to determine periods when activity outside burrows was concentrated. The 95% isopleth, that represents the time interval, in a 24 h period, in which 95% of activity occurs was considered the activity range (Oliveira-Santos et al., 2013). The 50% isopleth was considered the core activity period, the time range of peak activity. The precision of the estimates is defined by the 95% confidence intervals (CIs) based on 1000 bootstrap samples (Ridout and Linkie, 2009). We estimated the time of day when sunrise and sunset occurred for the each independent record using the sunriset function of the maptools package (Bivand and Lewin-Koh, 2015) in the R environment.

# Track plots and searches for burrows and sign

We complemented the camera trap surveys in the Aborigen Reserve and in Luján with 75 and 90 track plots, respectively. Track plots were 1 x 1 m square, 50 m apart along 2 km-long footpaths. We used three footpaths per site that were at least 6 km apart from each other and we installed 25 to 30 plots per footpath. We cleared all vegetation from these plots and sifted the soil. Each track plot was active for 5 to 7 consecutive days and was checked every 24 h (Wilson et al., 1996).

While we were setting and checking the camera traps, we searched on foot along trails and abandoned roads for any sign of giant armadillos. The number of kilometers searched at each location depended on the availability of trails and the logistical challenges of the moment. In cases where we returned along

Table 2

Camera trap effort at the five semi-arid Chaco locations surveyed for giant armadillos (*Priodontes maximus*), between October 2007 and January 2014.

Location	Survey dates	N° stations	Trap days	Average distance between cameras (km + SD)	MCP of camera trap layout (km²)
El Cantor	01 July to 09 September 2010	35	2129	$3.20 \pm 0.46$	362.7
Aborigen Reserve	23 June to 07 September 2008	30	1993	$3.04 \pm 0.98$	455.4
Aborigen Reserve	17 September to 03 October 2007	12	176	3.70	371.7
Copo NP	04 September to 19 November 2009	24	1204	$2.81 \pm 0.60$	367.3
Luján	04 to 13 October 2007	11	83	2.90	110.1
La Fidelidad	13 February 2013 to 18 January 2014	52	3498	2.82	1155.7

the same trail, we only collected data on the way out (Table 1).

# Compilation of anecdotal information

Opportunistically, at all the locations we visited homes of people living within or near the study area. In informal conversations with these residents and with natural reserve and park rangers, we asked about giant armadillo presence (current and past) in the area, how frequently animals or burrows were seen, why it was hunted, and challenges for the species' conservation.

# **RESULTS**

# Camera traps, track plots and searches for burrows and sign

We only registered giant armadillos at 3 of the 5 locations surveyed: Copo National Park, Aborigen Reserve, and La Fidelidad Resource Reserve. In Luján and El Cantor areas, we found no evidence of the species. In the Aborigen Reserve, we registered only 1 burrow and 1 track record, but no camera trap photos. In Copo National Park we obtained 1 camera trap photo (0.08 records/100 camera days), 1 track record and we documented 9 different burrows (Fig. 2).

In La Fidelidad Provincial Resource Reserve, we recorded giant armadillo in 8 (15.4%) of 52 camera trap stations. The 96 photographs from 14 independent capture events (Fig. 3) represent a capture rate of 0.40 records/100 camera days. We found 9 burrows and recorded 2 direct sightings (Ezcurra, Aguer and Geringelli pers. com., 2013). Burrows or sightings near camera trap stations where we photographed the species were grouped as single independent records. Considering burrows, sightings and camera trap photos all together, we identified 18 independent records of giant armadillo presence in La Fidelidad (not necessarily representing 18 different individuals) (Fig. 2). All but one record was in the central portion of the Reserve.

In the study area (UTC-3), and during the study period, sunrise ranged between 06:52 and 07:46 and sunset between 18:21 and 19:43 h (**Fig. 4**). Giant armadillo activity in La Fidelidad was strongly nocturnal. The estimated daily activity period (95% kernel) was 14.3 hours (95% CI = 9.7-15.6), lasting roughly from 18:00 h to 08:00 h, that is, from sunrise to sunset. The core activity period (50% kernel) was 4.5 hours (95% CI = 3.2-6.2) between 02:00 and 06:00 h (**Fig. 4**). The only camera

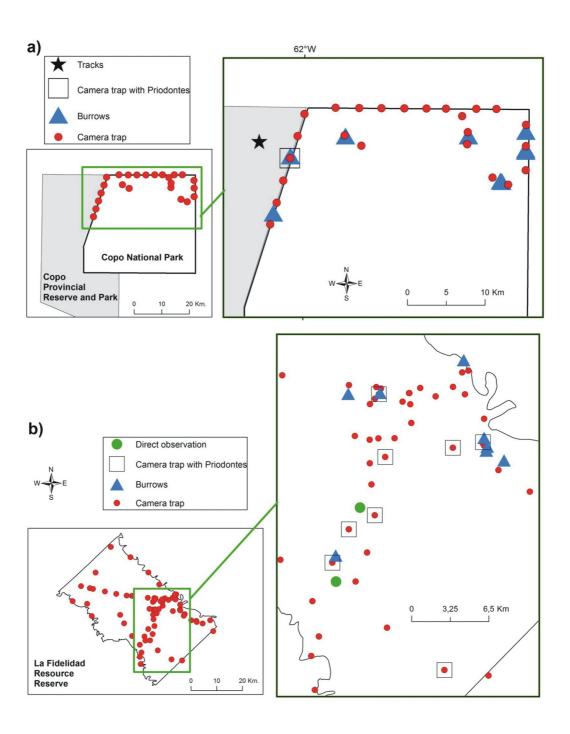


Fig. 2: Location of camera traps in Copo National Park and La Fidelidad Resource Reserve, and the detail of the area in each site where we obtained records of present points (camera trap photos, burrows, tracks and direct observations). a) Copo National Park; b) La Fidelidad Resource Reserve.

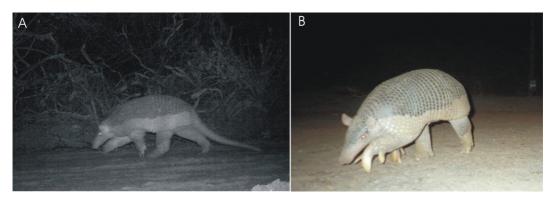


Fig. 3: Camera trap photographs of giant armadillos (*Priodontes maximus*) from surveys in the Argentine Chaco. A) La Fidelidad Resource Reserve, Chaco province, year 2013; B) Copo National Park, Santiago del Estero province, year 2009.

trap record from Copo National Park was also during this period (03:48 h).

# **Anecdotal Information**

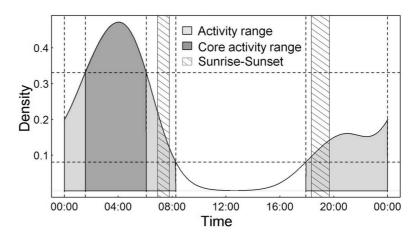
The compilation of anecdotal information from informal interviews provided qualitative information on giant armadillo presence in the area and on conservation challenges. Both in Luján and in El Cantor, local inhabitants asserted that the species has been absent in the area for twenty or thirty years. In the Aborigen Reserve, Copo National Park and La Fidelidad, interviewees confirmed the species' presence, and attributed the lack of direct sightings to its nocturnal and fossorial habits. Park guards did report 2 sightings (in 2004 and in 2015) of giant armadillos in Loro Hablador Provincial Park, 20 km north of Copo National Park. In general,

local residents indicated that giant armadillo meat does not taste good, so it is rarely hunted for food in the Argentine semi-arid Chaco. However, they noted that giant armadillos are highly valued as pets or as hunting trophies. Another threat for the species is the presence of dogs in the forest, near the ranches, because they attack giant armadillos when encountered.

#### DISCUSSION

Of 5 locations surveyed systematically with camera traps, we registered multiple records of giant armadillo only in the central portion of La Fidelidad Resource Reserve, the site with the least human disturbance. As in other locations across its range where the species faces human disturbance (Aguiar and Da Fonseca,

Fig. 4: Kernel density estimates for temporal activity range (kernel 95%) and the core activity range (kernel 50%) for giant armadillos in the Argentine Chaco. The activity range extends from roughly 18:00 h to 08:00 h the following day, and the core activity range from 02:00 to 06:00 h approximately.



2008; Vynne et al., 2009; Nuñez-Regueiro et al., 2015), giant armadillos in the Argentine Chaco are absent from areas with higher human population densities and disturbance (hunters, dogs from nearby ranch outposts, cattle, among others), as well as from protected areas that are not effectively managed. Camera trap surveys in Ecuador (Yasuní Biosphere Reserve), where the species is not hunted, found no correlation between giant armadillo presence and distance to settlements or to roads (Espinoza, 2012). Although in Argentina the species is not hunted for food, our results suggest that its current range is severely limited by the level of human disturbance except in effectively-managed protected areas. This is probably due to commercial hunting combined with habitat degradation.

Independent of habitat type, location, and human impacts, camera trap recording rates of giant armadillos across its distributional range are relatively low when compared to other mammal species (e.g., Blake and Mosquera, 2014), suggesting that the species is generally rare or difficult to detect. Comparing camera trap capture rates in the Argentine Chaco with rates from other locations across its range (Table 3), our results from La Fidelidad (0.40)

records/100 camera trap nights) represent an average recording rate for the species, with a mean (and SD) of 0.27 (0.24, N = 34 sites) photographic records/100 camera trap nights (estimated from Table 3, which excludes sites with no records). The capture rate at Copo National Park (0.10 camera trap records/100 nights) was lower than the mean value of other sites, but several other sites have recording rates as low or lower than this study site (Table 3). The relatively numerous records for giant armadillos at La Fidelidad contrast sharply with the scarce records (or lack of records) from other locations surveyed, suggesting that La Fidelidad may protect one of the few relict populations of giant armadillos in the Argentine Chaco. Copo National Park, on the other hand, despite its lower camera trap capture rate, is also important as a location for giant armadillo conservation, because the frequent observations of active burrows suggests that a population persists in this protected area.

The nocturnal activity pattern that we observed is similar to that reported from other locations across the species' distribution (Anacleto, 1997; Noss et al., 2004). It is likely that, in contrast to other Xenarthra (Cuellar, 2008;

Table 3
Capture rates for giant armadillos (records/100 camera days) at locations across South America.

Locality	Trap days	Events/100 trap days	Reference
Copo National Park, Argentine Chaco	1204	0.1	This paper
La Fidelidad Reserve, Argentine Chaco	3498	0.4	This paper
Ecological Ranch, Brazilian Pantanal	504	0.8	Trolle and Kéry, 2005
Santa Emilia Ranch, Brazilian Pantanal	450	0.2	Trolle, 2003
Serro do Amolar, Brazilian Pantanal	550	0.4	De Oliveira Porfirio et al. 2012
Humaitá Forest Reserve, Brazilian Amazon	850	0.2	Botelho et al., 2012.
Caixuanã National Forest, Brazilian Amazon	2838	0.1	Da Souza Martins et al. 2007
Emmas National Park, Brazilian Cerrado	9051	0.7	Silveira et al., 2009
Río Araguaia, Brazilian Cerrado	624	0.3	Zimbres et al., 2013
Municipio de Aruana, Brazilian Cerrado	2797	0.1	Zimbres et al., 2013
Emmas National Park, Brazilian Cerrado	8112	0.9	Zimbres et al., 2013
Areas around Emmas National Park, Brazilian Cerrado	1726	0.2	Zimbres et al., 2013

(Table 3 cont.)

Locality	Trap days	Events / 100 trap days	Reference
Emas-Taquari Ecological Corridor, Brazilian Cerrado	1926	0.1	Zimbres et al., 2013
Cocos Municipality, Brazilian Cerrado	681	0.2	Zimbres et al., 2013
Cantão State Park and surroundings, Brazilian Cerrado	10170	0.2	Zimbres et al., 2013
Rio Doce State Park, Brazilian Atlantic Forest	4200	0.1	Srbek-Araujo et al., 2009
Sooretama Biological Reserve and Vale Natural Reserve, Brazilian Atlantic Forest	6914	0.01	Srbek-Araujo et al., 2009
Madidi NP and Pilon Lajas Reserve, Bolivian Amazon	2450	0.04	Ayala and Viscarra, 2009a
Madidi NP, Bolivian Amazon	650	0.2	Ayala et al., 2009
Madidi NP, Bolivian Amazon and Bahuaja-Sonene NP, Peruvian Amazon	1525	0.1	Ayala, 2007
Madidi NP, Bolivian Amazon	830	0.1	Ayala, 2004
Madidi NP, Bolivian Amazon	1914	0.1	Ayala, 2002
Estación Isoso, Bolivian Chaco	2500	0.1	Romero Muñoz et al., 2007
Tucavaca, Bolivian Chaco	6924	0.4	Noss et al., 2004
Ravelo, Bolivian Chaco	3480	0.03	Noss et al., 2004
San Miguelito, Bolivian Chiquitano Forest	1695	0.2	Noss et al., 2004
San Miguelito, Bolivian Chiquitano Forest	1502	0.7	Arispe et al., 2005
Ángel Sandoval Forest Concession, Bolivian Chiquitano Forest	2192	0.05	Venegas et al. 2009
Cuyabeno Fauna Reserve, Ecuadorian Amazon	1656	0.3	Araguillín et al., 2010a
Tiputini Reserve, Ecuadorian Amazon	13400	0.4	Blake et al., 2012
Yasuní National Park, Ecuadorian Amazon	2015	0.7	Araguillín et al., 2010b
Yasuní National Park, Ecuadorian Amazon	1015	0.20	Blake and Mosquera, 2014
Bahuajua-Sonene NP and Tambopata Reserve, Peruvian Amazon	2950	0.1	Ayala and Viscarra, 2009b
Los Amigos Reserve, Peruvian Amazon	3780	0.3	Tobler et al., 2008

Di Blanco et al., 2017), giant armadillos may be less flexible in their daily activity pattern, remaining almost strictly nocturnal across their entire range. This lack of flexibility could be an important limitation for species that live in a region like the semi-arid Chaco with extreme hot and cold temperatures. In contrast, giant anteaters in northern Argentina are cathemeral in habits, but with seasonal shifts in daily activity patterns to avoid winter and summer extreme temperatures (Di Blanco et al., 2017). While giant armadillos lack this seasonal flexibility, the use of burrows may represent a buffer mechanism against extreme temperatures (Da Fonseca and Aguiar, 2004), as described for other species (McNab, 1980; Montaño et al., 2013). The giant armadillo may remain several days inside its burrow, where it can obtain

subterranean foods (Carter and Encarnação, 1983); thus, feeding is in part fossorial. These abilities allow the giant armadillo to avoid lethal hot or cold temperatures, to restrict its activity outside burrows to time periods that imply the lowest energy requirements, and/or to minimize risk from hunters, dogs and their natural predators.

Recent studies have demonstrated that the giant armadillo is a key component of the ecosystems it inhabits, acting as an ecosystem engineer through excavating its large burrows (Leite Pitman, 2004; Desbiez and Kluiber, 2013). Many other wildlife species use these burrows for shelter, while others feed on items in the excavated earth (Desbiez and Kluiber, 2013; Noss et al., 2013; Quiroga pers. obs.). This role as an ecosystem engineer, combined with the animal's beauty and unique characteristics, make the giant armadillo a keystone and flagship species around which conservation and management programs for the Chaco forest can be focused (Desbiez and Kluiber, 2013). Our results suggest that the population status of the giant armadillo in the Argentine semi-arid Chaco is worrisome. In this context the recent upgrading of La Fidelidad into El Impenetrable National Park, assuming the new national protected area is effectively managed and protected, will be essential for the conservation of the giant armadillo in Argentina and in the southern limits of its geographical range.

# **ACKNOWLEDGMENTS**

We thank the volunteers and field technicians, the provincial and national park guards, Gabriel Boaglio, Lucas Damer and all the personnel of La Fidelidad base camp, for their valuable collaboration in field surveys and data collection. We thank the Ministerio de Producción y Ambiente de Formosa, the Dirección de Fauna, Parques y Ecología de Chaco, Parque Nacional Copo, the Administración de Parques Nacionales (APN), the Universidad Nacional de Córdoba (UNC) and the Direccion Nacional de Fauna for permits and/or logistical support. We thank the Dirección de Fauna Parques y Ecología de Chaco, the Conservation Land Trust (CLT), CONICET, the Jaguar Conservation Program-WCS, the Rufford Small Grants Foundation, the Cleveland Metroparks Zoo and the Cleveland Zoological Society, the Mohamed bin Zayed Species Conservation Fund, Idea Wild, and Stephen F. Austin State University for financial and logistical support.

# LITERATURE CITED

- ABBA AM, MF TOGNELLI, VP SEITZ, J B BENDER and SF VIZCAÍNO. 2012. Distribution of extant xenarthrans (Mammalia: Xenarthra) in Argentina using species distribution models. Mammalia 76:123-136.
- AGOSTINELLI C and U LUND. 2013. R package 'circular': Circular Statistics (version 0.4-7). https://r-forge.rproject.org/projects/circular/.
- AGUIAR JM and GAB DA FONSECA. 2008. Conservation status of the Xenarthra. Pp. 215-231, in: The biology of the Xenarthra (SF Vizcaino and WJ Loughry, eds.). Gainesville: University of Florida Press.
- ALTRICHTER M. 2006. Wildlife in the life of local people of the semiarid Argentine Chaco. Biodiversity Conservation 15:2719-2736.
- ANACLETO TC 1997. Dieta e utilização de hábitat do tatu-canastra numa área de cerrado do Brasil Central. Teses de Mestrado, Univ. de Brasilia, Brasilia.
- ANACLETO TC, F MIRANDA, I MEDRI, E CUELLAR, AM ABBA and M SUPERINA. 2014. *Priodontes maximus*. The IUCN Red List of Threatened Species 2014: e.T18144A47442343. http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS. T18144A47442343.en. Revisado el 18 de Noviembre de 2015.
- ARAGUILLIN E, C URGILES and A NOSS. 2010a. Muestreo con trampas fotográficas de mamíferos medianos y grandes en la comunidad Cofán Zábalo (Reserva de Producción Faunística Cuyabeno). Technical Report #15. Quito, Ecuador: WCS, ICCA.
- ARAGUILLIN E, G ZAPATA-RIOS, V UTRERA and A NOSS. 2010b. Muestreo con trampas fotográficas de mamíferos medianos, grandes y de aves en el Bloque Ishpingo Tambococha Tiputini (ITT), sector Varadero (Parque Nacional Yasuní). Technical Report #9. Quito, Ecuador: WCS.
- ARISPE, R, D RUMIZ and C VENEGAS. 2005. Second camera-trap survey for jaguars (*Panthera onca*) and other mammals at San Miguelito Ranch. Technical Report. Santa Cruz, Bolivia: Wildlife Conservation Society.
- ARTEAGA MC and EM VENTICINQUE. 2010. Cuevas de armadillos (Cingulata: Dasypodidae) en la Amazonía central: ¿son útiles para identificar especies? Edentata 11(1):29-33.
- ARTEAGA MC and EM VENTICINQUE. 2007. Influence of topography on the location and density of armadillo burrows (Dasypodidae: Xenarthra) in the central Amazon, Brazil. Mammalian Biology 73(4):262-266.
- AYALA G. 2002. Uso de trampas cámaras para estimar densidad de jaguar y la diversidad de mamíferos en el valle bajo de los ríos Tuichi y Hondo. La Paz, Bolivia: WCS.
- AYALA G. 2004. Uso de trampas cámaras para estimar densidad de jaguar y la diversidad de mamíferos en Alto Madidi. La Paz, Bolivia: WCS.
- AYALA G. 2007. Estimando la densidad de jaguar y la abundancia relativa de mamíferos medianos y grandes en el río Heath, Parque Nacional Madidi, Bolivia y Parque Nacional Bahuaja-Sonene, Perú. La Paz, Bolivia: WCS.

- AYALA G and M VISCARRA S. 2009a. Estimando la densidad de jaguar y la abundancia relativa de mamíferos medianos y grandes en el Parque Nacional Madidi y la Reserva Pilón Lajas, Bolivia. La Paz, Bolivia: WCS.
- AYALA G and MS VISCARRA. 2009b. Estimando la densidad de jaguar y la abundancia relativa de mamíferos medianos y grandes en el Parque Nacional Bahuahua-Sonene y la Reserva Nacional Tambopata, Perú. La Paz, Bolivia: WCS.
- AYALA G, M VISCARRA, J MARTINEZ, F ZENTENO, S BARRERA and M MENDOZA. 2009. Investigaciones de biodiversidad en las Pampas del Madidi, Norte de La Paz, Bolivia. La Paz, Bolivia: WCS.
- BAXENDALI CA and GD BUZAI. 2009. Caracterización socio-espacial del Chaco argentino. Pp. 3-50, en: El Chaco sin bosques: la Pampa o el desierto del futuro (JH Morello y AF Rodríguez, eds.). Orientación gráfica editora, Buenos Aires.
- BIVAND R and N LEWIN-KOH. 2015. maptools: Tools for reading and handling spatial objects. R package version 0.8-34. http://CRAN.R-project. org/package=maptools.
- BLAKE JG, D MOSQUERA, BA LOISELLE, K SWING, J GUERRA and D ROMO. 2012. Temporal activity patterns of terrestrial mammals in lowland rainforest of eastern Ecuador. Ecotropica 18:137-146.
- BLAKE JG and D MOSQUERA. 2014. Camera trapping on and off trails in lowland forest of eastern Ecuador: Does location matter? Mastozoología Neotropical 21(1):17-26.
- BOTELHO ALM, AM CALOURO, LHM BORGES and W CHAVES. 2012. Large and medium-sized mammals of the Humaitá Forest Reserve, southwestern Amazonia, state of Acre, Brazil. Check List 8(6):1190-1195.
- CARTER TS. 1985. Armadillos of Brazil. National Geographic Society Research Reports 1979. 20:101-7.
- CARTER TS and CD ENCARNAÇAO. 1983. Characteristics and use of burrows by four species of armadillos in Brazil. Journal of Mammalogy 64(1):103-108.
- CAZIANI S, CE TRUCCO, PG PEROVIC, A TALAMO, EJ DERLINDATI, J ADÁMOLI, F LOBO, M FABREZI, M SRUR, VA QUIROGA and MI MARTINEZ OLIVER. 2003. Línea de Base y Programa de Monitoreo de Biodiversidad del Parque Nacional Copo. Proyecto de Conservación de la Biodiversidad-BIRF/GEF TF 028372-AR, Administración de Parques Nacionales, Argentina. 235 pp.
- CERESOLI N and E FERNANDEZ-DUQUE. 2012. Size and orientation of giant armadillo burrow entrances (*Priodontes maximus*) in western Formosa province, Argentina. Edentata 13:66-68.
- CUÉLLAR E. 2008. Biology and ecology of armadillos in the Bolivian Chaco. Pp. 306-312, in: The biology of the Xenarthra (SF Vizcaino and WJ Loughry, eds.). Gainesville: University of Florida Press.
- DA FONSECA GAB and JM AGUIAR. 2004. The 2004 Edentate species assessment workshop. Edentata 6:1-26.
- DA SOUZA MARTINS S, JG ANDERSON and J DE SOUZA E SILVA JUNIOR. 2007. Monitoring mammals in the Caxiuana National Forest, Brazil First results

- from the Tropical Ecology, Assessment and Monitoring (TEAM) program. Biodiversity and Conservation 16:857–870.
- DE OLIVEIRA PORFIRIO GE, P SARMENTO, NLX FILHO, SP DA SILVA LEAL, VF MOREIRA, FA RABELO, J CRUZ and C FONSECA. 2012. New records of giant armadillo *Priodontes maximus* (Cingulata: Dasypodidae) at Serra do Amolar, Pantanal of Brazil. Edentata 13:72-75.
- DESBIEZ ALJ and D KLUYBER. 2013. The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. Biotropica 45(5):537-540.
- DI BLANCO YE, KS SPØRRING and MS DI BITETTI. 2017. Time activity patterns of reintroduced giant anteaters (*Myrmecophaga tridactyla*): effects of extrinsic and intrinsic factors. Mammalia 81(1):11-21.
- ESPINOSA-ANDRADE SR. 2012. Road development, bush meat extraction and jaguar conservation in Yasuni Biosphere Reserve Ecuador. Thesis for Doctor of Philosophy presented to the University of Florida. 153 pp.
- LEITE PITMAN R. 2004. Habitat use and activity of the giant armadillo (*Priodontes maximus*): preliminary data from Southeastern Peru. 2004 Annual Meeting of the Society for Conservation Biology in New York.
- MCNAB BK. 1980. Energetics and the limits to a temperate distribution in armadillos. Journal of Mammalogy 61:606-627
- MERITT JR DA. 2008. Xenarthrans of the Paraguayan Chaco. Pp. 294-299, in: The biology of the Xenarthra. (SF Vizcaino and WJ Loughry, eds.). Gainesville: University of Florida Press.
- MONTAÑO RR, RL CUELLAR, LA FITZGERALD, F MEDOZA, F SORIA, CV FIORELLO, SL DEEM and A NOSS. 2013. Activity and ranging behavior of the red tegu lizard *Tupinambis rufescens* in the Bolivian Chaco. South American Journal of Herpetology 8(2):81-88.
- MORELLO J y J ADÁMOLI. 1974. Las grandes unidades de vegetación y ambiente del Chaco argentino. Segunda Parte: Vegetación y ambiente de la Provincia del Chaco. INTA Serie Fitogeográfica 13.
- MORELLO JH, AF RODRÍGUEZ y M SILVA. 2009. Clasificación de ambientes en áreas protegidas de las ecorregiones del Chaco húmedo y Chaco seco. Pp. 53-89, en: El Chaco sin bosques: la Pampa o el desierto del futuro (JH Morello y AF Rodríguez, eds.). Orientación Gráfica Editora, Buenos Aires.
- NOSS AJ, R PEÑA and DI RUMIZ. 2004. Camera trapping *Priodontes maximus* in the dry forests of Santa Cruz, Bolivia. Endangered Species update 2(21):43-52.
- NOSS AJ, RR MONTAÑO, F SORIA, SL DEEM, CV FIORELLO and LA FITZGERALD. 2013. *Chelonoidis carbonaria* (Testudines: Testudinidae) activity patterns and burrow use in the Bolivian Chaco. South American Journal of Herpetology 8(1):19-28.
- NOWAK RM. 1991. Walker's Mammals of the World, 5 ed. Johns Hopkins Univ. Press. Baltimore, 1629 pp.
- NÚÑEZ-REGUEIRO MM, L BRANCH, RJ FLETCHER JR, GA MARÁS, E DERLINDATI and A TÁLAMO. 2015. Spatial patterns of mammal occurrence in forest strips surrounded by agricultural crops of the Chaco region, Argentina. Biological Conservation 187:1926.

- OLIVEIRA-SANTOS LGR, CA ZUCCO and CAGOSTINELLI. 2013. Using conditional circular kernel density functions to test hypotheses on animal circadian activity. Animal Behaviour 85:269-280.
- PERES CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian Forest vertebrates. Conservation Biology 15(6):1490-1505.
- PORINI G. 2001. Tatú carreta (*Priodontes maximus*) en Argentina. Edentata 4:9-14.
- PROHASKA R. 1959. El polo de calor de América del Sur. INTA; IDIA 141:27-30.
- QUIROGA VA and GI BOAGLIO. 2006. Informe general del proyecto de evaluación poblacional y monitoreo de mamíferos en el Impenetrable Chaqueño. Dirección de Fauna Silvestre. SAyDS. 26 pp.
- QUIROGA VA and GI BOAGLIO. 2007. Informe general del proyecto de evaluación poblacional y monitoreo de mamíferos en el Impenetrable Chaqueño - Segundo año. Dirección de Fauna Silvestre. SAyDS. 19 pp.
- QUIROGA VA. 2013. Ecología y conservación del yaguareté (*Panthera onca*) y el puma (*Puma concolor*) en el Chaco semiárido argentino: su relación con la disponibilidad de presas y la presencia humana en la región. Tesis Doctoral para la Universidad Nacional de Córdoba. 216 pags.
- QUIROGA VA, GI BOAGLIO, AJ NOSS and M DI BITETTI. 2014. Critical population status of the jaguar in the Argentine Chaco: camera trap surveys suggest recent collapse and imminent regional extinction. Oryx 48(1):141-148.
- R CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.http://www.R-project.org/.
- REDFORD KH. 1994. The edentates of the cerrado. Edentata 1(1):4-10.
- RIDOUT MS and M LINKIE. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological and Environmental Statistics 14:322-337
- ROMERO MUÑOZ A, R PAREDES and L MAFFEI. 2007. Muestreo con trampas cámara de jaguares y otros mamíferos en la Estación Isoso (18°25'W, 61°46'W), Parque Nacional Kaa Iya del Gran Chaco. 7 de Julio-8 de septiembre, 2006. TechnicalReport#172. Santa Cruz, Bolivia: Wildlife Conservation Society.
- SILVEIRA LA, TA JÁCOMO and JAF DINIZ-FILHO. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological Conservation 114:351-355.
- SILVEIRA L, AT DE ALMEIDA JACOMO, MM FURTADO, NM TORRES, R SOLLAMANN and C VYNNE. 2009. Ecology of the giant armadillo (*Priodontes maximus*) in the grasslands of central Brazil. Edentata 8(10):25-34.

- SRBEK-ARAUJO AC, LM SCOSS, A HIRSCH and AG CHIARELLO. 2009. Records of the giant-armadillo *Priodontes maximus* (Cingulata:Dasypodidae) in the Atlantic Forest: are Minas Gerais and Espírito Santo the last strongholds of the species? Zoologia 26(3):461-468.
- SUPERINA M and AM ABBA. 2012. *Priodontes maximus*. In: IUCN 2012. IUCN Red List of Threatened Species.
- TARIFA T. 2009. *Priodontes maximus* (Kerr, 1792): Cingulata-Dasypodidae. Pp. 496-498, en: Libro Rojo de la fauna silvestre de vertebrados de Bolivia (LF Aguirre, R Aguayo, J Balderrama, C Cortéz y T Tarifa, eds.). La Paz, Bolivia: Ministerio de Media Ambiente y Agua.
- TOBLER MW, SE CARRILLO-PERCASTEGUI, R LEITE PITMAN, R MARES and G POWELL. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Animal Conservation 11:169-178.
- TORRES R and JP JAYAT. 2010. Modelos predictivos de distribución para cuatro especies de mamíferos (Cingulata, Artiodactyla y Rodentia). Típicas del chaco en argentina. Mastozoología Neotropical 17(2):335-352.
- TROLLE M. 2003. Mammal survey in the southeastern Pantanal, Brazil. Biodiversity and Conservation 12:823-836.
- TROLLE M and M KERY. 2005. Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. Mammalia 69(3-4):405-412.
- VENEGAS C, R ARISPE, D RUMIZ and K RIVERO. 2009. Censo de jaguares (*Panthera onca*) y otros mamíferos con trampas cámara en las concesiones forestales "Ángel Sandoval" y "San José" del bosque seco chiquitano. Santa Cruz, Bolivia: WCS, FCBC, MHNNKM, FAM.
- VYNNE C, RB MACHADO, J MARINHO-FILHO and SK WASSER. 2009. Scat-detection dogs seek out new locations of *Priodontes maximus* and *Myrmecophaga tridactyla* in central Brazil. Edentata 8-10:13-14.
- VYNNE C, JL KEIM, RB MACHADO, J MARINHO-FILHO, L SILVEIRA, MJ GROOM and SK WASSER. 2011. Resource selection and its implications for wide-ranging mammals of the Brazilian Cerrado. Plos one. 6(12):1-12.
- WILSON DE, FR COLE, JD NICHOLS, R RUDRAM and YM FOSTER. 1996. Measuring and monitoring biological diversity; standard methods for mammals. Smithsonian Institution Press; Washington and London. 409 pp.
- WORTON B. 1989. Kernel methods for estimating utilization distribution in home-range studies. Ecology 70:164-168
- ZIMBRES B, MM FURTADO, ATA JÁCOMO, L SILVEIRA, R SOLLMANN, NM TÔRRES, RB MACHADO and J MARINHO-FILHO. 2013. The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado. Landscape Ecology 28:259-269.