

Pelage Variation and an Update on the Geographic Distribution of the Black-tailed Marmoset *Mico melanurus*

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Abstract: The black-tailed marmoset, *Mico melanurus*, occurs in Brazil, Bolivia, and Paraguay. There are some gaps in our understanding of its distribution in the Brazilian states of Mato Grosso and Rondônia. Based on field surveys and a literature review, we present new records and an updated distribution map for the species. We also assess geographic and individual variation in the pelage of *M. melanurus*. For the surveys, we used the linear-transect method, adapted to include the use of playback. We also examined 11 specimens from museum collections—four from the mammal collection of the Cáceres campus of the Mato Grosso State University, and seven from the Goeldi Museum, Belém, Pará. Specimens from Vilhena and Chupinguaia had the darkest pelage, representing a previously unrecorded phenotype for the species, while specimens from the Guaporé, São Miguel, and Cautário river basins were of the palest phenotype. The thigh stripe, otherwise prominent, is inconspicuous or absent in some specimens. The new records extend the geographic distribution of *M. melanurus* to the northwest, suggesting contact zones with *Mico nigriceps* and *Mico intermedius*.

Key words: Amazonian marmoset, Platyrrhini, Callitrichidae, arc of deforestation, geographic variation

Introduction

The black-tailed marmoset, *Mico melanurus* (É. Geoffroy Saint-Hilaire in Humboldt, 1812), has the widest geographic distribution of any member the genus *Mico*, and is the only one to occur in biomes other than the Amazonian rainforest and outside Brazil (Rylands *et al.* 2009). This

species occupies the southern Amazon basin in Brazil and Bolivia, and, in the southernmost extreme of its distribution, the woodlands and riparian forests of the grassland-dominated ecosystems in parts of the Brazilian Cerrado, as well as the Pantanal wetlands (Rylands *et al.* 2019). To the west, the distribution of *M. melanurus* extends to the Río Mamoré in central Bolivia, and to the Chaco scrublands

of northeastern Paraguay, while to the east, it reaches the Rio Teles Pires in Brazil (Hershkovitz 1977; Stallings and Mittermeier 1983; Stallings 1985; Brown and Rumiz 1986; Vivo 1991; Rylands *et al.* 1993; Ferrari 2008; Mercado and Wallace 2010; Aguirre *et al.* 2019).

Vivo (1991) described *M. melanurus* as the darkest bare-eared *Mico*, with individuals having a uniformly dark-brown pelage on the dorsum, except for a buff stripe on the side of the thigh, together with a black tail and darkly pigmented face, except in the region around the nostrils. Vivo reported darker pelage on the dorsum of individuals collected in the central and southern parts of the Brazilian state of Mato Grosso, as compared to the lighter specimens from the Pantanal, in the municipality of Corumbá, in the state of Mato Grosso do Sul. Miranda Ribeiro (1914) also reported chromatic variation in the marmoset populations from Mato Grosso, and noted that one marmoset (*Hapale melanura*) collected on the upper Rio Jauru in southwestern Mato Grosso was darker than the individuals collected at Mata do Toscano, in the municipality of Cáceres (cited as “S. Luiz de Cáceres, Matta do Toscano”), also in Mato Grosso.

Intraspecific variation in pelage coloration is poorly documented in most mammal species (Caro 2009), and its role in the ecology and evolution of Neotropical primates has also been largely overlooked, except for some recent studies in species of the genera *Leontocebus* (Peres *et al.* 1996), *Alouatta* (Aguiar *et al.* 2008), *Lagothrix* (Mantilla-Meluk 2013) and *Leontopithecus* (Garbino *et al.* 2016). Understanding the biogeographic patterns of chromatic variation of *M. melanurus* populations will help to clarify the relevance of geographic barriers to gene flow between populations of this species, and, to a certain extent, in its congeners. Darker or lighter coat coloration may confer adaptive advantages on the individual (Mundy and Kelly 2003), depending on the vegetation structure, and in particular, the openness of the canopy, resulting in more shaded or sunlit environments in which the marmosets may be more or less exposed to predators. Here, we compile new records for *M. melanurus* populations over a wide range of the species' distribution, identify the location of populations with chromatic variations, and the degree of habitat loss that threaten these populations.

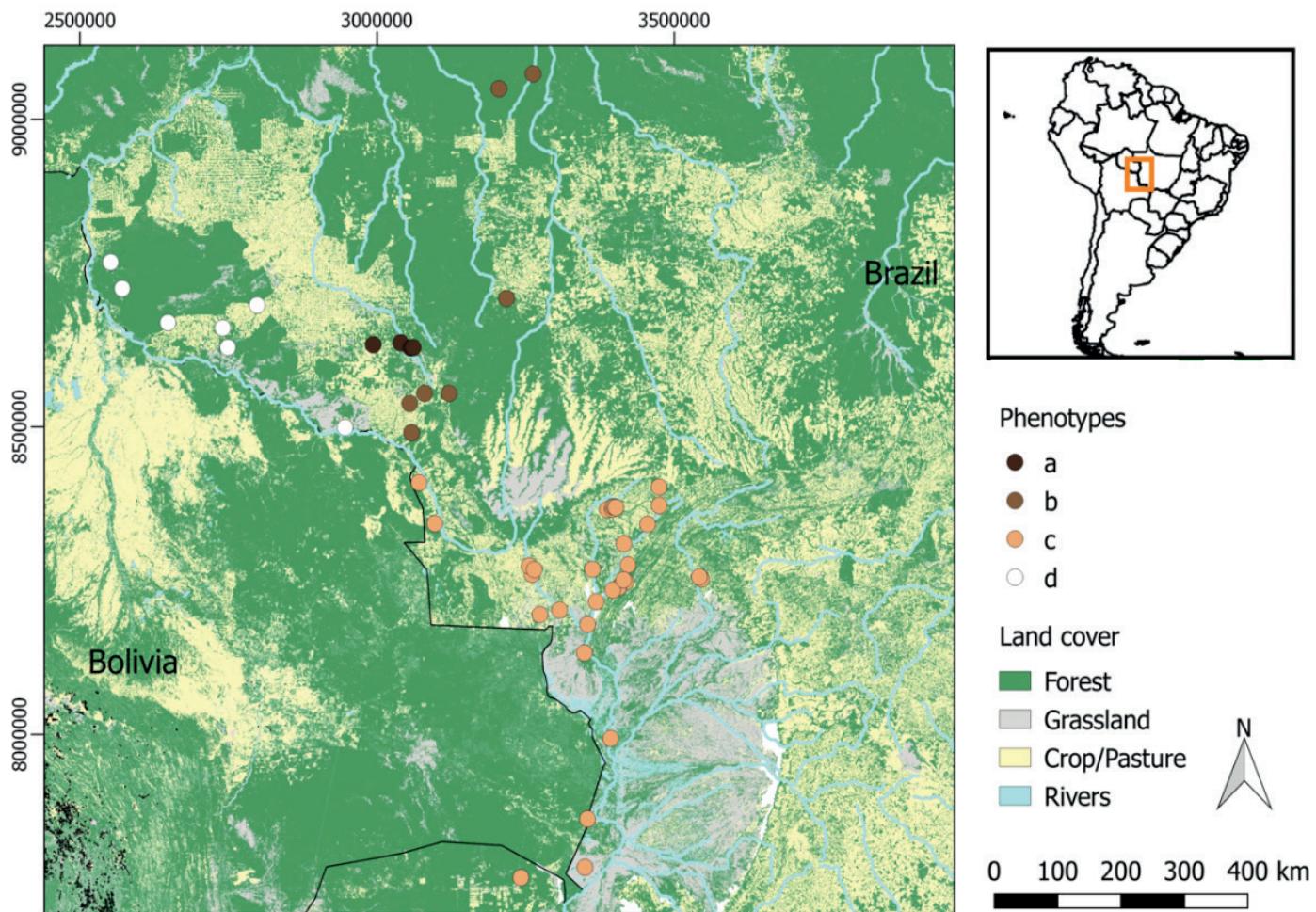


Figure 1. Localities of the new records of *Mico melanurus* obtained in the surveys conducted during the present study.

Methods

New records were obtained from 31 sites. The Rio Paraguai watershed (site 1 in Table 1) has a tropical Aw climate (Köppen 1948), with annual mean rainfall of 1500 mm and mean annual temperature of 22°C. The forest in this basin is of the seasonal, semideciduous submontane type (Radam-Brasil 1978). The sites numbered 2–6 in Table 1 are transitional between Amazonia and the Cerrado savanna of central Brazil (RadamBrasil 1978), with plateaus and cliffs, and elevations reaching 530 m above sea level in the Chapada dos Parecis. The forest remnants at these sites are small and surrounded by pasture. Sites 11–14 in Table 1 were surveyed using line transects, with a total of 112 km surveyed at site 11, 103 km at site 12, 106 km at site 13, and 102 km at site 14. All other records were obtained opportunistically. The new records are shown in Figure 1 and numbered on the map Figure 2.

Mico melanurus vocalizations were played back to lure the marmosets using a Sony Intelligent Noise Cut connected to a Supervoz II TSI-1210 amplifier. The recordings were obtained in the field in June 2015, on the left margin of the Rio Jauru, in the municipality of Indiavaí, in Mato Grosso, Brazil.

Photographs of the marmosets observed in the 23 study areas were compared with the specimens deposited in the Goeldi Museum, Belém (specimens MPEG 13289, 13290, 13296, 15266, 15267, 21395, 21396), and in the Mammal Laboratory of the Cáceres campus of Mato Grosso State University, UNEMAT (specimens CELBE-M-AC-337, CELBE-M-ODS-005, CELBE-M-ODS-006, CELBE-M-ODS-004) (Table 2, Fig. 3). We followed the species diagnosis and description provided by Hershkovitz (1977). We complemented our new records from the field with all the existing records compiled from a literature search (Table 3, Fig. 2).

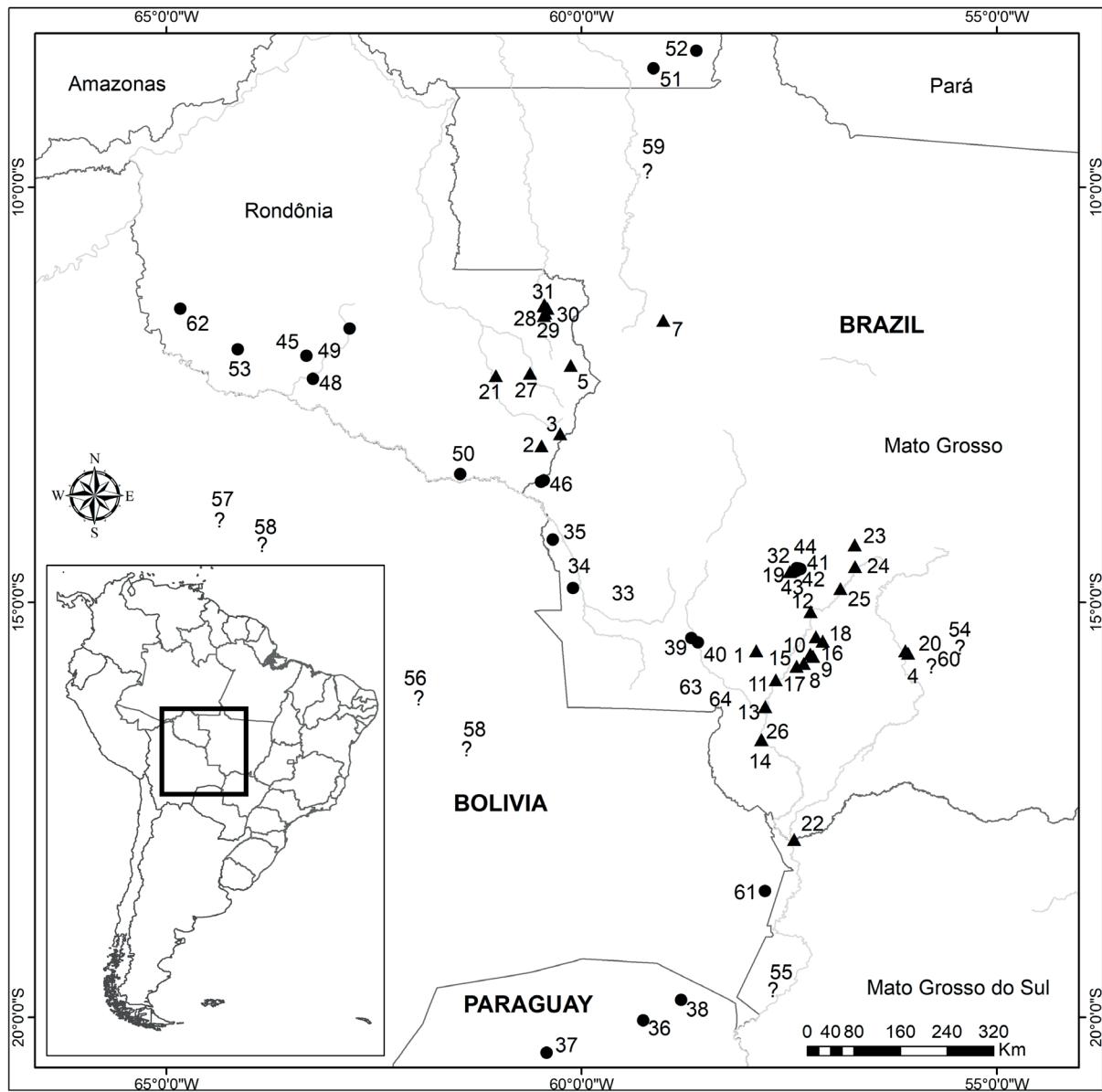


Figure 2. *Mico melanurus* localities. See Tables 1 and 3.

Table 1. Localities of the sightings of *M. melanurus* recorded in the present study, in Brazil. Brazilian states: MT = Mato Grosso; RO = Rondônia.

Site	Locality, municipality, state	N animals	Date	Coordinates	Region	Phenotype (Fig. 1)
1	Sítio Santo Antônio, Curvelândia, MT	8	18/12/2013	15°34'56"S 57°53'59"W	Pantanal	d
2	Campus IFRO, Colorado do Oeste, RO	7	13/03/2014	13°06'45"S 60°29'05"W	Amazonia	b
3	Sítio Santa Ana, Nova Conquista, RO	5	15/4/2014	12°58'05"S 60°15'33"W	Amazonia	b
4	Universidade Federal de Mato Grosso campus, Cuiabá, MT	13	27/04/2014	15°36'46.97"S 56°04'13.93"W	Cerrado	c
5	Sítio Cirio Libanés, Vilhena, RO	6	05/01/2015	12°58'05"S 59°53'10"W	Amazonia Cerrado	b
6	BR 174, km 180, Juína, MT	7	28/05/2016	11°36'07.49"S 59°01'07.71"W	Amazonia	b
7	Estação Ecológica Serra das Araras, Porto Estrela, MT	16	20/03/2017	15°39'1.45"S 57°12'50.21"W	Cerrado	b
8	MT 343, km 121, Porto Estrela, MT	3	28/03/2017	15°44'10.29"S 57°19'35.36"W	Cerrado	c
9	Estação Ecológica Serra das Araras, Cáceres, MT	3	28/03/2017	15°28'33.03"S 57°435.05"W	Cerrado	c
10	MT 343 km 142, Porto Estrela, MT	4	10/04/2017	15°24'49.61"S 57°10'51.47"W	Cerrado	c
11	Rancho do Reis, Cáceres, MT	7	07/07/2017 (2 groups)	15°56'03.70"S 57°39'46.24"W	Pantanal	c
12	Rio Paraguai, Barra do Bugres, MT	42	01-08/09/2017 (7 groups)	15°06'46.70"S 57°14'36.46"W	Pantanal	c
13	Pousada Recanto do Dourado, Cáceres, MT	8	11/10/2017	16°15'23.91"S 57°47'26.97"W	Pantanal	c
14	Fazenda Descalvados, Cáceres, MT	9	11/11/2017	16°39'20.35"S 57°50'27.33"W	Pantanal	c
15	MT 343, km 110, Porto Estrela, MT	2	28/03/2018	15°44'10.29"S 57°19'35.36"W	Cerrado	c
16	Vila Aparecida, Distrito de Cáceres, MT	2	12/04/2018	15°46'12.53"S 57°24'42.14"W	Cerrado	c
17	Salobra Grande, Distrito de Cáceres, MT	1	12/04/2018	15°37'32.57"S 57°14'53.88"W	Cerrado	c
18	MT 343, km 36, Cáceres, MT	3	17/04/2018	12°16'04.7"S 61°02'06.7"W	Cerrado	c
19	Parque Municipal, Tangará da Serra, MT	5	17/05/2018	14°37'37.98"S 57°29'36.54"W	Amazonia	c
20	Parque Mãe Bonifácia, Cuiabá, MT	9	20/08/2018	15°34'57.6"S 56°06'08.6"W	Cerrado	c
21	RO 391, km 36, Chupinguaia, RO	3	19/04/2019	12°16'04"S 61°02'07"W	Amazonia	a
22	Parque Nacional do Pantanal, Poconé, MT	3	21/03/2018	17°51'26"S 57°26'37"W	Pantanal	c
23	Fazenda Camargo Correa, Diamantino, MT	17	18-25/11/2018 (4 groups)	14°18'23"S 56°4244"W	Amazonia	d
24	Fazenda Águia Branca, Nortelandia, MT	6	19/11/2018	14°34'09"S 56°42'33"W	Amazonia Cerrado	c
25	Areal, MT 241, Denise, MT	15	20/11/2018	14°50'10"S 56°53'08"W	Amazonia Cerrado	c
26	Fazenda Morrinhos, Cáceres, MT	21	05-11/05/2018 (5 groups)	19°39'08"S 57°49'58"W	Pantanal	c
27	Rio Comemoração, Pimenta Bueno, RO	3	12/02/2018	12°14'23"S 60°37'16"W	Amazonia Cerrado	c

Cont'd...

Table 1. Cont'd.

28	Linha 90 Capa 120, Vilhena, RO	5	10/07/2020	12°9'44"S 60°27'9"W	Amazonia	a
29	Linha 90 Capa 120, Vilhena, RO	3	10/07/2020	12°7'58"S 60°27'14"W	Amazonia Cerrado	a
30	Linha 90 Capa 120, Vilhena, RO	2	10/07/2020	12°3'53"S 60°26'48"W	Amazonia Cerrado	a
31	Linha 90 Capa 120, Vilhena, RO	2	10/07/2020	12°2'0"S 60°25'12"W	Amazonia Cerrado	a

Results

New records

We registered 31 new populations of *M. melanurus*: six in the Amazon, nine in the Cerrado, seven in the Pantanal, and nine in the ecotonal zone between the Amazon and the Cerrado in the ombrophylous forests of the western portion of the Parecis Plateau, the Chapada dos Parecis (Fig. 1). Groups of *M. melanurus* were seen in pristine forest, but also in anthropogenic environments near pasture and in secondary forest, including, for example, one group feeding in a mango tree (*Mangifera indica*, an exotic species in Brazil), at Curvelândia in Mato Grosso state, and other groups observed in small forest fragments in Colorado do Oeste and Nova Conquista in the state of Rondônia. A total of 240 individuals were observed: 56 in the Amazon (9.3 per group), 56 in the Cerrado (5.8 per group), 37 in the ecotonal zone (4.7 per group), and 91 in the Pantanal (5.7 per group). Mean group size was 5.8 (Tables 1 and 2).

Geographic variation in pelage coloration

We identified four principal *M. melanurus* phenotypes (Figs. 1 and 4), based on the 31 visual records in the field,

11 specimens from museum collections, and six published descriptions (Vivo 1991; Tables 1–3).

Phenotype a (Figs. 4 and 5): a previously unknown phenotype observed in the extreme northwest (records 21, 28–31, Fig. 2) of the distribution of the species. This is the darkest of the known phenotypes, with an overall blackish brown coloration; dorsal region gray-brown, gradually darkening to blackish brown in the pelvic region; forelimbs dark gray-brown; hindlimbs brownish-black with a contrasting whitish-brown stripe on the thigh extending to the sacral region; face darkly pigmented but depigmented in the nasal region; tail black.

Phenotype b (Fig. 4): recorded in the Cabixi and Aripuanã river basins, and from the ESEC Serra das Araras (records 2, 3, 5, 6, and 7). This phenotype has a generalized brown agouti pattern; dorsal region light brown, gradually darkening to brown agouti in the pelvic region; forelimbs light gray-brown, gradually darkening to brown agouti at the extremities; hindlimbs brownish-black with a contrasting yellowish stripe on the thigh, which extends to the sacral region; face darkly pigmented, but depigmented in the nasal region; tail black.



Figure 3. Specimens from the Mammal Laboratory of Mato Grosso State University (UNEMAT). Photograph: Odair Silva-Diogo. 1. CELBE-M-AC-337, Municipality of Cáceres, Mato Grosso. 2: CELBE-M-ODS-005, Municipality of Barra do Bugres, Mato Grosso. 3: CELBE-M-ODS-006, Municipality of Barra do Bugres, Mato Grosso. 4: CELBE-M-ODS-004, Colorado d'Oeste Municipality, Rondônia.

Table 2. Museum specimens of *M. melanurus* examined at the Goeldi Museum in Belém, Pará (MPEG), and the Mammal Laboratory of the Cáceres campus of Mato Grosso State University (UNEMAT) in Mato Grosso, Brazil.

Collection	Locality	Number
MPEG	Cidade Laboratório de Humboldt, Aripuanã, MT	MPEG 13289, 13290, 13296, 15266, 15267, 21395, 21396
UNEMAT	Município de Colorado d'Oeste, RO	CELBE-M-ODS-004
UNEMAT	Município de Barra do Bugres, MT	CEUBE-M-ODS-005, 006
UNEMAT	Município de Cáceres, MT	CEUBE-M-AC 337

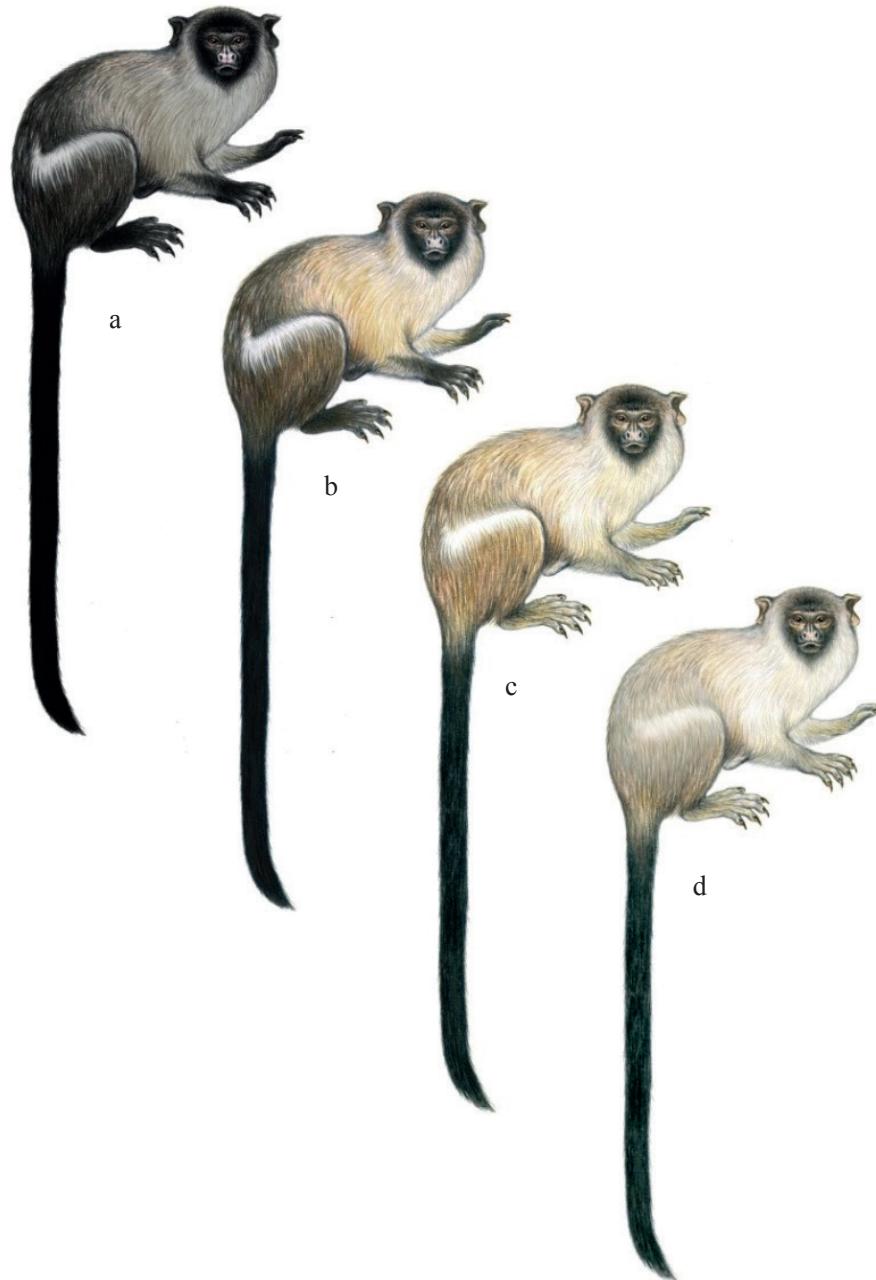


Figure 4. The four color-morphs of *Mico melanurus* observed in the field. See Figure 1. Illustrations by Stephen D. Nash.

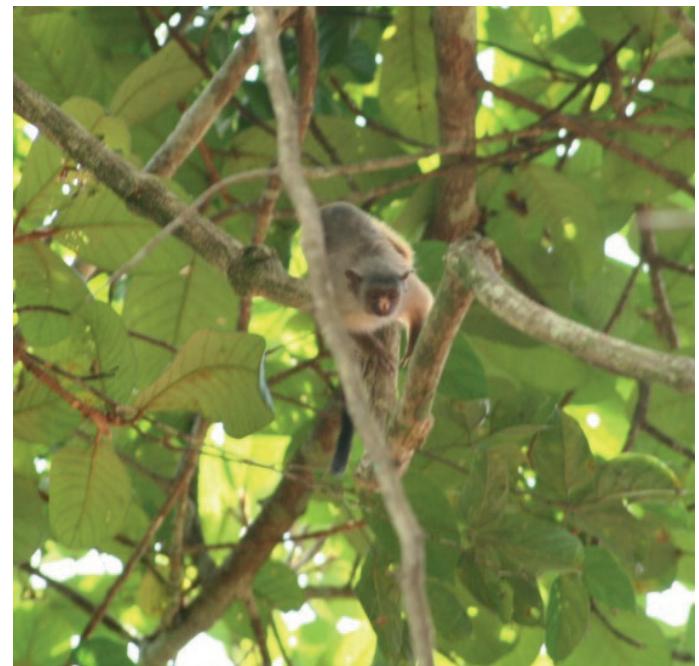


Figure 5. Left. *Mico melanurus* at Chupinguaia, southeastern Rondônia, Brazil, see Figure 2, locality 21 (photograph by Carlos A. Tuyama). Right. *Mico melanurus* in the Rio Cautário Extractivist Reserve, southwestern Rondônia, Brazil, see Figure 2, locality 45 (photograph by Almério C. Gusmão).

Phenotype c (Fig. 4): found throughout most of the geographic distribution of the species in Brazil, principally in the ecotonal zone from the headwaters of the Rio Guaporé, through the Paraguai and Cuiabá basins, to the Pantanal. This phenotype has a generalized brown pattern; dorsal region whitish, gradually darkening to brown agouti in the pelvic region; forelimbs whitish, gradually darkening to brown at their extremities; hindlimbs brown with a contrasting white stripe on the thigh, which extends to the sacral region; face with brownish pigmentation but depigmented in the nasal region; tail black.

Phenotype d (Fig. 4): found in the western extreme of the Brazilian distribution of the species, more precisely in the Guaporé/São Miguel interfluvium in the state of Rondônia. The general pattern of this phenotype is gray-brown; dorsum whitish in the scapular region, gradually darkening to grayish brown in the pelvic region; forelimbs whitish, gradually darkening to grayish brown at the extremities; hindlimbs light grayish-brown with a contrasting white-grayish stripe on the thigh, which extends to the sacral region; face lightly pigmented compared to other observed phenotypes but depigmented in the nasal region; tail black. These individuals appear to be lighter than those described by Vivo (1991). Alves (2012), in a long-term study, noted the pale color of *M. melanurus* from this region.

Geographic distribution and threats

Mico melanurus is found in the Amazon, Cerrado, and Pantanal. According to the map published by Rylands *et al.* (2008), which is based on the records of Hershkovitz (1977), the geographic distribution of the species is limited in the northeast by the southern margin of the Chapada dos Parecis highlands. New records of the species, reported in

the present study, at the Fazenda Sirio Libanês (site 5; Fig. 2) and at Linha 90, Capa 120 (sites 28–31; Fig. 2), extend the known distribution of the species approximately 80 km to the northwest, from the Chapada dos Parecis localities reported by Hershkovitz (1977). Rylands and Régis (2008) indicated that this area is part of the range of *M. intermedius*, although no data were available. The series of new records from the Apidá/Comemoração/Roosevelt interfluvia (sites 21 and 28–31; Table 1, Fig. 2) extend the known geographic range of the species further northwest in comparison with the ranges proposed by Vivo (1991), Noronha *et al.* (2008), and Rylands and Régis (2008).

In the state of Rondônia, *M. melanurus* is sympatric with *Mico rondoni* (see Ferrari *et al.* 2010) and *Leontocebus weddelli* (see Gusmão *et al.* 2015) south of the Serra dos Pacaás Novos and the east of the rios São Miguel and Urupá rivers, in the western extreme of the distribution of the species (Vivo, 1985). Records 28–31 (Fig. 2) also indicate that the species may be sympatric with *Mico nigriceps* to the northwest or, more precisely, at the headwaters of the rios Comemoração and Roosevelt.

The principal threats to *M. melanurus* detected in the present study were habitat loss due to the clearance of forest for crops and livestock. Forest fires and roadkill also result in considerable numbers of fatalities. At the sites on the BR 174 (site 6) and MT 343 highways (sites 8, 15 and 18), the marmosets were observed in disturbed and secondary forest at the roadside. Of the new *M. melanurus* records, 12 (1–4, 8, 10, 15, 16–19, and 21; Table 1, Fig. 2) were obtained in isolated forest fragments surrounded by a matrix of pasture, or in urban zones. At all other locations, the *M. melanurus* groups were observed in continuous old-growth forest.

Table 3. Occurrence records of *M. melanurus* available in the literature. Brazilian states: AM = Amazonas; MS = Mato Grosso do Sul; MT = Mato Grosso; RO = Rondônia.

Site	Locality, municipality, state or department, country	Coordinates	Region	Reference
32	Fazenda Monte Fusco, Indavai, MT, Brazil	15°32'54"S 58°38'02"W	Amazonia/Cerrado	Gusmão (2016)
33	Fazenda Pousada Guaporé - Vila Bela da Santíssima Trindade, MT, Brazil	14°49'36.5"S 60°06'15.6"W	Amazonia/Cerrado	Oliveira (2013)
34	Fazenda Rio do Meio - Vila Bela da Santíssima Trindade, MT, Brazil	14°14'40.4"S 60°20'39.9"W	Amazonia/Cerrado	Oliveira (2013)
35	Fazenda Curitiba, Comodoro, MT, Brazil	13°31'46.6"S 60°27'18.3"W	Amazonia	Oliveira (2013)
36	Parque Nacional Defensores del Chaco, Agua Dulce, Paraguay	20°25'34"S 60°25'16"W	Chaco	Stallings & Mittermeier (1983)
37	Agua Dulce, 3 km E on Linea, Paraguay	20°02'16"S 59°15'18"W	Chaco	Stallings & Mittermeier (1983)
38	20 km W. Mbariqui, Paraguay	19°47'38"S 58°48'07"W	Chaco	Cabral <i>et al.</i> (2017)
39	Sítio São Pedro, Indiavai, MT, Brazil	15°25'42"S 58°40'35"W	Amazonia/Cerrado	Gusmão (2016)
40	Pousada Rio das Luzes (APP Rio Jauru), Indiavai, MT, Brazil	15°28'49"S 58°35'55"W	Amazonia/Cerrado	Gusmão (2016)
41	MT 339, km 12 Sul, Tangará da Serra, MT, Brazil	14°37'13.83"S 57°24'54.89"W	Cerrado	Gusmão (2016)
42	MT 339, km 15 Sul, Tangará da Serra, MT, Brazil	14°35'19.51"S 57°24'30.04"W	Cerrado	Gusmão (2016)
43	Corrego Cachoeirinha region, Tangará da Serra, MT, Brazil	14°35'24.44"S 57°23'00.99"W	Cerrado	Gusmão (2016)
44	Corrego Cachoeirinha region, Tangará da Serra, MT, Brazil	14°35'56.34"S 57°21'52.19"W	Cerrado	Gusmão (2016)
45	Resex do Rio Cautário, Costa Marques, RO, Brazil	11°57'05.5"S 64°08'26.3"W	Amazonia	Gusmão <i>et al.</i> (2015)
46	Fazenda Curitiba, Comodoro, MT, Brazil	13°31'46.6"S 60°27'18.3"W	Amazonia/Cerrado	Oliveira (2013)
47	Rebio Guaporé, Costa Marques, RO, Brazil	12°18'23.64"S 63°14'04.71"W	Amazonia	Alves (2012)
48	Fazenda do Mansur, São Miguel, RO, Brazil	11°41'55"S 62°47'33"W	Amazonia	Ferrari <i>et al.</i> (2010)
49	Sítio do Geraldo, São Francisco, RO, Brazil	12°01'37"S 63°18'42"W	Amazonia	Ferrari <i>et al.</i> (2010)
50	Fazenda São Paulo, Pimenteiras, RO, Brazil	13°27'19"S 61°27'40"W	Amazonia	Ferrari <i>et al.</i> (2010)
51	Floresta Estadual Sucundurí, Apuí, AM, Brazil	08°34'S 59°08'W	Amazonia	Noronha <i>et al.</i> (2008)
52	Parque Estadual do Sucundurí, Apuí, AM, Brazil	08°21'S 58°37'W	Amazonia	Noronha <i>et al.</i> (2008)
53	Reserva Biológica do Traçadal, Costa Marques, RO, Brazil	11°27'35.19"S 64°49'53.43"W	Amazonia	Ferrari (2001)
54	Serra da Chapada, MT, Brazil	?	Cerrado	Hershkovitz (1977)
55	Urucum de Corumbá, Corumbá, MS, Brazil	?	Cerrado	Hershkovitz (1977)
56	Santa Cruz, Río Quiser, Chiquitos, Bolivia	?	?	Hershkovitz (1977)
57	Santa Cruz, Cercados, Bolivia	?	?	Hershkovitz (1977)
58	Santa Cruz, Palmarito, Río San Julian, Bolivia	?	?	Hershkovitz (1977)

Cont'd...

Table 3. Cont'd.

59	Aripuanã, Rio Roosevelt, MT, Brazil	?	Amazonia	Hershkovitz (1977)
60	Fazenda Maravilha, Vila Porto Antônio, Cuiabá, MT, Brazil	?	Cerrado	Hershkovitz (1977)
61	Porto Soarez, Departamento Santa Cruz, Bolivia	18°58'51"S 57°47'31"W	Pantanal	Cabral <i>et al.</i> (2017)
62	Ouro Preto Biological Reserve, Ouro Preto, RO, Brazil	11°04'44"S 65°00'25"W	Amazonia	Messias (2001)
63	Fazenda Icaroma, Cáceres, MT, Brazil	16°03'08"S 58°12'55"W	Cerrado	Gusmão (2016)
64	Floresteca Cáceres, MT, Brazil	16°07'05"S 58°30'56"W	Cerrado	Gusmão (2016)

Discussion

The occurrence records for *M. melanurus*, compiled in the present study, confirm the extensive geographic distribution of the species, which includes parts of the Amazon, Pantanal, and Cerrado, and their respective ecotonal zones. We have also redefined and extended the distribution of the species in the northwestern extreme of its range (Vivo 1991; Noronha *et al.* 2008). Our results also indicate a greater heterogeneity of color morphs than were described by Vivo (1991). The chromatic variation in phenotypes occurs systematically across the extensive geographic distribution of the species and may represent a cline related to climate or other factors. Similar clines in pelage coloration have not been reported in other *Mico* species.

Our study expands the number of records of *M. melanurus* considerably, and expands the area known to be occupied by the species in southern Amazonia. It seems unlikely, however, that *M. melanurus* occurs on the Guaporé floodplain between the Corumbiara State Park and the Rio Mequénis in southern Rondônia, as was suggested by Rylands *et al.* (2008). The absence of this species from flooded areas east of the Rio São Miguel to the Corumbiara State Park was also noted by Alves (2012) in his study in the Guaporé Biological Reserve. Based on this evidence, we consider that the species is absent from this region. Populations with paler pelage are found in the Branco/Guaporé/Cautário interfluvia and, as noted previously (Ferrari 2001; Ferrari *et al.* 2010; Alves 2012; Gusmão *et al.* 2015), they are isolated geographically from other populations in Rondônia. These populations are, nevertheless, contiguous with populations in Bolivia, on the opposite margin of the Rio Guaporé, a river that does not appear to represent a barrier to the dispersal of the species (see Rylands *et al.* 2008).

The darker *M. melanurus* morphs appear to coincide with the Cerrado woodlands (*Cerradão*) found at the headwaters of the Apidiá, Comemoração and Roosevelt rivers. This type of vegetation has a mean height of 8 m, with thick undergrowth and a well-developed canopy. In this area, the dense foliage of the trees provides intense shade, where the darker color morph may be less visible to predators.

The lighter color morph, observed at the western extreme of the species' range, coincides with tall Amazon

forest, with a mean height of 35 m and a more open canopy, with tall emergents that, upon toppling naturally, open large clearings in the forest. Another potential factor in this area is sympatry with *M. rondoni* (see Gusmão *et al.* 2015), which implies the potential for gene flow between populations, at least in the recent evolutionary past of the species. A similar mechanism has been suggested by Garbino *et al.* (2016) to account for the differentiation in coloration between *Leontopithecus chrysopygus* and *L. caissara*, two closely-related callitrichids from southeastern Brazil.

The four color-morphs identified by the present study occur in areas with very different conservation profiles, with the ecotonal zones representing the most altered landscapes, given their much longer history of human colonization. In these areas, the forest fragments are relatively old, and are mostly found in privately-owned reserves, and there is little current deforestation. By contrast, populations of the darker phenotype occur in areas subject to ongoing deforestation and frequent forest fires, that have been occupied more recently by humans, and where *M. melanurus* habitat is being lost at an alarming rate.

The least affected populations are in large protected areas, particularly those of the two intermediate phenotypes in the Pantanal, which, however, is currently (late 2020) suffering from a major drought and extensive wildfires.

The paler phenotype observed in the populations of the Guaporé river basin has the greatest cover of protected areas within the species' range. This region encompasses a mosaic of 12 protected areas: Reserva Extrativista (RESEX) do Rio Ouro Preto, RESEX Pacaás Novos, RESEX Federal Ribeirão das Antas, Pacaás Novos National Park (PARNA), Parna Serra da Cutia, Traçadal Biological Reserve (REBIO), REBIO Ouro Preto, REBIO Guaporé, and the Serra dos Reis State Park, and seven Indigenous Lands, the Igarapé Lourdes Indigenous Territory (TI), TI Rio Negro Ocaia, TI Uru-Eu-Wau-Wau, TI Guaporé, TI Pacaás Novos, TI Rio Branco, and TI Massaco). Although these areas are legally protected, recently they are being encroached upon by miners, illegal loggers, and squatters—a result of the dwindling financial resources for monitoring and enforcement (Rajão *et al.* 2020).

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