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Composition and Characteristics of a Diverse Didelphid Community (Mammalia: Didelphimorphia) in Sub-tropical South America

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Abstract

Few studies have reported didelphid communities of ≥10 species, and all of these have been from within the tropics *sensu stricto* of South America. Herein a community of 12 species of didelphids is described from a sub-tropical site in south-central South America. The Reserva Natural del Bosque Mbaracayú, in northeastern Paraguay, lies at the western margin of the Interior Atlantic Forest and the southwestern limit of the Cerrado, two important South American ecoregions. The rich didelphid community in this area likely results from the mosaic of habitats encountered at the distributional limits of these two ecoregions. Within the context of this mosaic, the species' habitat associations and vertical occupancy are discussed, as well as the reproductive patterns and population abundance variation of the more commonly encountered species. Three *Monodelphis* species were found in sympatry, all strictly terrestrial, along with *Cryptonanus chacoensis*. *Marmosa paraguayana* shared all habitats with *Gracilinanus agilis*, and both of these species primarily were arboreal. Although this natural reserve has been more extensively sampled than any other area in Paraguay, numerous questions remain unanswered regarding this rich didelphid community.

Key words: Cerrado, *Cryptonanus*, *Didelphis*, *Gracilinanus*, habitat association, Interior Atlantic Forest, *Marmosa*, *Monodelphis*, Paraguay, vertical occupancy

Resumen

Pocos estudios han registrado comunidades de didélfidos de ≥10 especies, y todas ellas han sido de los trópicos *sensu stricto* de América del Sur. Aquí reportamos una comunidad de 12 especies de didélfidos de un sitio subtropical en el centro sur de América del Sur. La Reserva Natural del Bosque Mbaracayú, en el noreste de Paraguay, se encuentra en el margen occidental del Bosque Atlántico Interior, y el límite suroeste del Cerrado, dos ecorregiones sudamericanas importantes. La rica comunidad de didélfidos en esta área es probablemente el resultado del mosaico de hábitats encontrados en los límites de distribución de estas dos ecorregiones. Dentro del contexto de este mosaico, discutimos las asociaciones de hábitats y la ocupación vertical de las especies, los patrones reproductivos y la variación de la abundancia de las poblaciones de las especies más comúnmente encontradas. Encontramos tres especies de *Monodelphis* en simpatría,

y todas estrictamente terrestres, junto con *Cryptonanus chacoensis*. *Marmosa paraguayana* compartió todos sus hábitats con *Gracilinanus agilis*, y ambas especies eran principalmente arbóreas. Enfatizamos que a pesar de que esta reserva natural ha sido muestreada más extensamente que cualquier otra área en Paraguay, muchas preguntas siguen sin respuesta con respecto a esta rica comunidad de didélfidos.

Palabras claves: asociación de hábitat, Bosque Atlántico Interior, Cerrado, *Cryptonanus*, *Didelphis*, *Gracilinanus*, *Marmosa*, *Monodelphis*, ocupación vertical, Paraguay

INTRODUCTION

South America is remarkable for its faunal diversity, which includes two ancient but extant mammalian superorders, Xenarthra (sloths, anteaters and armadillos) and Ameridelphia (New World marsupials) (Simpson 1980; Jansa et al. 2013). Both of these lineages experienced broad and successful radiations in South America before the emergence of the Panama land bridge and ensuing biotic interchange between North and South America. They continue to be important components of Neotropical fauna, with several species of both orders also occurring in Central America and even into temperate North America. In South America, approximately 100 species of marsupials are recognized, with 93 belonging to the Order Didelphimorphia with its single Family, Didelphidae (Gardner 2005, 2007).

Willig and Gannon (1997) evaluated marsupial species density (number of species per equal-area grid unit) in North and South America and found the highest densities in a latitudinal band at 15–20 degrees south latitude. Reports of didelphid species richness from specific South American sites generally reflect this pattern (Table 1, Fig. 1). Paraguay, lying at ca. 19.3–27.5 degrees south latitude, lies mostly within two bands of considerably lower marsupial species density (Willig and Gannon 1997). Nevertheless, the country lies at the nexus of several major ecoregions, and exhibits high mammalian species richness for a relatively small country (de la Sancha et al. 2017). For example, its 406,752 km^2 is only about 2.3% of South America's surface area, but its 18 recognized species of didelphid marsupials (de la Sancha et al. 2017) represent 19.4% of the known South American species.

To our knowledge, nine sites in South America have been reported as having ≥10 didelphid species, and none of these sites lies outside of the Tropics (Table 1). The highest reported species richness is from the Lower Urubamba River (12.0°S, Cusco Region, Perú), with 17 didelphid species (Solari et al. 2001). Other South American sites with ≥10 species lie from 5.3°N (Paracou, French Guiana) to 17.6–23.2°S (Maracaju Mountain Range, Mato Grosso do Sul, Brazil). This report describes the didelphid community within the Reserva Natural del Bosque Mbaracayú (ca. 24.0–24.3°S, in northeastern Paraguay), where 12 species are confirmed. In addition, this report discusses habitat associations and vertical occupancy, body mass, reproductive patterns, microsympatry, and population densities of the more commonly encountered species.

Table 1. Summary of data for Neotropical localities that have ≥ 10 didelphid species.

Latitude	Locality	Division	Country	Number of confirmed didelphid species	Reference
5.3° N	Paracou		French Guiana	12	Voss et al. 2001
4.1° N	Les Nourages		French Guiana	10	Guillemin et al. 2001
4.0° S	Estación Biológica Allpahuayo	Loreto	Perú	13	Hice 2003
6.2° S	Carajás National Forest	Para	Brazil	12	Gettinger et al. 2012
9.6° S	Panguana Biological Station	Ucayali	Perú	10	Hutterer et al. 1995
10.1° S	Balta	Ucayali	Perú	11	Voss and Emmons 1996
11.9° S	Cocha Cashu / Pakitza	Madre de Dios	Perú	12	Voss and Emmons 1996
12.0° S	Lower Urubamba River	Cusco	Perú	17	Solari et al. 2001
17.6–23.2° S	Maracaju Mountains	Mato Grosso do Sul	Brazil	11	Hannibal and Neves-Godoi 2015
24.1° S	Reserva Natural del Bosque Mbaracayú	Canindeyú	Paraguay	12	This report

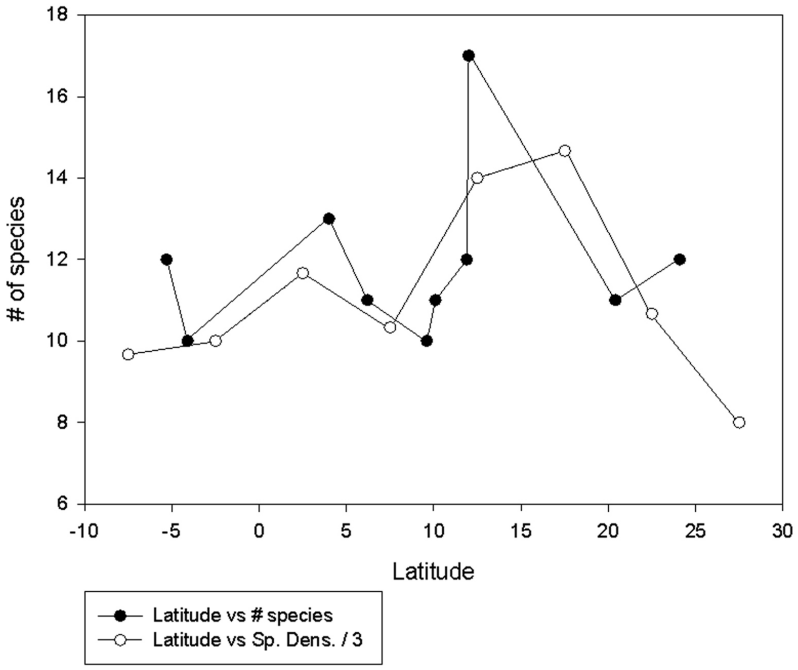

Figure 1. Closed circles indicate the number of verified didelphid species, by latitude, within South American tropics and near-tropics. Open circles indicate didelphid species densities by mid-point of latitudinal band. Species densities were taken from Willig and Gannon 1997 (Fig. 2) and divided by 3.0 to facilitate graphic visualization. See Table 1 for localities and references for didelphid species richness reports.

MATERIALS AND METHODS

Study site.—The Reserva Natural del Bosque Mbaracayú (RNBM) encompasses ca. 65,000 ha in Canindeyú Department, Paraguay (Fig. 2). The Reserve is located near the western margin of the Interior Atlantic Forest and near the southwestern extent of the Cerrado, both of which are extensive ecoregions lying primarily within Brazil and extending into eastern Paraguay (Olson et al. 2001). Most of the vegetation of the RNBM is mature forest, some of which was selectively logged in the past, but undisturbed for at least the last 35 years. In addition, an isolated patch of Cerrado (ca. 6,000 ha) is located in the eastern portion of the reserve. Elevation in the reserve ranges from 175 to 460 m, including an escarpment of the Cordillera de Mbaracayú at the northeastern edge of the reserve. This cordillera is a southern extension of the Maracaju Mountain Range, a north-south range of low mountains in Mato Grosso do Sul, Brazil. This range constitutes the divide between the Paraná and Paraguay river watersheds, to the east and west respectively.

Annual rainfall in the region averages around 1,650 mm. Historically, annual weather cycles include a hot rainy season from November to February, another less pronounced wet season in April, and a less rainy period in the cooler months of May–October, although rains may occur at any time of the year (Owen et al. 2010). A detailed digital map depicts 10 types of vegetation cover within the RNBM (Fig. 2). Information on the data and development of this map is provided in Naidoo and Hill (2006) and Peña-Chocarro et al. (2010), and the habitats are described in Table 2.

Field methods and data.—An extensive survey and inventory of Paraguayan small mammals by crews from Texas Tech University, and a long-term project on ecology and zoonoses of small mammals in the RNBM by personnel from Texas Tech University and the University of Tennessee Health Sciences Center, have included multi-year sampling of small mammals in the RNBM. This has included both collecting and mark-recapture sampling, and has been conducted in various areas within and around the reserve during the years 1995–96, 2001–08, and 2014–17. In total, the resulting database includes approximately 7,780 capture records of small mammals from the RNBM, and verifies a high diversity both of sigmodontine rodents and small didelphid marsupials (Barreto Cáceres 2017; Eastwood et al. 2018). In particular, two mark-recapture sampling studies provided much of the data summarized in this report. A two-year study described in detail in Owen (2013) included 12 sampling sessions on two grids in the Cerrado portion of the RNBM during 2001–2003, and another study was conducted on six sampling grids in the forest habitats of the RNBM, which were sampled six times between July 2015 and February 2017. Each of the six grids included 144 traps stations (12 x 12) placed 10 m apart. Each station included three standard Sherman traps—two placed on the ground and one located in branches or vines, 2–3 m above ground. Table 3 provides the location and a brief description of the vegetation for these six grids.

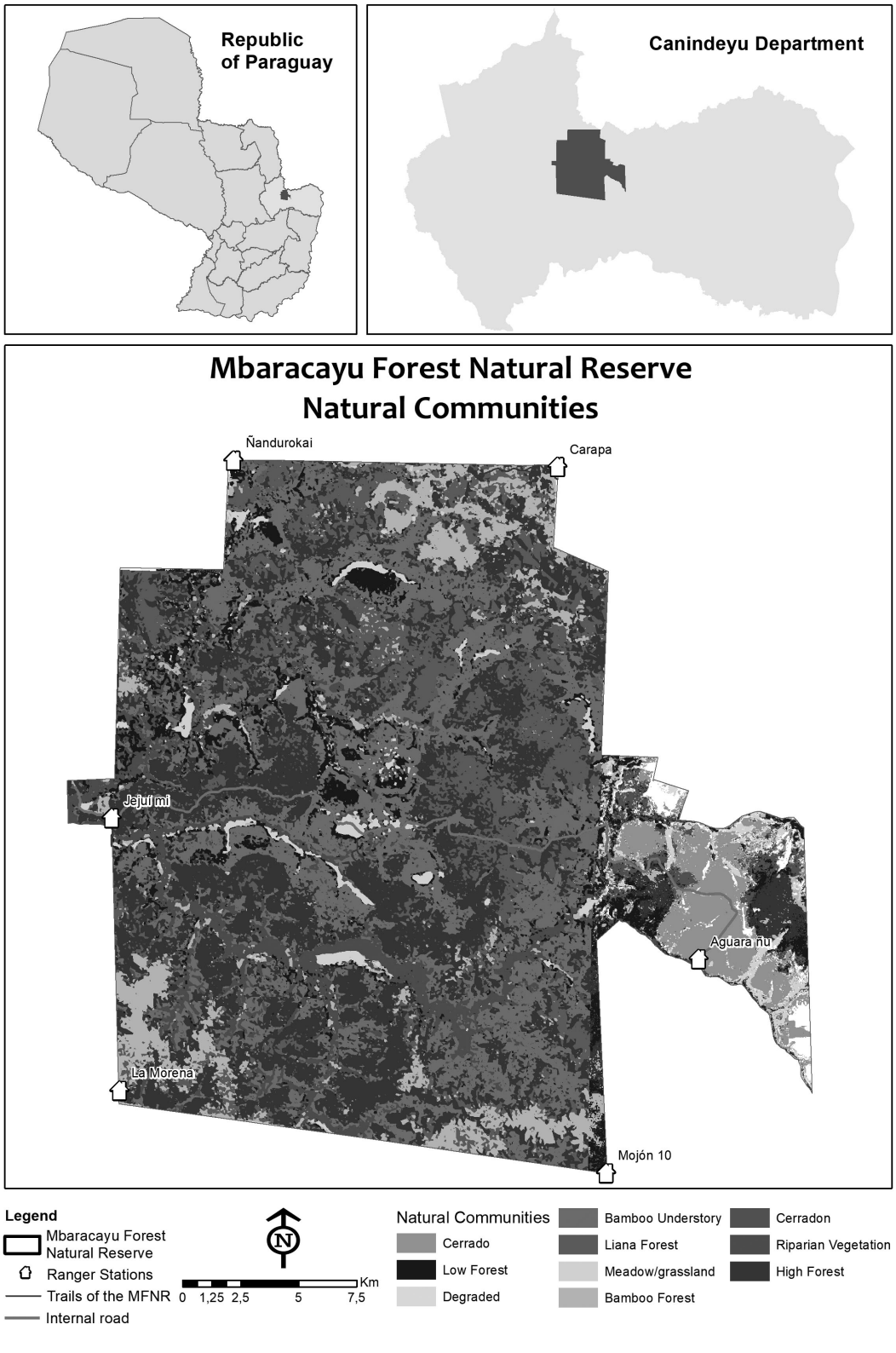

Figure 2. Location of Reserva Natural del Bosque Mbaracayú within Paraguay and habitat types within the Reserva Natural del Bosque Mbaracayú.

Table 2. Ten habitat types encountered in the Reserva Natural del Bosque Mbaracayú, Canindeyú Department, northeastern Paraguay. Habitat designations are based on Naidoo and Hill (2006) and Peña-Chocarro (2010).

Acronym	Habitat type	Habitat description
BF	Big Bamboo Forest	Few trees and a predominance of *Guadua angustifolia* bamboo that can reach 10–15 m in height.
BU	Bamboo Understory	Canopy trees 15–25 m in height, and with a thick undergrowth of *Merostachys clausseni* bamboo, which grows 1–3 m in height.
CE	Cerrado	Wide range of open woodland, open scrub and grassland forms, with grasses, palms, and legumes.
CN	Cerradon	Woody formation of variable tree density, reaching 15 m in height. Tree species are characterized by cork-like bark, enabling them to tolerate fire.
DH	Degraded Habitat	Partially or completely deforested areas with an open upper canopy, now in secondary succession, favoring the appearance of invasive species such as *Brachiaria brizantha* or *Ricinus communi*. Species of the families Lauraceae and Myrtaceae predominate.
HF	High Forest	Dominated by trees reaching heights of 25 m or greater; ground cover is sparse, and composed of ferns, heliconias, and bromeliads.
LF	Low Forest	Most trees less than 15 m high, and less than 10 cm in diameter at breast height, with ground cover dominated by bromeliads.
LiF	Liana (Vine) Forest	Medium to high forests with an abundance of lianas in the understory.
MG	Meadow (Grassland)	Few trees and a predominance of grassy vegetation. They are usually wet for at least part of the year.
RV	Riverine Forest	Locational, reflects proximity to a geographical feature, rather than a unique vegetation community.

Table 3. Description of vegetative components of six mark-recapture grids, sampled six times between July 2015 and February 2017. Each grid included 144 traps stations (12 x 12), with trap stations placed 10 m apart. Each station included three standard Sherman traps—two placed on the ground and one located in branches or vines, 2–3 m above ground. Coordinates (latitude and longitude) indicate the center of each grid.

Grids	Disturbance	Description and location
B, H	Low	The densest forest formation, associated with large trees of average height of approximately 15 meters. Tree-falls leave visible clearings, with rapid colonization of lianas covering the grasses and shrubs. Undergrowth mainly dominated by Poaceae and ferns in the most humid areas, and a very low percentage of bare soil. Grid B, -24.1412, -55.3664; Grid H, -24.1212, -55.4651.
A, D	Medium	Characterized by fairly homogeneous vegetation formation. Trees do not exceed 20 meters in height and average 10–12 meters in height. Soil is rather poor in organic matter, with *Citrus aurantium* (an invasive exotic species) distributed in several points of the plots. Undergrowth characterized by the predominance of grasses in more than 80% of the seasons, at times precluding the growth of other species. Grid A, -24.1239, -55.5048; Grid D, -24.1314, -55.4326.
C, G	High	Vegetative conformation visibly altered by the action of past and present adjacent communities, presenting few large trees. The most frequent species forming part of the lower layer is *Citrus aurantium*. Forest floor characterized by a large percentage of herbaceous plants, and in most of the seasons a high percentage of bare soil is observed. The undergrowth is quite homogeneous and presents high moisture content in many parts of the plots. Grid C, -24.1316, -55.5020; Grid G, -24.1306, -55.5369.

RESULTS

The presence of 12 didelphid species was verified in the RNBM or its immediate proximity (within 5 km) (Table 4). Supplemental file Table S1 (available as a PDF file at http://www.faunaparaguay.com/didmbaracayu.pdf) includes all capture records of didelphids resulting from sampling in the reserve, plus five specimens in the Museo Nacional de Historia Natural del Paraguay (MNHNP, San Lorenzo, Paraguay), one in the mammal collection of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Asunción, one in the Instituto de Bioecología e Investigaciones Subtropicales (IBIS—Pilar, Paraguay), and one photographic record of an individual captured and released (Vazquez and Ramírez Pinto 2014, p. 23; M. Velazquez pers. com.).

Species accumulation.—The first didelphids were recorded from the RNBM in 1988 (Table S1; Fig. 3), and no new species have been encountered since 2013. Three additional species which eventually may be encountered in the RNBM are *Marmosa constantiae, Philander quica*, and *Thylamys macrurus* (Gardner 2007; Voss et al. 2018). De la Sancha Saenz (2010) reported *Gracilinanus microtarsus* from the reserve, but this presumably was in error, as it is not included in a recently published list of Paraguayan mammals (de la Sancha et al. 2017).

Habitat associations and vertical occupancy.—Of the 204 capture records for which habitat association data are available, the number of habitats occupied by

Table 4. Listing of 12 species of Didelphidae verified by voucher specimens (11 species) or photographs (one species) to occur in or within 5 km of the RNBM. Habitat associations based on 204 captures for which precise locality data enables specific habitat designation. For each species the number of records is given, followed by the number of records with a voucher specimen. Species are ordered by number of habitats occupied; habitats are ordered by number of didelphid species recorded there. For three species (*Chironectes minimus*, *Didelphis albiventris*, *Lutreolina crassicaudata*) no record has precise locality information, and thus no habitat association can be specified. Trap height indicates the number of capture records recorded at ground level, followed by the number of above-ground captures (traps on branches or vines). Trap height data were available for several specimens without habitat information. No information (NI) on trap height is available for *Caluromys lanatus*, *Didelphis albiventris*, or *Lutreolina crassicaudata*. See Table 2 for habitat acronyms and descriptions.

Species	Records / Specimens	Trap height	HF	LiF	MG	BF	BU	RV	CE	DH	CN	LF	Totals
Monodelphis domestica	64/50	32/0	X	X	X	X	X	X	X	X	X		9
Gracilinanus agilis	107/38	4/98	X	X	X	X	X	X					6
Cryptonanus chacoensis	5/4	4/0	X		X			X		X			4
Marmosa paraguayana	9/6	1/10	X	X	X		X						4
Metachirus nudicaudatus	3/2	1/0		X	X	X							3
Monodelphis dimidiata	5/4	3/0		X	X	X							3
Monodelphis kunsi	5/5	3/0	X	X					X				3
Didelphis aurita	5/1	1/0	X				X						2
Caluromys lanatus	1/0	NI	X										1
Chironectes minimus	1/1	1/0											1
Didelphis albiventris	1/0	NI											1
Lutreolina crassicaudata	1/0	NI											1
Totals	207/111		7	6	6	4	4	3	2	2	1	0	

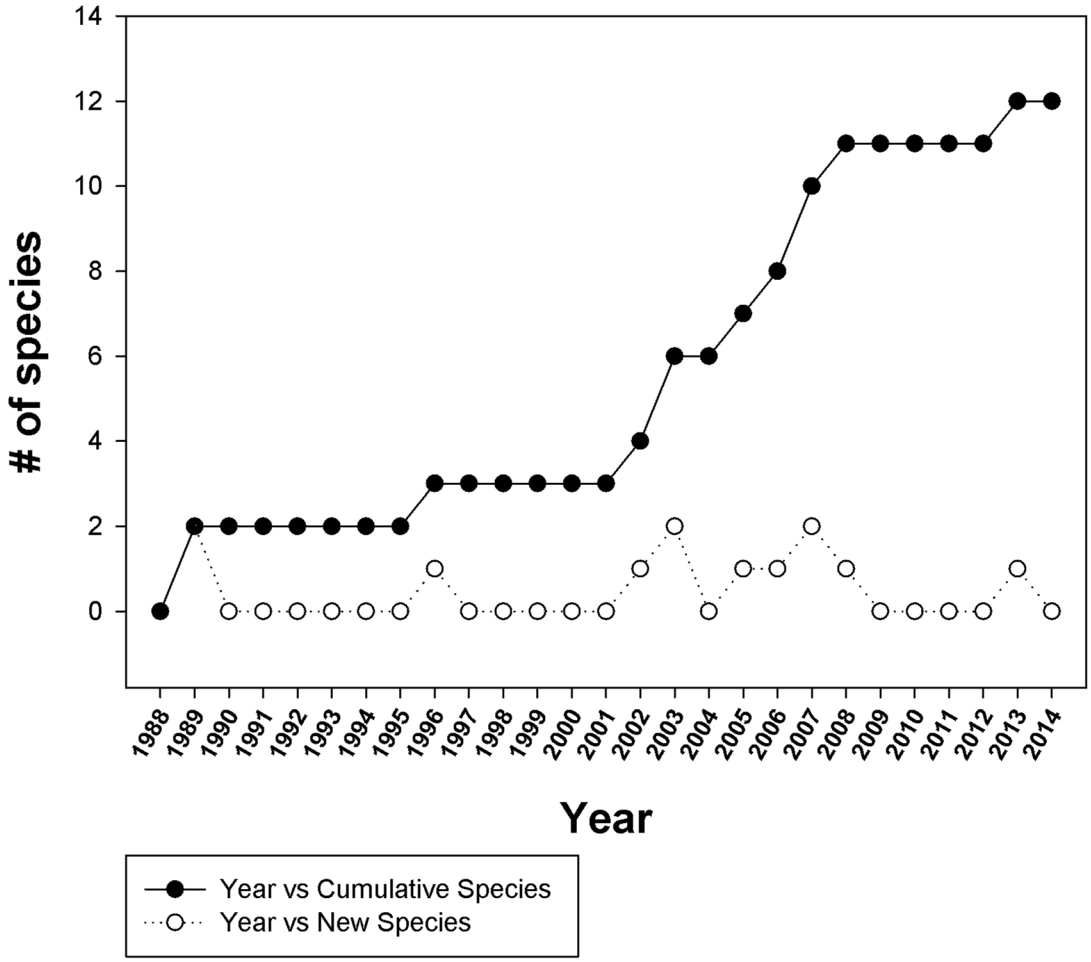

Figure 3. New didelphid species records for the RNBM by year. Open circles indicate the number of new species recorded each year; closed circles indicate cumulative species totals.

the species encountered ranged from nine (*Monodelphis domestica*, which was encountered in all habitats except Low Forest) to one (*Caluromys lanatus*, found only in High Forest) (Table 4). The habitat with the highest number of species was High Forest, with seven of the nine species for which habitat was known; whereas Cerradón had only one species (*M. domestica*), and no species were recorded for Low Forest. However, neither Cerradón nor Low Forest have been sampled extensively in the RNBM.

The three *Monodelphis* species and *Cryptonanus chacoensis* were all captured exclusively on the ground (including pitfall traps) (Table 4). *Gracilinanus agilis* and *Marmosa paraguayana* were captured primarily (but not exclusively) in above-ground traps (branches and vines). *Chironectes minimus, Didelphis aurita,* and *Metachirus nudicaudatus* also were captured only at ground level or in the water. However, there is only one capture record for each of these species, and the records are considered insufficient to comment on their vertical occupancy. No information on capture height is available for *Caluromys lanatus*, *D. albiventris*, or *Lutreolina crassicaudata*.

Body mass.—Extant didelphid species are considered to be "small mammals", and in fact they rarely weigh more than 1 kg. Nevertheless the range of body mass spans two orders of magnitude. In the RNBM, mean adult mass ranges from 8.8 gm (*M. kunsi*) to 640 gm (*D. albiventris*), with extremes of 8.5 gm (*M. kunsi*) to 1,000 gm (*D. aurita*, recorded as 1 kg by the

collector). Table 5 lists mean, minimum, and maximum for standard external measurements and body mass for each species, sex, and age class, where the information is available.

Reproductive patterns.—Reproductive status was not recorded consistently during the field sampling reported in this study, which encompassed more than 20 years (1995–2017). Information is available regarding six of the species present in the RNBM. Table 6 lists months in which juveniles and subadults, as well as female reproductive activity (open vagina, pregnant or lactating) were observed. Because many of these captures were in mark-recapture sampling, these data are often based on external features observable in the live animal.

Gracilinanus agilis was the species most frequently captured (107 captures recorded). Juveniles or subadults were recorded from five months of the year, in both the rainy season (November, December, and February) and the dry season (June and July). An adult female with vagina open was noted in February, and a pregnant female (seven embryos, 21 x 15 mm) was encountered in August. Both male and female adults were captured in both the warm rainy season (October–February) and the cooler dry season (May–July).

A subadult female *Monodelphis dimidiata* (mass = 40 gm) was captured in July. All other captures of this species were in November, and were males (two listed as adults [mass = 76 and 88 gm], two without age or mass recorded). These ages and weights correspond well with those reported by Pine et al. (1985), who reported this to be a semelparous annual species. *Monodelphis domestica* was well represented in the sampling results (65 records). Juveniles or subadults were encountered in the rainy months of the year (November, February, March). A pregnant female was captured in October, and lactating females were found in October, November, and March (the warmer months of the year). No juvenile or subadult *Monodelphis kunsi* were recorded. Adult individuals were captured during four months of the year (5 captures total), in both the autumn (February and April) and spring (October and November).

A juvenile *Cryptonanus chacoensis* was captured in June, and a subadult in December. A subadult *Marmosa paraguayana* was captured in December. No age-class or reproductive information was recorded for *Didelphis albiventris*, *D. aurita,* or *Lutreolina crassicaudata*.

Longevity and philopatry.—Because this report is based entirely on field studies (mark-recapture and specimens collected), we have no direct information concerning maximum longevity for any of the species encountered. However, mark-recapture sampling produced records for two species for which individuals were recorded during more than one mark-recapture sampling session. A subadult male *G. agilis* was captured and released in November 2016, and was captured again about three months later, in February 2017, at a trap station approximately 22 m distant from the first capture site, when it was recorded as an adult. A subadult female *G. agilis* was captured in December 2015 and again (as an adult) 11 months later, in November 2016, approximately 14 m from the first capture. An adult female *Mondelphis domestica* was captured three times in November 2016, at stations forming a triangle with sides of 51, 81, and 92 m. It was captured again three months later (February 2017) at a station located 20 m from the first point of capture in November.

Population densities.—Monodelphis domestica population densities varied from zero to five individuals/ha in two Cerrado grids (Owen, 2013) and from zero to 4.2 ind/ha in six forest grids (Table 7). This species was encountered in only two of the six forest grids and only during the second of two years of sampling.

Gracilinanus agilis densities varied from zero to 9.0 ind/ha on the six forest grids during the two-year sampling period 2015–17. The species was encountered on all six of the grids, but on every grid it was absent during one or two sampling sessions (Table 7; Fig. 4).

Sympatry and habitat associations of Monodelphis *species*.—Three species of *Monodelphis* were encountered during the mark-recapture sampling conducted on six forested grids, 2015–2017: *M. dimidiata, M. domestica*, and *M. kunsi*. All three of these species were not encountered on the same grid. However, the three possible pairs of species were each found together on different grids, although only once in the same sampling session. *Monodelphis dimidata*

Table 5. Standard measurements of all species for which specimens are available. For each species, measurements are given separately for each age class and sex for which data are available. Where more than one specimen is included, the mean, minimum and maximum values are listed. External measurements are given in mm, mass in gm.

Genus	Species	Age[1]	Sex[2]	N[3]	Total Length	Tail Length	Hind Foot Length	Ear Length	Mass
Caluromys	*lanatus*	3	1	1,1	506	300		28	250
Cryptonanus	*chacoensis*	2	1	1,1	172	96	13	15	11
Cryptonanus	*chacoensis*	3	1	1,2	194	109	14	17	19.5 (12-27)
Didelphis	*albiventris*	U	1	2,2	595.0 (570-620)	277.0 (276-278)	47.0 (42-52)	50.0 (48-52)	640.0 (460-820)
Didelphis	*aurita*	U	1	1,1	530	255	42	37	836
Didelphis	*aurita*	U	2	1,2	731	349	59	54	597.5 (195-1000)
Gracilinanus	*agilis*	1	2	0,1					25
Gracilinanus	*agilis*	2	1	1,13	225	125	16	16	13.5 (7-29)
Gracilinanus	*agilis*	2	2	8,26	199.8 (174-222)	112.4 (100-122)	14.5 (13-16)	15.5 (13-18)	16.6 (9-28)
Gracilinanus	*agilis*	3	1	13,29	229.5 (217-261)	130.4 (115-150)	15.6 (14-17)	18.5 (16-21)	24.8 (17-37)
Gracilinanus	*agilis*	3	2	13,23	216.7 (182-244)	121.6 (108-134)	15.1 (13-17)	18.0 (14-20)	20.9 (14-31)
Lutreolina	*crassicaudata*	3	2	1,1	522	257	40	25	309
Marmosa	*paraguayana*	2	2	0,1					36
Marmosa	*paraguayana*	3	1	1,2	350	214	27	26	112.5 (78-147)
Marmosa	*paraguayana*	3	2	3,3	333.3 (314-361)	192.0 (185-200)	24.7 (23-27)	34	49.0 (38-63)
Metachirus	*nudicaudatus*	3	1	1,1	535	313	44	11	225
Monodelphis	*dimidiata*	3	1	2,2	228.0 (227-229)	81.5 (76-87)	20.0 (20-20)		82.0 (76-88)
Monodelphis	*domestica*	1	1	1,1	126	43	12		17
Monodelphis	*domestica*	2	1	0,6					18.2 (17-19)
Monodelphis	*domestica*	2	2	3,5	173.0 (168-180)	61.0 (58-65)	14.7 (14-15)	20.9 (19-23)	28.4 (17-29)
Monodelphis	*domestica*	3	1	11,11	210.5 (167-245)	72.4 (61-80)	19.1 (15-22)	20.9 (19-23)	57.3 (36-90)
Monodelphis	*domestica*	3	2	12,12	212.4 (173-234)	73.0 (60-90)	18.6 (16-21)	10.0 (10-10)	55.8 (30-107)
Monodelphis	*kunsi*	3	2	2,2	118.0 (117-119)	39.0 (39-39)	11.5 (11-12)	14.0 (14-14)	8.8 (8.5-9)

[1] Age: 1 = juvenile, 2 = subadult, 3 = adult, U = unknown

[2] Sex: 1 = male, 2 = female

[3] N: number of specimens for external measurements, mass

Table 6. Age-class and reproductive activity. Months in which juveniles and/or subadults, or apparent female reproductive activity were observed. Numbers refer to months of the year, i.e., 06 = June, 12 = December.

Genus	Species	Age[1]	Months[2]	Reproductive Condition[3]	Months[4]
Cryptonanus	*chacoensis*	1	06		
Cryptonanus	*chacoensis*	2	12		
Gracilinanus	*agilis*	1	06, 11		
Gracilinanus	*agilis*	2	02, 06, 07, 11, 12		
Gracilinanus	*agilis*	3		4	02
Gracilinanus	*agilis*	3		5	08
Marmosa	*paraguayana*	2	12		
Metachirus	*nudicaudatus*	3		5	02
Monodelphis	*dimidiata*	2	07		
Monodelphis	*dimidiata*	3	11		
Monodelphis	*domestica*	1	12		
Monodelphis	*domestica*	2	02, 03, 11		
Monodelphis	*domestica*	3		5	10
Monodelphis	*domestica*	3		6	03, 10, 11

[1] 1=juvenile, 2=subadult, 3=adult
[2] Months in which the age class was encountered
[3] 4=vagina open, 5=pregnant, 6=lactating
[4] Months in which the reproductive condition was encountered

Table 7. Population abundances of *Monodelphis domestica* and *Gracilinanus agilis* on six mark-recapture sampling grids in forested areas, in six sampling sessions during two years, 2015–17. Density is calculated as minimum number known alive, divided by grid area (1.44 ha).

Sampling session	Mark-recapture sampling grid						Total
	A	B	C	D	G	H	
				Monodelphis domestica			
Jul 15	0	0	0	0	0	0	0
Nov 15	0	0	0	0	0	0	0
Feb 16	0	0	0	0	0	0	0
Jul 16	0	0	0	2	0	2	4
Nov 16	0	0	0	5	0	0	5
Feb 17	0	0	0	6	0	0	6
				Gracilinanus agilis			
Jul 15	2	12	2	2	3	1	22
Nov 15	1	0	1	2	2	2	8
Feb 16	0	1	1	0	1	2	5
Jul 16	2	5	0	13	6	0	26
Nov 16	4	0	0	5	0	1	10
Feb 17	0	2	6	7	7	3	25

was found on Grid B (low disturbance) in November 2016, and *M. kunsi* was on that grid in February 2017. *Monodelphis dimidiata* was captured in July 2016 on Grid D (medium disturbance), and *M. domestica* was captured on the same grid on numerous occasions from August 2016 to March 2017. Finally, on Grid H (low disturbance), *M. domestica* and *M. kunsi* were both encountered in October 2016.

Some of these captures were in Sherman traps during regular mark-recapture sampling, whereas others were in pitfall or Sherman-trap sampling conducted between the regular mark-recapture periods. *Monodelphis dimidiata* was captured only in Sherman traps, on grids of both low and medium disturbance of the forest habitat. *M. domestica* was captured in both Sherman and pitfall traps, on grids of both low and medium disturbance. Finally, *M. kunsi* was captured in both types of traps, but only in forest with a low level of disturbance.

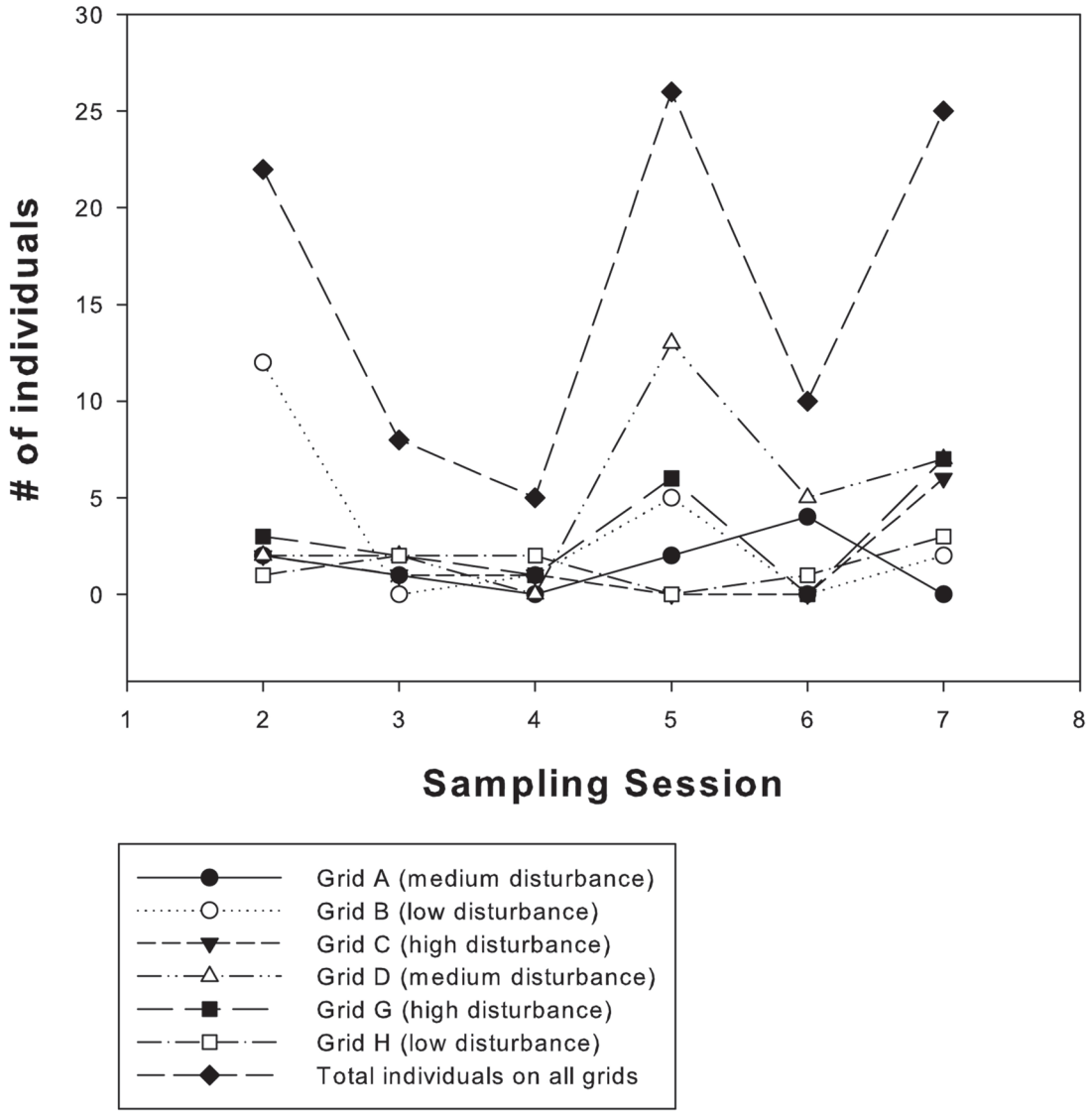

Figure 4. Plots of population densities of *Gracilinanus agilis* per grid through six sampling sessions (session 2, July 2015; 3, November 2015; 4, February 2016; 5, July 2016; 6, November 2016; and 7, February 2017). See Table 3 for descriptions of each grid. Sampling session numbers are consistent among this and companion papers to be published based on data from this project. Sampling sessions 1 (August 2014) and 8 (February 2019) did not or will not involve mark-recapture sampling on these grids, and thus no population densities were or will be calculated for those two sessions.

DISCUSSION

This paper provides detailed information on the most species-rich didelphid community reported to date from outside the Tropics. Several studies have reported on didelphid species richness or diversity (e.g., Fleck and Harder 1995; Mares and Ernest 1995; Flores et al. 2000; Guillemin et al. 2001; Solari et al. 2001; Asfora and Pontes 2009; Di Napoli and Caceres 2012; Owen 2013). However very few reports have provided the breadth of information about a didelphid community that is reported here, which includes information on species richness, habitat associations and vertical occupancy, external measurements and body mass, reproductive cycles, longevity and philopatry, population densities, and intrageneric microsympatry, to the extent that this information is available in this didelphid community. Smith et al. (2012) provided detailed information regarding the community composition, habitat associations, and external and cranial measurements for the didelphid community of Reserva Natural Laguna Blanca, Paraguay. That locality, which lies ca. 85 km WNW of RNBM, just south of the Tropic of Capricorn, also contains a mixture of Cerrado and Interior Atlantic Forest habitats, and is home to six didelphid species, five of which are shared with the RNBM.

Species richness.—Nine previous reports from tropical sites have listed from 10–17 didelphid species present. The present study is the first that we are aware of from a subtropical locality that includes 12 confirmed species. Willig and Gannon (1997) found South American didelphid species densities to be highest in latitudinal bands of 0–5, 10–15 and 15–20° S, decreasing sharply in the 20–25°S band (where the RNBM is located) and further south. The high didelphid species richness of RNBM is likely due to its location at the nexus of Interior Atlantic Forest and Cerrado ecoregions.

Hutterer et al. (1995) and Voss and Emmons (1996) stress the importance of long-term field efforts in arriving at realistic estimates of mammal species richness. For didelphids, the report of Smith et al. (2012) is based on 28 specimens from a locality, the highest didelphid species richness previously reported for a locality within Paraguay. The present report of 12 species is based on 218 captures of 204 individuals, 122 of which are preserved as specimens. Similarly, the report of 10 species at Les Nourages, French Guiana was based on 257 captures of 128 individuals (Guillemin et al. 2001), and that of 12 species at Paracou, French Guiana on 148 specimens (Voss et al. 2001). Hice's (2003) report of 13 species was based on 219 specimens, although many of those were of larger species.

Habitat associations and vertical occupancy.—Guillemin et al. (2001) stressed the importance of two "dimensions" of habitat partitioning (vertical stratification and open versus forest habitat) among didelphid marsupials. Additionally, they found each of three size classes to be dispersed among the distinct habitat and vertically defined niche spaces, thereby facilitating the sympatry and consequent high species richness in their site in French Guyana. Among the six most commonly encountered species in our data, both vertical and habitat preferences were found. Four of these species were captured exclusively on the ground, and two were primarily in arboreal traps. One of the two preferentially arboreal species (*Marmosa paraguayana*) was found only in habitats also occupied by the other (*Gracilinanus agilis*). These two species differ substantially in size.

Some controversy exists over the arboreal tendencies of *G. agilis* and *Cryptonanus chacoensis*. Hannibal and Caceres (2010), Andreazzi et al. (2011) and Cruz et al. (2017) reported that in central and southwest Mato Grosso do Sul, and Sergipe, Brazil, *G. agilis* was encountered predominantly on the ground. In contrast, this species was found almost exclusively (96%) in above-ground traps in the present study, whereas the externally similar *Cryptonanus chacoensis* was exclusively in ground-level traps. Similarly, Smith et al. (2012) captured *C. chacoensis* only in pitfall traps and *G. agilis* only in arboreal Sherman traps. Moreover, field observations of behavior support the conclusion that *Gracilinanus* is more arboreal than *Cryptonanus*. When released, the *Gracilinanus* in this study always climbed rapidly up the nearest available small tree or vine, and the *Cryptonanus* always went to the ground (sometimes jumping from a branch or vine where it had been placed) and escaped by running on the ground. Assuming no mis-identifications in any of the cited studies (*Cryptonanus* was only recently distinguished from sympatric *Gracilinanus* species—Voss et al.

2005), the contrasting reports suggest that further investigation is needed to understand the apparent geographic variation in vertical occupancy patterns of *G. agilis*.

The four most abundant ground-dwelling species in this site all are of small size (< 100 gm). Of these, one (*Monodelphis domestica*) was captured in nearly all habitats. Each of the other three (*Cryptonanus chacoensis, M. dimidiata,* and *M. kunsi*) was captured in only three or four habitats, and each of these three species shared only one habitat with each of the other two species. Nonetheless, the localities where the three species were encountered are all within a few kilometers of each other, within a continuous expanse of forest, and thus these species may be regarded as sympatric within the RNBM. Solari et al. (2001) found three species of *Monodelphis* sympatric in the Lower Urubamba region of eastern Peru and suggested that sympatric species of this genus would tend to be members of different subgenera. The data from the present study support this suggestion, as *M.* (*Monodelphiops*) *dimidiata*, *M.* (*Monodelphis*) *domestica*, and *M.* (*Mygalodelphys*) *kunsi* are referable to distinct subgenera (Pavan and Voss 2016).

Biology of Gracilinanus agilis.—Lopes and Leiner (2015) reported population densities of *G. agilis* of 19.8 and 16.7 individuals/ha in July or August of two succeeding years. In the present study, high overall abundances were found in July in both years, with substantial decreases in November of both years. The summer (February) samples differed considerably between years, with lowest overall abundances in February of 2016 and high overall abundances in the same month of the following year. Five of the six grids followed this overall trend, whereas Grid A (of medium disturbance) did not, having highest abundance in November of the second year (when overall abundances were low) and lowest in February of that year (when overall abundances were high).

Adult males and females of *G. agilis* in the present study averaged 24.8 and 20.9 gm, respectively, which is considerably heavier than the 13.9 and 10.5 gm reported for males and females by Smith et al. (2012), but similar to the 23.56 and 16.15 gm reported by Costa et al. (2003). Lopes and Leiner (2015) reported a pattern of considerable temporal variation in adult mass in a Brazilian Cerrado locality, with both sexes heaviest in the summer (October–February). Maximum mean adult mass in their study was ca. 40 gm for males, and ca. 32 gm for females. In contrast, the heaviest individuals (≥ 30 gm) in the present study were found in winter and spring (June, July, August, and October).

Andreazzi et al. (2011) reported biased sex ratios in *Gracilinanus agilis* in the Brazilian Pantanal, with males significantly outnumbering females. They found that breeding activity was confined to December–February, and resulted an unusually high population during May–August of one year, which was not repeated in the following year. Similarly, Lopes and Leiner (2015) found female reproductive activity was seasonal and synchronized in Cerrado habitat in Minas Gerais state, Brazil, but occurred July–February, with a post-mating male die-off. Females generally disappeared after weaning their young. These reports and others (e.g., Mares and Ernest 1995; Puida and Paglia 2015) indicate that *G. agilis* has discrete, non-overlapping generations. However, the samples from the present study do not support this description of *G. agilis* demography. Juvenile and young were found in both the cool-dry and warm-wet seasons, and one female was encountered which survived for at least 11 months on one of the sampling grids. Evidence of female reproductive activity was found in both seasons, and adult animals were found throughout the year.

The results reported here serve to emphasize the importance of extensive and long-term sampling to understand patterns of species habitat associations and community composition, annual reproductive and demographic patterns, and annual and multi-annual variation in population abundances. The area of the RNBM was first sampled extensively for small mammals in the early 1980s (P. Myers pers. comm.), and the first didelphid was collected in 1988. The following three decades of sampling in the reserve have resulted in 218 captures of didelphids, including the nine genera and 12 species reported here. Of these, fully half (six species) were unrecorded before 2005. This and the recent report of two new species of sigmodontine rodents from this reserve (Owen et al. 2018), indicate that much remains to be documented, even in relatively well-sampled sites.

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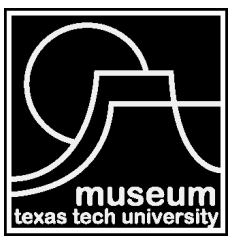

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