RESEARCH ARTICLE

Reduced range of the endangered crested capuchin monkey (Sapajus robustus) and a possible hybrid zone with Sapajus nigritus

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US Fish and Wildlife Service; Palm Beach Zoo; Idea Wild; Los Angeles Zoo; Nature Conservancy; Margot Marsh Biodiversity Foundation The crested capuchin monkey (Sapajus robustus) is an endangered species endemic to the highly fragmented Atlantic Forest of Brazil. Surveys for S. robustus were carried out over a 25-month period (2003-2005) to obtain more precise geographical limits for the western range of the species. Previously published localities for S. robustus were mapped, and each point was given a 25-km radius "buffer zone." The largest forest remnants in the buffer zones (>300 ha) in Minas Gerais were visited in order to interview the local people and/or survey the forests directly using playback recordings of S. robustus. Camera traps were used in key localities if interviews suggested the presence of capuchins but no animals were sighted during the surveys. Of 127 valid interviews, only 39 people reported the presence of Sapajus in nearby forest fragments. We confirmed the presence of Sapajus in only 19 of these. S. robustus occurred in four, and S. libidinosus, S. nigritus, S. xanthosternos, or S. robustus × S. nigritus (hybrids?) occurred in the remaining 15. Based on our study, the estimated geographical distribution of S. robustus is 119,654 km², which represents a reduction of more than 70,000 km² when compared to its formerly described range. The geographical limits as defined in this study are: northeast-the Jequitinhonha River; northwest and west-the Jeguitinhonha River; southwest-the Suacuí Grande River and the Espinhaco mountains; southeast-the Doce River; east-the Atlantic Ocean. A probable hybrid zone where capuchin monkeys have morphological features of both S. nigritus and S. robustus was found between the Santo Antônio and the Suaçuí Grande rivers. The elucidation of the geographical distribution of S. robustus is important for its conservation, facilitating the delineation of priority areas for the creation of reserves and the initiation of studies of the species' ecology and behavior.

KEYWORDS

conservation, geographic distribution, historic range, hybridization, intergradation zone, range reduction, robust capuchin monkeys, *Sapajus*

1 | INTRODUCTION

The taxonomy of capuchin monkeys is complex (Cabrera, 1957; Hill, 1960; Groves, 2001; Rylands et al., 2000; Silva, 2001). The main causes

of confusion are the high degree of population level polymorphism stemming from ontogenetic changes, sexual dimorphism, and individual variation, as well hybridization in adjacent populations (

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Torres, 1988; Torres de Assumpção, 1983; see also Rylands, Kierulff, & Mittermeier, 2005).

The crested capuchin monkey, *Sapajus robust*us (Kühl, 1820), is endemic to the Atlantic Forest of Brazil. The common name crested capuchin monkey, or macaco-prego-da-crista in Portuguese, refers to the conspicuous pelage of its crown, with two long tufts converging to form a median crest (Figure 1). It was formerly considered a subspecies of *Cebus apella* (Linnaeus, 1758), then a subspecies of *C. nigritus* (Goldfuss, 1809) (Groves, 2001; Rylands et al., 2000, 2005), and now, based on genetic and morphological evidence, this taxon has been elevated to the species level, in the robust or tufted capuchin genus, as *S. robustus* (Lima et al., 2017; Lynch Alfaro et al., 2012; Silva, 2001).

Abundant in the past, crested capuchins are now threatened because of habitat destruction and hunting (Oliver & Santos, 1991). According to the most recent *IUCN Red List of Threatened Species* (IUCN, 2017), they are categorized as "Endangered." *S. robustus* occurs in protected areas in the state of Espírito Santo and the south of the state Bahia, but at the onset of this study it had not been reported in any of the reserves in Minas Gerais, the state which makes up the bulk of its range (Oliver & Santos, 1991).

Previous surveys of the distributional limits of *S. robustus* described its distribution as follows: south of the Jequitinhonha River in southern Bahia and Minas Gerais, with its congener *S. xanthosternos* north of the river (Kierulff et al., 2005; Oliver & Santos, 1991), and north of the Doce River in northern Espírito Santo, with *S. nigritus* to the south. In southern Minas Gerais, the Doce and Piracicaba rivers form another boundary separating *S. robustus* and *S. nigritus* (Hirsch, 2003; Pinto, 1941; Silva, 2001). The western limit to the distribution of *S. robustus* was postulated as the São Francisco River (Rylands et al., 1988), with *S. libidinosus* (Spix, 1823) occurring to the west.

The aim of our survey was to obtain a more precise description of the western and southwestern geographical limits of *S. robustus* and to assess evidence for intergradation, sympatry, replacement or hybridization with other *Sapajus* species in the regions within the limits of the currently identified species distribution. To this end, we 1) mapped known historical locations for *S. robustus* from the literature and



FIGURE 1 The crested capuchin monkey, *S. robustus*, eating an oil palm fruit

museum collections; 2) visited the largest fragments in a 25-km radius of each of those locations, in order to question local people about the presence or otherwise of *S. robustus*; 3) surveyed forests using playback recordings of capuchin vocalizations in order to determine the presence of *S. robustus* or other *Sapajus* species when local people indicated that they still occurred there; 4) used camera traps in key localities when the presence of *S. robustus* was indicated but playback surveys failed to confirm its presence; and 5) used the new and historical locality data to create a new map of the present distributional limits of *S. robustus* and of any area of potential sympatry, hybridization, intergradation and/or parapatry with other *Sapajus* species.

2 | METHODS

2.1 | Scope of the survey

A survey of crested capuchin monkey populations across the presumed western and southwestern distributional limits of the species (as postulated by Rylands et al. [1988] and Oliver & Santos [1991], see Figure 2) was carried out over a 25-month period from June 2003 to June 2005. The research was non-invasive, no animals were touched or harmed, and we complied with protocols approved by the Post-Graduate program of Wildlife Management at Federal University of Minas Gerais (UFMG). The research adhered to the legal requirements of Brazil (no IBAMA permit was required because it did not involve the capture or collection of animals) and to the American Society of Primatologists' Principles for the Ethical Treatment of Non Human Primates.

2.2 | Field localities for interviews and surveys

The contested boundaries of the distribution of crested capuchins are in the western part of their range, and so we focused on populations in Minas Gerais, including those along the upper Jequitinhonha River, the Espinhaço Mountains, and along the Suaçui Grande and Santo Antônio rivers (see Table 1, Supplementary Table S1, and Figure 3 for the municipalities surveyed). In order to determine which forest fragments to visit, we mapped distribution points of S. robustus from the literature, as compiled by Hirsch et al. (2002). We then created "buffer zones" by marking a circular area with a radius of 25 km around each locality (see Figure 4). We also mapped the forest remnants within the known distributional limits of the crested capuchin monkey in Minas Gerais, using Landsat7 ETM+ satellite images in photographic format obtained through the National Institute of Space Research (INPE), Brazil. The images were color composites, including three spectral bands (3/4/5-B/G/ R). We used maps with a scale 1:100,000 that were published by the Brazilian Institute for Geography and Statistics (Brazil, IBGE 1992, 1993). These images were interpreted by using the software ERDAS Imagine v.8.4 (ERDAS, 1997a,b) following the protocol established by Landau, Hirsch, and Musinsky (2008) to obtain vegetation cover and land use.



FIGURE 2 Map of historical distribution of crested capuchin monkey (*S. robustus*). Points indicate localities where presence of capuchin monkeys was confirmed in this study, either through direct observation or by indication of presence from interviewees

We prioritized the largest forest fragments (>300 ha) within these sub-regions (buffer zones), using the satellite imagery data, for carrying out interviews with local people and/or surveys of *S. robustus* (see interview and survey methods below). When multiple buffer zones were overlapping, we visited at least one location in the combined area. We also visited rivers and mountains that were believed to be important in defining the distributional limits of the species. The localities visited for interviews and surveys are listed in Table 1, with geographic coordinates for localities with capuchins present in Supplementary Table S1. We surveyed both sides of the Piracicaba River, which was previously described as the southwestern geographical limit for *S. robustus* (Pinto, 1941), and we visited the Espinhaço Mountains.

WPM visited the collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, and the Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro, in order to examine morphological variation in the genus *Sapajus* to assist in the correct identification of the capuchin monkeys seen in the field. Skins cited in the literature and important for the establishment of geographical limits for *S. robustus* were examined with particular care (see section 4).

2.3 | Survey techniques—interviews

Locality buffer zones in 39 municipalities in Minas Gerais were visited to interview local people about their knowledge of the

presence or absence of capuchin monkeys. Capuchin monkeys are easily identified and described because of their distinct behavioral characteristics, such as their skill at manipulating objects and their propensity to forage in cornfields. Local residents-hunters and people who spend time in the forests-were interviewed because of their skill at recognizing animals and their ability to distinguish among different species of primates (Davis & Wagner, 2003). Interviewees were asked to identify monkeys from photos of all the primates recorded for Minas Gerais. They were also encouraged to describe the animals' physical characteristics (size, color) and some aspect of the behavior or the ecology of each species that they recognized (e.g., group size, calls, or typical behaviors). An interview was considered valid if the interviewee had some knowledge of the behavior or morphology of the monkeys and had spent time in the forest fragments in question. In practice, interviews describing the presence of capuchins were highly reliable because locals easily recognized the unique characteristics of these monkeys. Some people hated capuchin monkeys while some admired them for their propensity to attack cornfields, a behavior that has been described for Sapajus only among Atlantic Forest primates.

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Interviewees were also asked the exact location where they had seen each type of monkey. If an interviewee reported knowledge of a local capuchin monkey population somewhere other than the adjacent forest fragment, then further interviews were conducted at the location described.

TABLE 1 Results from valid interviews and corresponding forest surveys (corresponding geographic coordinates available in Supplementary Table S1).

Forest fragment			
number	Municipality	Primate genera reported	Primate species observed
1	Central de Minas	Sapajus	S. robustus
2	Senador Modestino Gonçalves	Alouatta; Sapajus	S. robustus
3	Turmalina/Leme do Prado	Sapajus	S. robustus
4	Poté	Alouatta; Callithrix; Sapajus	S. robustus; Callithrix geoffroyi
5	Carmésia	Alouatta; Callicebus; Callithrix; Sapajus	S. robustus × S. nigritus(Hybrid?)
6	Carmésia	Alouatta; Callicebus; Callithrix; Sapajus	S. robustus × S. nigritus(Hybrid?)
7	Guanhães	Callicebus; Callithrix; Sapajus	S. robustus × S. nigritus(Hybrid?)
8	Peçanha	Brachyteles; Sapajus	S. robustus × S. nigritus(Hybrid?)
9	Bocaiuva	Sapajus	Sapajus xanthosternos
10	Francisco Dumont	Callicebus; Sapajus	Sapajus xanthosternos; Callicebus personatus
11	Botumirim	Alouatta; Callicebus; Callithrix; Sapajus	Sapajus xanthosternos; Callithrix penicillata
12	Itinga	Alouatta; Callicebus; Callithrix; Sapajus	Sapajus xanthosternos; Callithrix penicillata
13	Lassance	Sapajus	Sapajus libidinosus
14	Lassance	Sapajus	Sapajus libidinosus; Callithrix penicillata
15	Lassance	Sapajus	Sapajus libidinosus; Callithrix penicillata
16	Carmo do Cajuru	Sapajus	Sapajus nigritus
17	Nova Era	Callithrix; Sapajus	Sapajus nigritus
18	Santa Maria de Itabira	Sapajus	Sapajus nigritus
19	Iguatama	Alouatta; Callicebus; Callithrix; Sapajus	Sapajus nigritus; Callithrix penicillata
20	Peçanha	Brachyteles	Brachyteles hypoxanthus
21	Virgolândia	Brachyteles	Brachyteles hypoxanthus
22	Felixlândia	Alouatta; Sapajus	Callithrix penicillata
23	Itinga	Alouatta; Callicebus; Callithrix; Sapajus	Callithrix penicillata
24	Turmalina/Leme do Prado	Callithrix	Callithrix penicillata
25	Varzea da Palma	Alouatta; Callithrix	Callithrix penicillata
26	Curvelo	Alouatta; Callithrix; Sapajus	Callithrix penicillata; Alouatta caraya
27	Botumirim	No primates reported	
28	Bocaiuva	No primates reported	
29	Bom Jesus do Amparo/ Barào de Cocais	Callicebus; Callithrix	No species observed
30	Botumirim	Callithrix; Sapajus	No species observed
31	Botumirim	Callithrix; Sapajus	No species observed
32	Botumirim	Sapajus	No species observed
33	Botumirim	Callithrix	No species observed
34	Botumirim	No primates reported	
35	Buenópolis	No primates reported	
36	Catas Altas	Callicebus; Callithrix	No species observed
37	Central de Minas	Callithrix; Callicebus	No species observed
			(Continues)

(Continues)

TABLE 1 (Continued)

TABLE I (Continued)			
Forest fragment number	Municipality	Primate genera reported	Primate species observed
38	Central de Minas	Callithrix	No species observed
39	Central de Minas	No primates reported	
40	Corinto	No primates reported	
41	Corinto	No primates reported	
42	Couto de Magalhães	Alouatta; Sapajus	No species observed
43	Curvelo	Alouatta; Callithrix	No species observed
44	Curvelo	Alouatta; Callithrix	No species observed
45	Curvelo	Alouatta; Callithrix	No species observed
46	Curvelo	Alouatta; Callithrix	No species observed
47	Diamantina	No primates reported	
48	Diamantina	No primates reported	
49	Diamantina	No primates reported	
50	Felicio dos Santos	Callicebus; Sapajus	No species observed
51	Felixlândia	No primates reported	
52	Felixlândia	No primates reported	
53	Felixlândia	Callithrix; Sapajus	No species observed
54	Felixlândia	Alouatta	No species observed
55	Felixlândia	Sapajus	No species observed
56	Felixlândia	Alouatta	No species observed
57	Felixlândia	Alouatta	No species observed
58	Felixlândia	No primates reported	
59	Felixlândia	Sapajus	No species observed
60	Felixlândia	Sapajus	No species observed
61	Felixlândia	No primates reported	
62	Felixlândia	No primates reported	
63	Felixlândia	No primates reported	
64	Felixlândia	Sapajus	No species observed
65	Ferros	Callicebus; Callithrix	No species observed
66	Ferros	Callithrix	No species observed
67	Ferros	No primates reported	
68	Francisco Dumont	No primates reported	
69	Francisco Dumont	No primates reported	
70	Francisco Dumont	No primates reported	
71	Francisco Dumont	Callithrix	No species observed
72	Galiléia	Callithrix; Callicebus	No species observed
73	Guanhães	Callicebus; Callithrix	No species observed
74	Guanhães	No primates reported	
75	Guanhães	Callicebus; Sapajus	No species observed
76	Guanhães	Callicebus	No species observed
77	Guanhães	No primates reported	
78	Guanhães	No primates reported	
79	Itacambira	No primates reported	
80	Itacambira	Sapajus	No species observed
81	Joaquim Felício	Alouatta	No species observed
			(Continues)

(Continues)

TABLE 1 (Continued)

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Forest fragment number	Municipality	Primate genera reported	Drimate species observed
number 82	Municipality Joaquim Felício	Primate genera reported No primates reported	Primate species observed
		• •	
83	Lassance	No primates reported	
84	Lassance	Sapajus	No species observed
85	Monjolos	Callithrix	No species observed
86	Monjolos	Alouatta; Callithrix	No species observed
87	Montes Claros	Callicebus	No species observed
88	Morro do Pilar	No primates reported	
89	Nova Era	No primates reported	
90	Nova Era	No primates reported	
91	Nova Era	No primates reported	
92	Nova Era	Callicebus; Sapajus	No species observed
93	Nova Era	Callithrix	No species observed
94	Nova Era	No primates reported	
95	Nova Era	Sapajus	No species observed
96	Nova Era	Sapajus	No species observed
97	Pocrane	Callithrix	No species observed
98	Poté	No primates reported	
99	Santa Maria de Itabira	No primates reported	
100	Santa Maria de Itabira	No primates reported	
101	Santa Maria de Itabira	Callicebus	No species observed
102	Santa Maria de Itabira	No primates reported	
103	Santa Maria de Itabira	Callicebus; Callithrix	No species observed
104	Santa Maria de Itabira	Callicebus; Callithrix	No species observed
105	Santa Maria de Itabira	No primates reported	
106	Santa Maria de Itabira	No primates reported	
107	Santo Hipólito	Alouatta; Callithrix	No species observed
108	Santo Hipólito	No primates reported	
109	Santo Hipólito	No primates reported	
110	Santo Hipólito	Alouatta; Callithrix	No species observed
111	São Gonçalo do Rio Abaixo	Callicebus; Callithrix	No species observed
112	São Gonçalo do Rio Abaixo	Sapajus	No species observed
113	São José do Buriti	No primates reported	
114	Senador Modestino Gonçalves	No primates reported	
115	Senador Modestino Gonçalves	No primates reported	
116	Senador Modestino Gonçalves	No primates reported	
117	Senador Modestino Gonçalves	No primates reported	
118	Senador Modestino Gonçalves	No primates reported	
119	Turmalima	No primates reported	
120	Turmalina	No primates reported	
121	Turmalina/Leme do Prado	Sapajus	No species observed
122	Varzea da Palma	No primates reported	
123	Varzea da Palma	No primates reported	
124	Varzea da Palma	Alouatta; Callithrix	No species observed
125	Várzea da Palma	Callithrix	No species observed
			(Continues)

TABLE 1 (Continued)

Forest fragment			
number	Municipality	Primate genera reported	Primate species observed
126	Várzea da Palma	Alouatta	No species observed
127	Várzea da Palma	Alouatta	No species observed

All municipalities listed are within the state of Minas Gerais, Brazil.

2.4 | Surveys with playbacks of vocalizations

When interviews suggested the presence of capuchin monkeys, the area was surveyed directly to confirm the presence or absence of the monkeys. Playback recordings of the calls of *S. robustus* and other *Sapajus* species were used to attract capuchin monkeys. The recordings were of a captive *S. robustus* in a colony at the Centro de Primatologia do Rio de Janeiro (CPRJ), and of *Sapajus* species from the audio recordings of Emmons, Whitney, and Ross (1998).

We used the playback method of previous studies (Diego, Ferrari, & Mendes, 1993; Kierulff, 1993; Mendes, 1993; Pinto, 1994), using existing trails and/or roads in the forest fragments. Fragments were sampled at an average walking speed of 2 km/hr, and the playback recording was played three times (at 3-min intervals) every 400 m,

pointing the speaker in the four compass points. When a group of capuchins approached in response to the calls, we identified the species, and observed if there was a mixed appearance to the group as a whole (i.e., if there were features typical of more than one *Sapajus* species present in individuals in the group).

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2.5 | Camera traps

In key locations where interviews suggested the presence of capuchin monkeys but we failed to find them using the playback recordings, we used camera traps, following the protocol established by Kierulff, Santos, Canale, Guidorizzi, and Cassano (2004). A camera trap was set on a platform with bait (banana or corn) during one month and photos



FIGURE 3 Detailed map of study area in Minas Gerais. All municipalities surveyed in the study are coded as follows: black, presence of *S. robustus* confirmed by direct observation in at least one location in that municipality; dark gray, presence of *Sapajus* asserted by at least one interviewee, but no *S. robustus* directly observed in that municipality; stipled, *S. robustus* × *S. nigritus* presumed hybrids observed in that municipality; striped, no evidence for *S. robustus* at localities or from interviews in that municipality



FIGURE 4 Map showing buffer zones and forest remnants overlaid on the historical distribution of the crested capuchin monkey (*S. robustus*). Only the buffer zones in Minas Gerais were visited for this study, as these encompassed the areas of uncertainty about crested capuchin distribution

were reviewed once a week. If, after this period, no capuchin monkeys were caught in camera trap photos, they were considered absent at that location.

2.6 | Geographical distribution map

The geographic coordinates of every capuchin monkey sighting were plotted, by species, using the software ArcGis 8.2 (ESRI, 2001). We then compared these locations to the locations from the literature (Hirsch et al., 2002) and to the provenance of museum skins. We defined the current geographical boundaries among *Sapajus* species in this region through this comparison of localities from the literature and the new information based on the present survey.

3 | RESULTS

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3.1 | Interviews and surveys using playback

The local presence of the genus *Sapajus* was reported in 39 of 127 valid interviews from 39 municipalities in Minas Gerais (Table 1 and Figure 3). We surveyed all 39 forest fragments where local people indicated that capuchin monkeys were present. Of these, we were able to confirm the presence of *Sapajus* through surveys in 19 forest fragments.

S. robustus was observed in four forest fragments, while other capuchin species were observed in 15 forest fragments (*S. robustus* × *S. nigritus* [hybrid?] in four, *S. xanthosternos* in four, *S. libidinosus* in three and *S. nigritus* in three). We never found two *Sapajus* species in the same municipality, except for the *S. robustus* × *nigritus* populations (described below). Field observations confirmed local interviewees' reports of the presence of capuchin monkeys as described in Table 1.

From the north bank of the Santo Antônio River to the Suaçuí Grande River there is a probable hybrid zone, as the capuchin monkey groups observed in this area contained morphological features common to or intermediate between *S. nigritus* and *S. robustus*.

No crested capuchin monkeys were found along the Piracicaba River, previously defined as the southwestern limit to their range (Pinto, 1941). At this location we found only a single group of *S. nigritus* (Forest fragment 17). Another group of *S. nigritus* was recorded north of the Piracicaba River near the Santo Antônio River (Forest fragment 18).

3.2 | Camera traps

Camera traps were used in only two localities, both on the west bank of the Das Velhas River, an important region for defining the western limits of the distribution of *S. robustus*. Using camera traps we recorded *S. libidinosus* at Lassance (Forest fragments 13, 14, and 15, see Figure 5), but no capuchin species were found at Curvelo (Forest fragment 43, represented as a question mark icon in the map on Figure 6).

3.3 | Distributional limits

We plotted all our positive results (forest fragments with the confirmed presence of *S. robustus*) and previously described locations (when not contradicted by our current results) to delimit the geographical distribution of *S. robustus* (Figure 6), and update the previously described limits of *S. robustus* (Table 2). Our revised estimated distribution is 119,654.18 km², most of which (58% or 69,399.49 km²) is in the state Minas Gerais, the remainder divided between Bahia (24% or 28,717.11 km²) and Espírito Santo (18% or 21,537.78 km²). This is a reduction of about 70,000 km² from our estimate of the previously described total range for *S. robustus*.

4 | DISCUSSION

The major findings in our study include (1) a significant decrease in the western and southwestern range of *S. robustus* in Minas Gerais; and (2) a potential hybrid zone between *S. robustus* and *S. nigritus* between the Suaçui Grande and Santo Antônio rivers. Our results also indicate the expansion of previously described distributional limits for *S. xanthosternos*, *S. libidinosus*, and *S. nigritus*.

The range of *S. robustus* is delimited by rivers in the north and south, the Atlantic Ocean in the east and the Espinhaço Mountains in the west. Interviews suggested that crested capuchin monkeys were capable of crossing the Jequitinhonha River in certain places, although this was not confirmed. In its upper reaches the river flows through a narrow valley and in some places the tree crowns on either side of the river are close or in contact, providing potential bridges. In the middle reaches it is conceivable that monkeys can cross the river during the dry season. On the western (right) bank of the river there is a forest large enough to support a group of capuchin monkeys. However, even if the monkeys cross the river, heading west, the forest is quickly replaced by shrubs and



FIGURE 5 The bearded capuchin (*Sapajus libidinosus*) at Lassance, east of the São Francisco River, in Minas Gerais. Photo taken with camera trap at Forest Fragment 13 (see Table 1)

grasslands at higher elevations on the Espinhaço Mountains, limiting the monkeys' ability to disperse farther west.

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The previously described western limit for *S. robustus* was based on specimens in the Museu Nacional, Rio de Janeiro, collected in 1947 from the municipality of Curvelo, just east of the upper São Francisco River and west of the Das Velhas River (Forest fragment 43; see Figure 6) (see Kinzey, 1982). We visited the municipality of Curvelo, where the skins were reported to have been collected in 1947. Kinzey (1982) and Silva (2001) concluded that the skins collected there are hybrids of *S. robustus* and *S. libidinosus*. The forest where they were collected has since been divided into four small farms with only one forest patch remaining. We sampled this forest extensively (seven expeditions, using playback recordings and camera traps with bait) but no capuchins were seen, heard, or photographed.

A group of bearded capuchin monkeys (S. libidinosus) was photographed with a camera trap (Figure 5) just 65 km north from Curvelo, in the municipality of Lassance (Forest fragment 13, also observed at Forest fragments 14 and 15), also on the western bank of the Das Velhas River. We also recorded a group of yellow-breasted capuchin monkeys (S. xanthosternos) on the eastern bank of the Das Velhas River (Forest fragment 10). Our results suggest that for S. robustus to occur at Curvelo, it would have to cross the upper Jequitinhonha River (its currently identified western geographical limit), the Espinhaço Mountains (in which the Atlantic Forest vegetation is replaced by shrub and grassland on the west side of the mountains), the southwestern limit of its congener S. xanthosternos, and the Das Velhas River. This seems unlikely, and suggests that perhaps the labels of the skins were accidentally changed since 1947. We identified the museum skins currently tagged with these labels as belonging to the black horned capuchin S. nigritus.

Previous studies of the southwestern limit of S. robustus contain several discrepancies. Pinto (1941) contradicted himself as to which bank of the Doce River he collected specimens of S. robustus. He indicated the collection locality as on the left bank at Doce River on page 111, and on the right bank of the river at Doce River on page 113. The locality was considered to mark the southwestern limit for the species. Pinto (1941; pp.116-117) also made an ambiguous remark about the features of a specimen (MZUSP-5921) collected in the municipality of Nova Era (formerly Presidente Vargas): "in females, however, you can notice very important differences that could motivate observers at first to suppose they belong to another species. These differences are the encephalic helmet, whose configuration never looks like the other species described above [S. robustus], and their hairs, besides not being that long are distributed ordinarily in two tufts or a tuft laterally separated." He gave a similar morphological description in the same paper referring to Cebus cirrifer (currently known as S. nigritus). In a later reanalysis, the same female skin (MZUSP-5921) was ambiguously assigned to species by Silva (2001). Torres de Assumpção (1983) described the collection locality of this same specimen in Nova Era (formerly Presidente Vargas) as "Fazenda Esperança" and not its correct name, "Fazenda Boa Esperança." In our survey, we found that capuchin monkeys in the municipality of Nova Era (Forest fragment 18) displayed the morphological features of



FIGURE 6 Map showing revised geographical distribution of crested capuchin monkey (S. robustus) and its intergradation zone with S. nigritus

S. nigritus. We concluded that the Nova Era specimen MZUSP-5921 should be assigned to S. nigritus.

North of Nova Era, from the northern bank of the Santo Antônio River to the southern bank of the Suaçui Grande River, we found evidence for capuchin monkeys with morphological features of both S. robustus and S. nigritus, even in the same group; some individuals displayed characteristics intermediate between S. nigritus and S. robustus, such as two narrowly spaced but distinct tufts near the center of the top of the head. This hybrid zone is quite large; it extends over 14,394 km² (Figure 6). In three municipalities visited there-Pecanha (Forest fragment 8), Guanhães (Forest fragment 7), and Carmesia (Forest fragments 5 and 6)-capuchin groups included some

TABLE 2 Geographical limits identified for S. robustus (see Figure 6)

Northeast	Jequitinhonha River in Bahia and Minas Gerais
Northwest	Jequitinhonha River in Minas Gerais
West	Jequitinhonha River and Espinhaço Mountains in Minas Gerais
Southwest	Suaçuí Grande River and Espinhaço Mountains in Minas Gerais
Southeast	Doce River in Minas Gerais and Espírito Santo
East	Atlantic Ocean
Probable hybrid zone	Between the Santo Antônio River and Suaçuí Grande River in Minas Gerais

individuals with hybrid features as well as "typical" individuals of S. nigritus travelling in groups of S. robustus. The "typical" S. nigritus individuals were identified as such based on morphological features such as a white facial mask and two high and erect tufts forming two separate horns (Silva, 2001). Their presence in groups of crested capuchin monkeys suggests hybridization. More studies of morphological and genetic variation are needed to understand the crossspecies dynamics for capuchin monkeys in this region.

4.1 | Conservation implications

The discrepancy between the reports of the interviewees noting the local presence of capuchin monkeys and the negative results from surveys and playback in many forests in Minas Gerais suggest that the crested capuchin monkey population is in decline and has been extirpated in many forests. The combined results of the loss of monkey populations in forest patches, a smaller range than was previously believed, and a hybrid zone within the former range for this species highlight the urgency for conservation action and research on this species.

4.2 | Expansion of the ranges of S. nigritus, S. xanthosternos, and S. libidinosus

Our surveys unexpectedly revealed new data points for the presence of three capuchin species beyond their described ranges. The distribution

of *S. nigritus* was extended north to Nova Era (Forest fragment 17) and Santa Maria de Itabira (Forest fragment 18), formerly thought to be within the range of *S. robustus. Sapajus libidinosus* was recorded in Lassance (Forests fragments 13, 14, and 15) extending its known range to the east of the São Francisco River. We observed *S. xanthosternos* on the east bank of the Das Velhas River (Forest fragment 10), a region also previously described as in the range of *S. robustus.* Continued monitoring of these border areas will be important in understanding the dynamics of peripatry, species boundaries, interspecific competition, and hybridization for *Sapajus* species.

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