An Introduction to the *Callithrix* Genus and Overview of Recent Advances in Marmoset Research

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Abstract

We provide here a current overview of marmoset (*Callithrix*) evolution, hybridization, species biology, basic/biomedical research, and conservation initiatives. Composed of 2 subgroups, the *aurita* group (*C aurita* and *C flaviceps*) and the *jacchus*

group (*C geoffroyi*, *C jacchus*, *C kuhlii*, and *C penicillata*), this relatively young primate radiation is endemic to the Brazilian Cerrado, Caatinga, and Atlantic Forest biomes. Significant impacts on *Callithrix* within these biomes resulting from anthropogenic activity include (1) population declines, particularly for the *aurita* group; (2) widespread geographic displacement, biological invasions, and range expansions of *C jacchus* and *C penicillata*; (3) anthropogenic hybridization; and (4) epizootic Yellow Fever and Zika viral outbreaks. A number of Brazilian legal and conservation initiatives are now in place to protect the threatened *aurita* group and increase research about them. Due to their small size and rapid life history, marmosets are prized biomedical models. As a result, there are increasingly sophisticated genomic *Callithrix* resources available and burgeoning marmoset functional, immuno-, and epigenomic research. In both the laboratory and the wild, marmosets have given us insight into cognition, social group dynamics, human disease, and pregnancy. *Callithrix jacchus* and *C penicillata* are emerging neotropical primate models for arbovirus disease, including Dengue and Zika. Wild marmoset populations are helping us understand sylvatic transmission and human spillover of Zika and Yellow Fever viruses. All of these factors are positioning marmosets as preeminent models to facilitate understanding of facets of evolution, hybridization, conservation, human disease, and emerging infectious diseases.

Key words: arbovirus; biological invasion; biomedical; Brazil; callitrichid; conservation; endangered; hybridization; neotropical; pathogen

BACKGROUND

The small, charismatic Brazilian monkeys that compose the *Callithrix* genus have special relevance in biomedicine, evolutionary/hybridization studies, and burgeoning conservation work. In this review, we first give a general overview of the 6 *Callithrix* species by discussing their biogeography, evolutionary relationships, and demographic history. Then we focus on unique behavioral, ecological, demographic, and/or conservation aspects of individual species. The final section of this review summarizes a number of recent, novel, and neglected aspects of captive and wild *Callithrix* research. Specifically, we discuss (1) unique aspects of *Callithrix* biology relative to biomedical research; (2) recent comparative, functional, and population *Callithrix* genomics work; (3) biomedical relevance of *Callithrix* in viral studies, *Callithrix* susceptibility to viral disease, and the *Callithrix* virosphere; (4) natural and anthropogenic *Callithrix* hybridization; (5) legislative and conservation aspects of *Callithrix* population management; and (6) anthropogenic impacts on *Callithrix* populations. We conclude this review by identifying new avenues for wild and captive *Callithrix* research.

AN OVERVIEW OF THE *CALLITHRIX* GENUS

Callithrix Biogeography and Evolutionary History

The *Callithrix* genus is composed of 6 naturally allo- and parapatric species (Figure 1) endemic to Brazil.[1] Phylogenetic analysis of mitogenomes (Figure 2) shows that this genus diverged from the Amazonian *Cebuella*/*Mico* clade approximately 6.83 million years ago (MYA) (Node E, Figure 2).[2] Then the genus separated into 2 subgroups, the *aurita* group (*C aurita* and *C flaviceps*) and *jacchus* group (*C geoffroyi*, *C jacchus*, *C kuhlii*, *C penicillata*), approximately 3.54 MYA (Node D, Figure 2). Within the *jacchus* group, *C geoffroyi* represents the most basal lineage, having arisen approximately 1.18 MYA (Node C, Figure 2). Mitochondrial (mtDNA) phylogenies show *C kuhlii* and *C penicillata* clades as polyphyletic, likely due to incomplete lineage sorting.[2] Finally, the *C jacchus* clade arose approximately 0.5 MYA as the sister clade to one of the polyphyletic *C penicillata* clades (Node A, Figure 2).

Callithrix marmosets likely originated within the southeastern Atlantic Forest, after a vicariant event split them from the Amazonian marmosets, and then spread northward along the coast and into the Brazilian interior.[3] *Callithrix aurita*, *C*

flaviceps, *C geoffroyi*, and *C kuhlii* are endemic to the Atlantic Forest biome.[1,3] However, *C geoffroyi* is also found in the semi-arid regions of northeastern Minas Gerais and southern Bahia.[1] *C jacchus* can be found in the Atlantic Forest and the semi-arid Caatinga biome of northeastern Brazil.[1] *C penicillata* mostly occurs in the semi-arid Cerrado of central and central-western Brazil[1] but also is found in the Caatinga (personal observation, Joanna Malukiewicz, Luiz CM Pereira).[4]

Callithrix Natural Geographic Ranges

C aurita, or the buffy-tufted-ear marmoset, inhabits submontane and montane forests of the Atlantic Forest biome at altitudes above 500 m.[5] Environmental factors such as altitude, climate, and phytophysiognomy may play key roles in determining *C aurita*–suitable habitats.[6,7] The northwestern limits of the *C aurita* range reach transitional regions between the Atlantic Forest and Cerrado in São Paulo and Minas Gerais states.[1,5] Hershkovitz[8] placed the northeastern limit of the species' distribution in Minas Gerais state at the right bank of the Muriaé river. However, Mittermeier et al[9] noted that the species also inhabits the region north of the Rio Doce State Park in Minas Gerais state but does not exceed the northern limits of the Doce river. More specifically, the northern distribution of *C aurita* may occur at the confluence of the Piracicaba and Doce rivers, north of the Rio Doce State Park in Minas Gerais.[9] The southern limit of *C aurita*'s range is undefined but it probably advances through the Serra do Mar mountain range, possibly to the forest massif of Paranapiacaba.[10]

With a geographical distribution of 30 815 km², *C flaviceps*, or the buffy-headed marmoset, possesses the smallest *Callithrix* geographic distribution.[11] This species occurs in mountainous regions of Espírito Santo and Minas Gerias states at altitudes up to at least 1200 m.[11] Its range begins south of the Doce river[5] and continues into the Serra da Mantiqueira mountain range in the south of Espírito Santo where this state borders Rio de Janeiro state.[1] However, the *C flaviceps* range may reach to the far north of Rio de Janeiro state.[1,12] An unconfirmed *C flaviceps* occurrence was reported in the municipality of Varre-Sai, northern Rio de Janeiro state.[13]

The northern distribution limit of *C kuhlii*, or Wied's marmoset, occurs at the Contas river in Bahia state and the southern limit is the Jequitinhonha river in Minas Gerais state.[1] There are recent reports of *C kuhlii* to the north beyond the
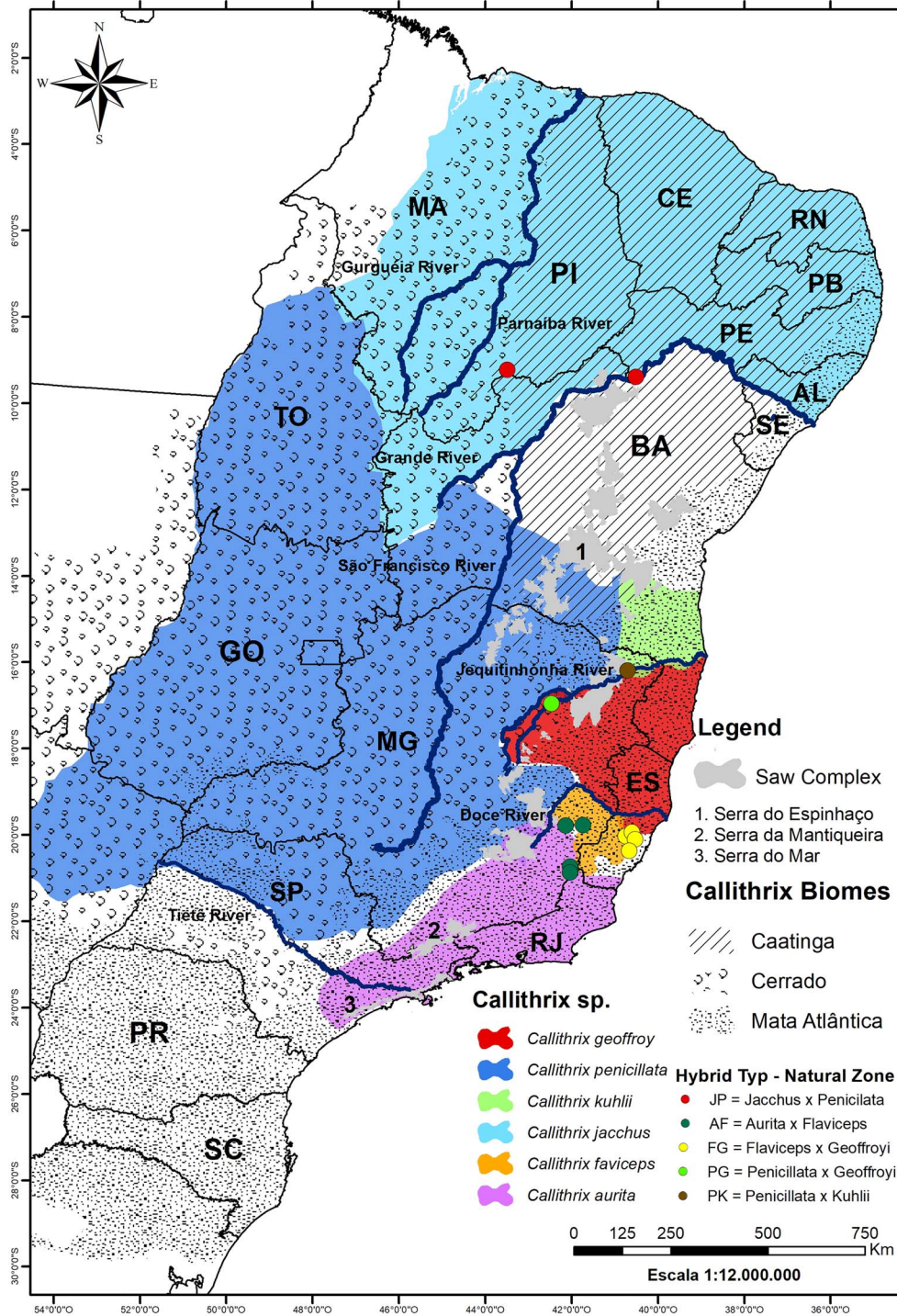
Figure 1: Maps of natural Brazilian *Callithrix* ranges, following Rylands ,[1] and natural hybrid zones, following Malukiewicz.[21] Each range is color-coded by species, and respective hybrid zones are shown as points. Abbreviations stand for Brazilian states: AL = Alagoas; BA = Bahia; ES = Espírito Santo; CE = Ceará; GO = Goiás; MA = Maranhão; MG = Minas Gerais; PB = Paraíba; PI = Piauí; PE = Pernambuco; PR = Paraná; RJ = Rio de Janeiro; RN = Rio Grande Do Norte; SE = Sergipe; SP = São Paulo; TO = Tocantins. Hybrid zone: AF = *C aurita* × *C flaviceps*; FG = *C flaviceps* × *C geoffroyi*; JP = *C jacchus* × *C penicillata*; PG = *C geoffroyi* × *C penicillata*; PK = *C penicillata* × *C kuhlii*.

Contas river, in the region of Valença, Bahia,[12] and within the vicinity of Todos os Santos Bay, Bahia (personal observation, Vanner Boere and Ita de Oliveira e Silva).[14] The eastern limit of *C kuhlii*'s distribution reaches the Atlantic Ocean, and the Cerrado likely terminates the species' natural distribution to the west.[15]

C geoffroyi, or Geoffroy's tufted-ear marmoset, generally occurs in the Atlantic Forest at altitudes below 500–700 m.[1] The southern bank of the Jequitinhonha river and eastern bank of the Araçuai river represent upper limits of the *C geoffroyi* range.[1] *C geoffroyi* occurrences have also been recorded in the Espinhaço Mountains, Minas Gerais state (see Figure 1), which are located
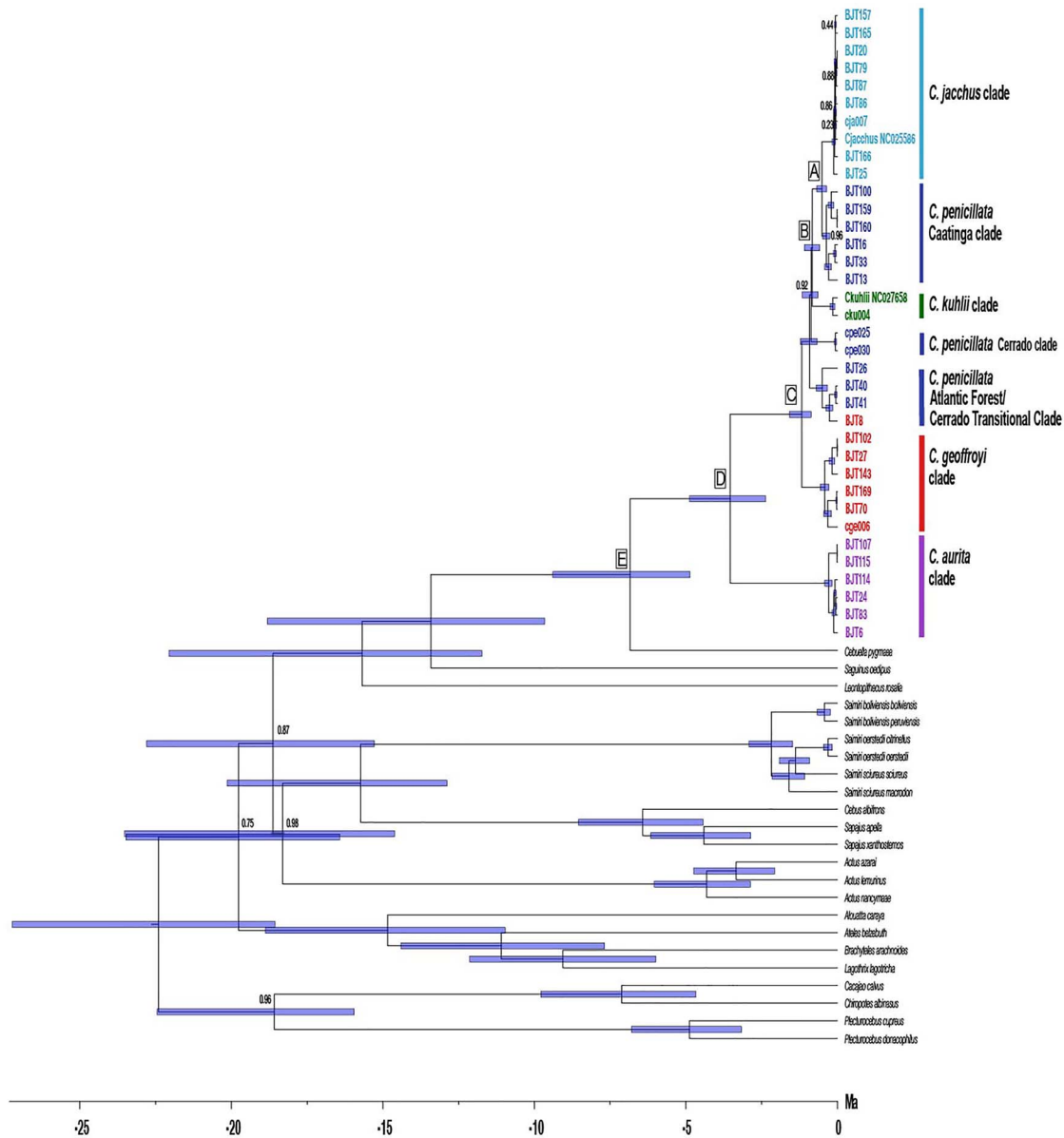
Figure 2: BEAST - Bayesian phylogeny showing divergence patterns and temporal divergence estimates between *Callithrix* mitogenomic lineages, modified from Malukiewicz et al.[2] Boxed letters represent major divergence nodes among *Callithrix* clades. "Ma" stands for millions of years.

at the western Atlantic Forest limit.[16] Additionally, the species has been observed in the region between the Jequitinhonha and Doce rivers, in the north and northeast of Minas Gerais state, but it is not clear whether *C geoffroyi* was introduced there or occurs there naturally.[15,17] Although *C geoffroyi* is considered a lowland species, it has been observed in the Serra do Cipó National Park, Minas Gerias state, at 1274 m above sea level.[1,12] The species has also been observed in a semi-arid region of northeastern Minas Gerais state on the western bank of the Araçuai river in Berilo municipality (personal observation, Joanna Malukiewicz).

C penicillata, or the black-tufted marmoset, has the widest *Callithrix* geographic distribution, with an area of approximately 1 300 000 km[2].[15,16,18] The northern *C penicillata* range seems limited by the Grande and São Francisco rivers.[15,16] The eastern limits of the *C penicillata* range seem bounded by the Araguaia river's course through Goiás, Mato Grosso, and Tocantins states. This species can also be found in the north of São Paulo state,

north of the Tietê and Piracicaba rivers,[8] as well as eastern Minas Gerais and southern Bahia states, where *C penicillata* has contact zones with *C geoffroyi*, *C aurita*, *C flaviceps*, and probably *C kuhlii*.[1,15,16]

For the currently recognized *C penicillata* distribution, several unfilled gaps still exist in the occurrence of this species, particularly within the Caatinga biome. Although the southern portion of the Caatinga is recognized by Rylands et al[1] as part of the natural distribution of *C penicillata*, we have observed occurrences of *C penicillata* in northern parts of the Caatinga (Figure 3) (personal observation, Luiz CM Pereira and Joanna Malukiewicz). The dataset of da Rosa et al[19] lists several occurrences of *C penicillata* as "alien" in the northern Caatinga, where no *Callithrix* are thought to occur naturally. We, however, would like to note that the Caatinga *sensu stricto* is one of the youngest Brazilian vegetation formations, originating approximately 15–10 MYA.[20] Further, the *C penicillata* Caatinga clade and the
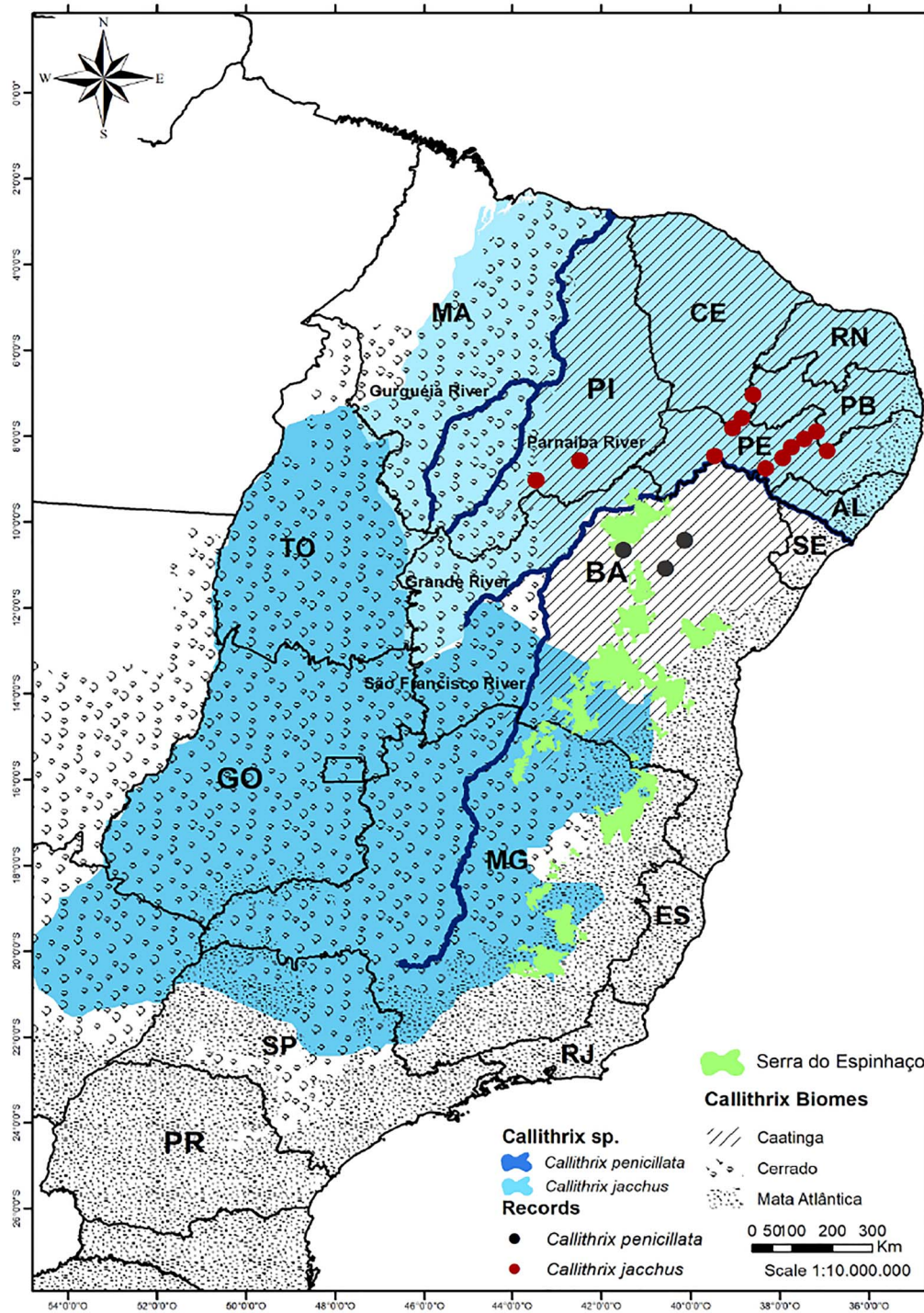
Figure 3: Light blue and darker blue regions respectively represent natural *C jacchus* and *C penicillata*, ranges following Rylands et al.[1] Maroon and black dots respectively represent unpublished *C jacchus* and *C penicillata* occurrences observed by Luiz CM Pereira and Joanna Malukiewicz. Abbreviations stand for Brazilian states: AL = Alagoas; BA = Bahia; ES = Espírito Santo; CE = Ceará; GO = Goiás; MA = Maranhão; MG = Minas Gerais; PB = Paraíba; PI = Piauí; PE = Pernambuco; PR = Paraná; RJ = Rio de Janeiro; RN = Rio Grande Do Norte; SE = Sergipe; SP = São Paulo; TO = Tocantins.

C jacchus clade represent the 2 youngest clades within the phylogeny shown in Figure 2. Thus, these occurrences of *C penicillata* in the Caatinga may be part of a natural expansion of this marmoset species from the Cerrado into the Caatinga.

C jacchus, or the white-tufted marmoset, occurs in northeastern Brazil.[1] The southern portion of its geographic distribution extends to the northern bank of the São Francisco river and the west bank of the Rio Grande river.[1] Whereas the northern and eastern portion of the *C jacchus* natural distribution is limited by the Brazilian Atlantic coast, the species' western limits are less clear.[1] Currently recognized limits of the natural *C jacchus* distribution are at the boundary between Tocantins and Maranhão states, but the species may also occur in the northeast of Tocantins state.[1]
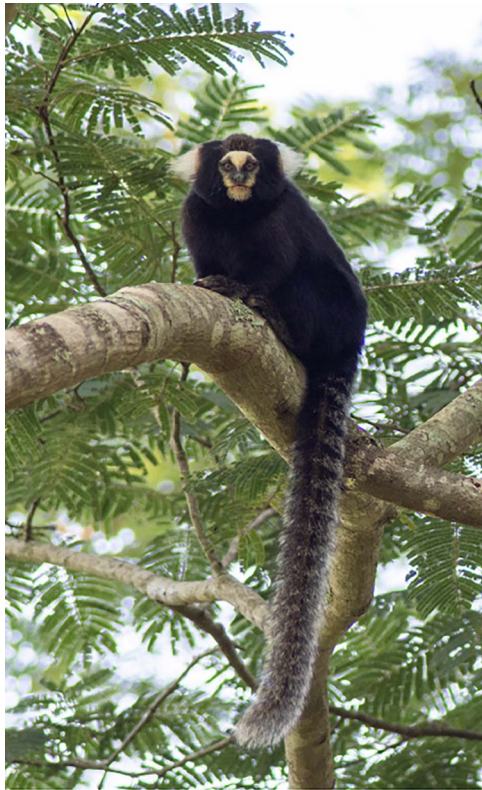
Figure 4: Image of *C aurita*. Photo credit: Orlando Vital.

Natural *Callithrix* Hybridization

Callithrix species are a relatively recent primate radiation, and secondary contact between *Callithrix* species at the borders of their natural geographical distributions can result in natural hybridization (Figure 1). One natural hybrid zone exists in the mountains of Espírito Santo state, where hybrids of *C flaviceps* and *C geoffroyi* occur in an area of overlap between altitude limits for each parental species.[5] A number of natural hybrid zones occur at major river boundaries between *C penicillata*'s natural distribution and that of other congeners (Figure 1).[21] *C aurita* and *C flaviceps* hybridize naturally in a region that roughly overlaps the borders of Minas Gerais, Rio de Janeiro, and Espírito Santo states. Climatic factors that shape *C flaviceps*' natural distribution and past climatic fluctuations may determine locations of natural *C aurita* and *C flaviceps* hybrid zones.[22] We have observed natural *C jacchus* and *C penicillata* hybrids along the banks of the São Francisco river between Petrolina, PE, and Juazeiro, BA,[4,21] as well as in Xique-Xique, BA (personal observation, Luiz CM Pereira). Natural hybrids between the 2 species have also been observed at the northern tip of the Espinhaço mountain range, where there is a mixture of Cerrado, Caatinga, and semi-deciduous forests (personal observation, Luiz CM Pereira).

CHARACTERISTICS AND DIFFERENCES BETWEEN CALLITHRIX SPECIES

C aurita

The total population size of adult *C aurita* (Figure 4) is estimated to be 10 000 individuals, and the species is currently listed as endangered.[10] *C aurita* social groups usually possess a single male–female breeding pair, although groups with multiple breeding females have been noted.[23,24] Group size varies from 5 to 11 individuals.[7,25] Population density for *C aurita* also varies from 2.8 individuals/km² in the Serra do Brigadeiro State Park, MG,[26] to 14.76 individuals/km² in the Pouso Alegre Municipal Natural Park, MG.[27] The home range size for a *C aurita* group is approximately 11 hectares.[28] The suitability of a given habitat for *C aurita*, considering topography and forest composition, may ultimately determine population density within a given region.[6] While conducting linear transect surveys, Norris et al[6] estimated a general population of 1892 individuals in a 250.7-km² area of Atlantic Forest in southern São Paulo state.

Several morphological differences distinguish *C aurita* from other *Callithrix* species. *C aurita* is perhaps the largest *Callithrix* species considering body weight and overall body size (Figure 5; Table 1). *C aurita* shares morphological similarities with *C flaviceps* [eg,[29]], likely due to the close evolutionary relationship between them.[5] For example, Souza[29] noted a larger brain case size in the *aurita* group, relative to the *jacchus* group, as well as retrusions of the upper and lower jaws. Differences in cranial morphology between *C aurita* and *C flaviceps* include greater lateral expansion of the parietal bone and elongation of the occipital bone in *C aurita* but more lateral nasal compression and larger incisors in *C flaviceps*.[29]

Morphological differences between the *aurita* and *jacchus* groups are likely related to stronger morphological specialization for gumnivory in the latter group.[28,29] In a 17-ha forest fragment in Minas Gerais state, *C aurita* consumed 50.5% gums, 11% fruits, and 38.5% prey.[30] Gums are generally accessed by *C aurita* from sources that do not require gouging.[10] The species also consumes fungi fruiting bodies from bamboo of the Poaceae family.[10]

C flaviceps

C flaviceps (Figure 6) is one of the least studied *Callithrix* taxa. The species is listed as critically endangered,[11] because a total of approximately 2000 adult *C flaviceps* individuals likely remain in the wild.[11] In secondary forests, *C flaviceps* occupies areas sized between 15 ha and 35.5 ha,[31–33] but in denser forests, 138.5-ha home ranges have been observed.[34] These home range sizes are among the largest for any *Callithrix* species.[32,33] On average, *C flaviceps* travels 1222.5 m/d, but food scarcity during the dry season likely causes the species to have longer daily travel than in the rainy season.[7] The size of *C flaviceps* social groups is between 3 and 15 members.[31] Although social groups tend to have 1 reproductive female, there are occasionally 2 or more reproductive females and several adult helpers that care for offspring.[35]

The *C flaviceps* dentition, like that of *C aurita*, is less specialized for gummivory than that of the *jacchus* group,[36] and the species' consumption of fruits, insects, and fungi varies seasonally.[34] *C flaviceps* uses a "scan and pounce" approach to foraging for small prey.[37] The consumption of fungi is especially high in this species and can compose up 65% of the total items consumed.[34,38] Gum consumption by *C flaviceps* is mostly opportunistic, because this species exploits gums from tree holes made by wood-digging insects.[7]

C geoffroyi

C geoffroyi is characterized by a white face and black voluminous ear tufts. The species appears to be the largest *jacchus* group for average body weight and size (Figure 5; Table 1).
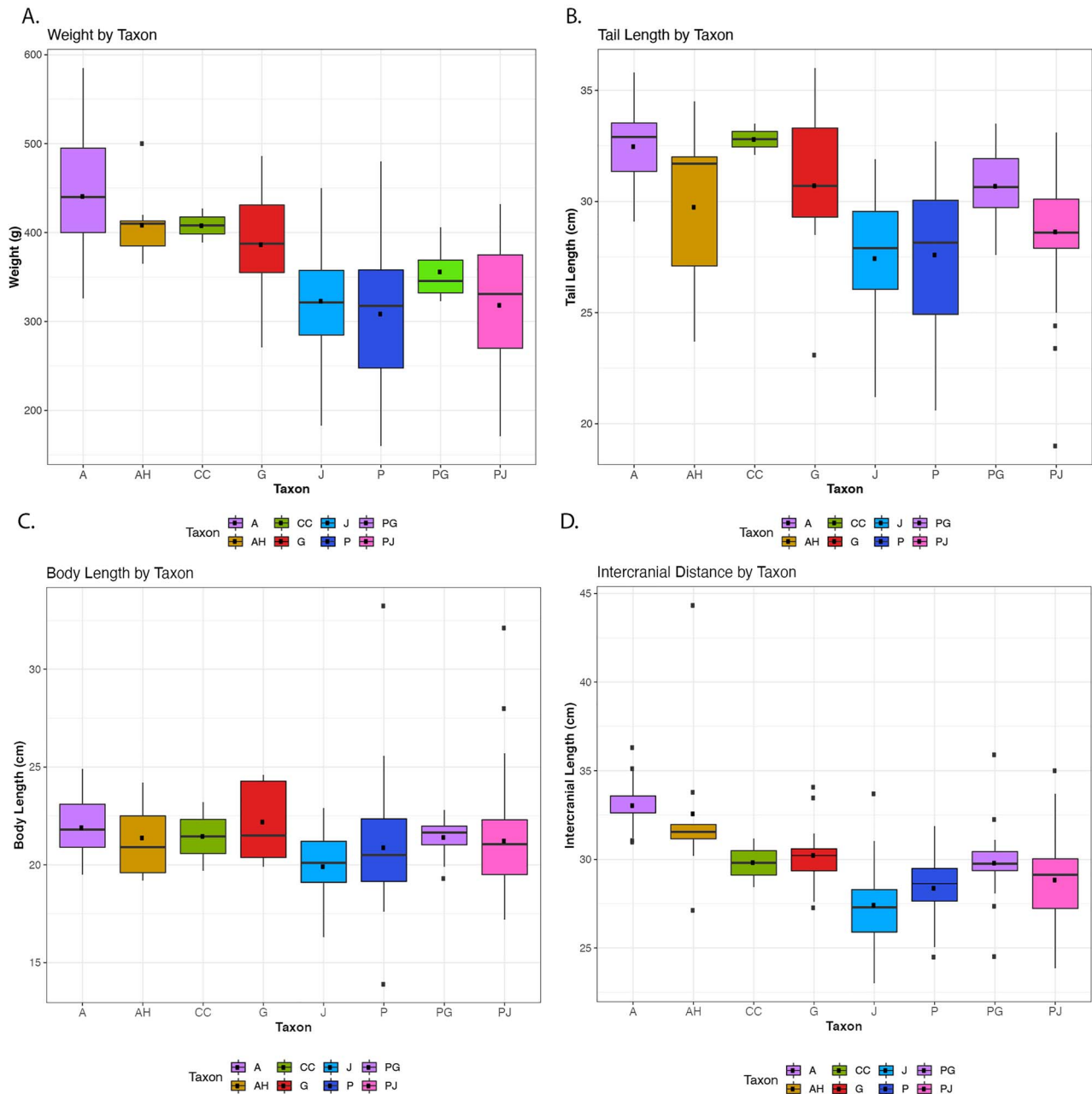
Figure 5: Boxplots of body weight (A), tail length (B), body length (C), and intercranial length for select *Callithrix* species and hybrid types. Modified from Malukiewicz et al. (unpublished data). A = *C aurita*; AH = *C aurita* hybrid; CC = unidentified hybrid; G = *C geoffroyi*; J = *C jacchus*; P = *C penicillata*; PG = *C penicillata* × *C geoffroyi* hybrid; PJ = *C penicillata* × *C jacchus* hybrid.

One *C geoffroyi* social group in an Atlantic Forest patch was composed of a single female, 2 males, and 2 juveniles.[39] The same group had a total home range size of 23.3 ha, but that varied between 4.9 ha in the rainy season and 7.2 ha in the dry season,[39] which is likely related to distribution of nutritional resources. The group's daily ranging distances varied from 480 to 1980 m.[39] In a 110-ha forest fragment in Espírito Santo state, major food categories for 1 *C geoffroyi* group were, on average, gums (68.6%) fruits (15%) and prey (invertebrates 14.6% and vertebrates 0.8%), although utilization of these items varied seasonal.[40] This same group preyed on insects, arachnids, gastropods, lizards, and frogs.[41] Population densities for *C geoffroyi* in northern Espírito Santo ranged from 0.7 groups/km^2

to 7.5 groups/km^2, generally being higher in larger fragments (approximately 20 000 ha) than in smaller fragments (approximately 200 ha).[41]

In general, *C geoffroyi* seems highly flexible in the types of habitats that it can occupy. Forested environments occupied by *C geoffroyi* include dense and semi-deciduous forests of the Atlantic Forest as well as deciduous Caatinga forests.[15] The species is tolerant of secondary habitats, for example, being able to utilize forest fragments surrounded by eucalyptus monoculture.[40,41] Across all of its range, the species also occurs commonly in urban areas, where it occupies orchards, backyards, and forest fragments (personal observation, Joanna Malukiewicz, Vanner Boere).

Table 1 Means of 13 Morphometric Measures

Taxa	Weight (g)	Tail (cm)	Body (cm)	IC (mm)	FO (mm)	Zyg (mm)	Jaw (mm)	Hand (mm)	Humerus (cm)	Forearm (cm)	Femur (cm)	Tibia (cm)	Foot (mm)
A	440.6 (25)	32.3 (26)	21.9 (27)	33.1 (27)	42.6 (27)	31.4 (23)	23.7 (23)	30.5 (21)	5.4 (26)	5.2 (27)	6.5 (27)	7.2 (27)	61.1 (24)
AH	408.1 (9)	29.7 (9)	21.4 (9)	32.6 (9)	38.8 (9)	30.3 (9)	26.3 (9)	39.0 (9)	5.2 (9)	5.2 (9)	6.4 (9)	7.2 (9)	57.9 (9)
G	386.2 (14)	30.7 (14)	22.2 (14)	30.2 (14)	40.2 (14)	30.1 (14)	25.7 (14)	36.3 (13)	5.3 (14)	4.8 (14)	6.3 (14)	7.1 (14)	55.4 (14)
J	322.6 (30)	27.4 (30)	19.9 (29)	27.4 (29)	39.7 (24)	28.7 (29)	22.2 (29)	35.4 (28)	4.7 (29)	4.5 (29)	5.5 (29)	6.6 (29)	54.7 (27)
P	308.4 (54)	27.7 (54)	20.9 (52)	28.4 (54)	39.8 (50)	28.6 (51)	22.9 (52)	35.2 (48)	4.6 (54)	4.6 (54)	5.8 (54)	6.5 (54)	54.2 (54)
PG	355.8 (18)	30.7 (18)	21.4 (18)	29.8 (18)	37.7 (18)	30.3 (18)	22.7 (18)	36.8 (9)	5.1 (18)	4.8 (18)	6.6 (18)	7.1 (18)	53.3 (16)
PJ	317.9 (53)	28.7 (53)	21.3 (54)	28.9 (54)	39.2 (49)	29.1 (53)	23.7 (53)	34.4 (50)	4.7 (54)	4.6 (54)	5.8 (54)	6.7 (54)	54.4 (54)

Numbers in parentheses represent the number of samples for a given measure. Taxa abbreviations are as follows: A = *C aurita*; AH = *C aurita* × *Callithrix sp*; G = *C geoffroyi*; J = *C jacchus*; P = *C penicillata*; PG = *C penicillata* × *C geoffroyi*; PJ = *C penicillata* × *C jacchus*. Modified from Malukiewicz et al (unpublished data). FO = cranial frontal-occipital distance; IC = intercranial distance; jaw = intermandibular distance; Zyg = distance between zygomatic arches.

C jacchus

C jacchus (Figure 7) is one of the smallest *Callithrix* species (Table 1; Figure 5), and several of its biological traits seem associated with a high level of specialization for exudivory.[28] Exudivory adaptations of *C jacchus* include chewing muscles for production of relatively large tree-gouging gapes[42] and an enlarged caecum as part of a digestive system that optimizes digestion of tree gums.[43] Further, Souza[29] attributed the compressed brain case and protruding zygomatic arches of the *jacchus* group to tree-gouging adaptations. *C jacchus* and its sister species, *C penicillata*, also share derived dentition patterns,[36] which also likely represent exudivory adaptations.

Few *Callithrix* species have home ranges as small as those of *C. jacchus*. In comparing Atlantic forest–living marmosets and Caatinga-living marmosets, the former had a mean group composition of 8.3 individuals whereas Caatinga mean group size was 5.9.[44] When comparing the animals' home range between these 2 environments, Atlantic forest–living animals had a slightly smaller mean home range (4.1 ha) than Caatinga-living animals (mean 5.3 ha).[44] Castro and Araújo[45] found that *C jacchus* feed on fruit, gums, and invertebrates, but fruit and gum consumption was negatively related and influenced by seasonality. In contrast, Abreu et al[46] did not observe a seasonal difference in gum consumption in Caatinga-living individuals. However, insect consumption was significantly higher in the rainy season.

Common marmosets are highly adaptive,[44,46,47] and their inhabitance of the Caatinga represents an ecological challenge related to heat stress and limited resources such as water.[48] The species' adaptability warrants the question as to what makes their ecological success possible. The species' funnel-shaped teeth and ability to cling vertically on tree trunks facilitate exudate extraction.[49] Having a cooperative breeding system and production of 2 litters per year[50] coupled with complex cognitive abilities[51] certainly contribute to *C jacchus*' ecological success. However, behavioral adjustments might be the key factor for navigating the challenges of the Caatinga.[46,47] Behavioral modification for dealing with heat stress can be observed by Caatinga common marmosets, who rest twice as much as Atlantic Forest marmosets,[47] live in smaller groups, and appear to have a higher ratio of surface area to body mass.[49] Additionally, Caatinga marmosets eat cactus, which requires cognitive skills to access the resource while avoiding injury.[46]

C kuhlii

The home range of *C kuhlii* varies from 10 to 58.3 ha,[52] and daily ranging distance is estimated to be as far as 1498 m, which is the longest among *Callithrix* species.[53] In this species, group size averages 4.3 individuals, with 1 breeding female and 1–2 adult males.[52] The diet of Wied's marmoset is heavily fruit and nectar based, with invertebrates and small vertebrates complementing the diet.[53] In many regions, *C kuhlii* co-occurs with golden-headed lion tamarins (*Leontopithecus chrysomelas*), although it is not clear whether there is a niche overlap of the 2 species.[52]

C kuhlii utilizes various habitats, including restinga forest, riverside forests, secondary forests, mangroves, fruit groves, and coconut and palm oil palm trees.[52] In the region of Itabuna and Ilhéus, Bahia state, the species also occupies old growth forests where cocoa is cultivated.[52] The species has a preference for occupying degraded areas close to wood edges.[52] The species is common in urban areas of Southern Bahia state, where

Figure 6: Image of *C flaviceps*. Photo credit: Sarisha Trindade.

social groups can be seen in backyards, orchards, and public squares.[54] Urban *C kuhlii* groups travel along poles, electrical wires, and houses.[54] At dusk, the animals retreat to clumps of bromeliads and vines, which is believed to be an anti-predatory and thermoregulatory strategy.[52]

C penicillata

Like its sister species, *C penicillata* is among the smallest *Callithrix* species (Table 1; Figure 5). The home range of *C penicillata* varies between 2.0 ha[55] and 18.5 ha,[56] and social groups are composed of 2–19 individuals.[28,57] *C penicillata* exploits many sources of food such as fruit, buds, flowers, leaves, young stems, small prey, and bird eggs.[28,56] Additionally, this species also heavily exploits tree gums, which seems to be advantageous in adapting to degraded environments and secondary forests.[28] Given the close evolutionary relationship between *C jacchus* and *C penicillata*,[2] the latter likely possesses similar adaptations for gumnivory as the former.

Cosmopolitan *C penicillata* populations have significantly expanded their ranges beyond their natural distribution,[2] likely in part due to illegal pet trafficking of the species between northeastern and southeastern Brazil.[17] The species has been introduced to portions of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Paraná, Santa Catarina, São Paulo, and Rio Grande do Sul states ([17,58]; personal observation JM,VB,IOS). Mathematical models predict that the expansion of *C penicillata* may be greater than expected and that this species may even replace marmosets native to the Atlantic forest.[58–60]

Although deforestation threatens other marmoset species, *C penicillata* may have instead benefited through the opening of new niches favoring a population expansion of the species.[28] Additionally, *C penicillata* shows great flexibility in occupying altered areas and secondary vegetation.[61] Other anthropogenic factors that may favor the range expansion of *C penicillata*, especially within urban areas, include planting of exotic trees and reductions of predators such as constrictor snakes, birds of prey, and wild cats.

A SUMMARY OF RECENT *CALLITHRIX* RESEARCH

Relevance of *Callithrix* Biological Traits in Biomedical Research

Reproduction and Growth Patterns in Callithrix Small body size and a fast life history, characteristics that make marmosets prized primate biomedical models (eg, pediatric obesity[62]; Zika infection during pregnancy[63]), are related to the evolution of *Callithrix* reproductive function. Four marmoset traits related to size and life history are likely inextricably linked: reproductive suppression, miniaturization, production of litters, and chimerism. However, it is important to note that, as biomedical models, marmosets have a delayed period of embryogenesis relative to

Figure 7: Image of *C jacchus*. Photo credit: Antonio Souto.

humans.[64] Understanding this difference is extremely important to ensuring appropriate use of marmosets to model pregnancy and development.[63]

Evidence for positively selected growth factor-insulin like growth factor axis genes that may have driven miniaturization in *C jacchus* has been found at *GHSR*, *IGF2*, *IGF1R*, *IGFBP2*, and *IGFBP7*.[65,66] Further, *Callithrix* growth patterns are likely tied to selection in marmosets for routine ovulation of multiple ova that leads to dizygotic twinning.[67] Altered placental and fetal growth patterns in marmosets may provide protection against discordant growth and placental pathologies of gestating litters in a simplex uterus.[66] The 4 positively selected genes with a likely role in regulating ova number and multiple gestations in *C jacchus* are *GDF9*, *BMP15*, *BMP4*, and *WFIKKN1*.[66]

Several factors associated with small body size, twin-rearing, and the fact that marmosets do not display anovulation have led to a marmoset social structure in which generally 1 female reproduces regardless of the number of other adult females within the group. This reproductive suppression has been the subject of extensive study over the past 30 years, but the mechanisms behind it are still somewhat unclear.[67] Impaired ovulatory function, which can be maintained for up to several years, is associated with suppressed pituitary secretion of luteinizing hormone and chorionic gonadotropin. Suppressed pituitary function is in turn likely associated with enhanced negative-feedback sensitivity to low levels of estrogen or blunted responsiveness to increasing estrogen. Some marmoset daughters escape suppression while in the presence of their mothers and ovulate, though they often display impaired luteal function, which raises questions about the fertility of these females. However, even if daughters ovulate, as long as a social group remains intact, with only the daughter's father and brothers and potential breeding partners, these females rarely become pregnant.

Callithrix Chimerism

Perhaps the most poorly understood *Callithrix*-derived trait is chimerism, which occurs when a single organism possesses

individual cells with >1 distinct genotype. Marmoset litters usually consist of twins or triplets that share a bidiscoid placenta with a fused chorion and vascular anastomoses.[68] Fusion of the chorionic membranes during embryonic development may allow blastocyst stem and precocial cells to cross the anastomoses, rendering littermates chimeric.[69] Marmosets are therefore hematopoietic chimeras with blood-derived tissues containing cells of the individual as well as their littermates.[70] However, the selection pressures that may have led to this trait remain obscure.

Benirshke et al[70] noted that approximately 90% of *C jacchus* pregnancies result in chimerism, but the degree of marmoset chimerism within a tissue and the extent of the tissues involved are not resolved. An evaluation of microsatellites from *C kuhlii* pregnancies with known parentage and samples from multiple tissue lineages estimated that all tissues could be chimeric, but blood-derived tissues were significantly more likely to be chimeric than other tissues.[69] Accordingly, Ross et al[69] showed that blood-derived tissues from deceased and living *C kuhlii* were between approximately 50% and 100% chimeric. Malukiewicz et al[4] found similar results for *C jacchus* when comparing blood and skin tissues via microsatellite genotyping. Another chimerism tissue analysis based on the SRY gene concluded that germ line cells were not chimeric and only hematopoietic lineages were chimeric.[71] Therefore, the contribution of embryonic cells to the overall phenotypic impact of chimerism on individual marmosets remains unknown.

An interesting question is how chimerism in marmosets impacts different levels of gene regulation. With respect to the epigenome, it is known that both underlying genetic signatures and environmental factors influence epigenetic changes.[72,73] Thus, in marmosets, the complication of how chimerism levels vary between tissue types may result in different genetic and epigenetic signatures across tissues. Further, the external signals that chimeric cells provide to one another within particular tissue environments may promote additional epigenetic changes. This idea has led to the hypothesis that chimerism may be a mechanism by which founder populations can rapidly increase their genetic diversity and gene expression variance, making them more adaptable to a range of novel environments.[74] However, although chimerism may affect such phenotypic plasticity through variation in genetic and epigenetic regulation, this relationship has not explicitly been tested in marmosets.

In most cases of biomedical modeling, it remains unclear whether chimerism may play a role in the variability found between individuals. However, chimerism in marmosets may be particularly well suited to questions designed to take advantage of the close relatedness of multizygotic litters using techniques such as adoptive transfer or paired design using litter mates as controls vs treatment subjects in immunology studies. Additionally, marmosets may be a natural model in which to study the impact of genomic conflict for questions of stem cell transfer, maternal-fetal microchimerism, or transplants.

Callithrix Cognition

Cognition studies is one of the growing areas of research for common marmosets (reviewed in[51]). Although laboratory studies dominate *C jacchus* research from the last 5 years, field studies should gain more attention because of their complementary value in relation to laboratory studies.[51] In this regard, field studies can have particular importance in areas that need integration between cognition and ecology. For instance, a recent study showed that common marmosets use spatial cognitive abilities to effectively obtain food in nature.[75] Studies such as this one, in which wild animals face the constraints and limitations imposed by the environment, can help us better understand the selective pressures that ultimately shaped their cognitive abilities.

Common marmosets are a particularly promising model for studying evolutionary and functional questions in primate personality due to their explorative and highly social character and adaptability to different natural environments.[44,51] Marmosets display personality traits when assessed with tools such as personality tests (eg,[76]) and behavioral observations (eg,[77]). In particular, marmosets exhibit short-term and long-term consistency of non-social and social personality traits.[78] Personality structure under captive and wild conditions is rather similar.[78] Inoue-Murayama et al[77] found that *C jacchus* sociability was positively linked with increased subjective well-being and cortisol levels, whereas neuroticism and dominance were associated with certain genetic polymorphisms. Interestingly, group-level similarity in marmoset personality has been found,[76] possibly as a product of shared social environment, genetics, or social facilitation. Future studies are needed to further explore links between inter-individual behavioral and cognitive variation in this species.

Callithrix Genomics and Genetics

Callithrix Genomic Assemblies   A high-quality genome is required for animal models, and in 2014 *C jacchus* became the first New World monkey whose genome was sequenced and assembled. Sanger sequences from a female marmoset were generated by an international consortium and assembled into extended continuous arrays of nucleotides (contigs). The published assembly (designated CalJac3 in the NCBI genomics database) consisted of 2.26 billion base pairs covering all *Callithrix* chromosomes.[65] However, the large number of continuous sequences were broken by gaps so that no chromosome sequence was complete end-to-end. Nonetheless, this genome allowed analysis of marmoset twinning genes[65,66] and detection of primate-specific constrained elements.[79]

Tables 2 and 3 list several genomic assemblies now available for *C jacchus*, some of which have been published (eg,[80]), as well as 1 unpublished assembly for the *C penicillata* genome. A recent *C jacchus* genome assembly by the Vertebrate Genomes Project is based on a novel technique called trio-binning in which the reads from parental and maternal haplotypes are assembled separately, resulting in a diploid assembly.[81] The most recent *C jacchus* assembly is designated cj1700_1.1/caljac4, which has now replaced calJac3 as the reference genome for that species. Cj1700_1.1 has a contig N50 (defined as the length of an individual contig for which one-half of all the available sequence occurs in contigs larger than that figure) of 25.2 megabases, an approximately 860-fold improvement over calJac3 in terms of contiguity. An unpublished genomic assembly for *C penicillata* has recently been sequenced and annotated (personal observation, Joanna Malukiewicz). The total length of this *C penicillata* genome is 2.6 GB and the contig N50 is 32.659 kilobases megabases (unpublished data, Malukiewicz et al).

More accurate and (largely) complete reference genome sequences for marmosets are opening tremendous opportunities for novel research. For example, CRISPR/Cas9 gene knock-in[82] has generated transgenic marmosets to model human disease. Further, the newer *Callithrix* genomic assemblies contain fewer gaps and better assembly of duplicated regions, which will provide better genomic annotation, leading to improved analysis of assays that require alignment of short reads to

Table 2 Marmoset Genome Assemblies From Short-Read Next-Generation Sequencing

Genbank Accession	Submitter	Date	Sequencing Technology	Contig N50 (Kb)	Scaffold N50 (Mb)	No. Contigs	No. Scaffolds
GCA_002754865.1 (ASM275486v1)	Broad Institute	2017/11/06	Illumina HiSeq	155.3	129.2	88 439	39 944
GCA_001269965.1 (CIEA01)	Keio University	2015/08/07	Illumina GAIIx, Illumina HiSeq	61.0	NA	109 198	NA
GCA_000832365.1 (ASM83236v1)	UN-NHPGC	2015/01/29	Ion Torrent	0.859	NA	1 992 178	NA
GCA_000004665.1 (caljac3)	Washington University (WashU)	2010/01/22	ABI 3730	29.3	5.2	201 371	16 399

Table 3 Marmoset Genome Assemblies From Long-Read Sequencing

Genbank Accession	Submitter	Date	Sequencing Technology	Contig N50 (Kb)	Scaffold N50 (Mb)	No. Contigs	No. Scaffolds
GCA_013373975.1 (CJA1912RKC)	Keio University/RIKEN	2020/06/03	PacBio RSII	24 828.9	132.3	3719	1872
GCA_009663435.2 (cj1700_1.1)	McDonnell Genome Institute at Washington University	2020/05/22	PacBio, Illumina	25 227.1	98.2	1336	994
GCA_011078405.1 (mCalJa1c.mat, maternal alternate haplotype)	Vertebrate Genomes Project	2020/03/10	PacBio Sequel I CLR; Illumina NovaSeq; Arima Genomics Hi-C; Bionano Genomics DLS	8609.0	146.9	1284	216
GCA_011100535.1 (mCalJac1.pat; paternal alternate haplotype)	Vertebrate Genomes Project	2020/03/10	PacBio Sequel I CLR; Illumina NovaSeq; Arima Genomics Hi-C; Bionano Genomics DLS	14 650.8	137.0	1124	336
GCA_011100555.1 (mCalJac1.pat.X, principal haplotype of the diploid genome)	Vertebrate Genomes Project	2020/03/10	PacBio Sequel I CLR; Illumina NovaSeq; Arima Genomics Hi-C; Bionano Genomics DLS	13 255.6	137.9	1312	353
GCA_009811775.1 (CJ2019)	Keio University	2019/12/13	PacBio RSII	6375.4	143.9	1812	65
calPen (genome assembly not yet submitted to GenBank)	Arizona State University	N/A	Dovetail Hi-C; Illumina	32.659	124.262	194 780	12 090

a reference genome (RNA-seq, ATAC-seq, ChIP-seq, etc). The diploid assemblies will facilitate the study of haplotype structure and structural variation in marmosets.[83]

Callithrix Functional Genomics and Epigenomics Marmoset epigenetics studies have examined DNA methylation patterns in a wide sampling of tissues such as bone[84] and placental tissue.[85] DNA methylation variation can be associated with variation in transient traits like body weight, and when such changes in gene regulation occur in developmentally important tissues like the placenta, they can potentially impact phenotypic development in offspring.[85] Interestingly, Housman et al[84] found that DNA methylation variation in marmosets is not strongly associated with variation in static traits such as bone morphology. This study also noted higher levels of DNA methylation heterogeneity compared with other nonhuman primate species, which led these researchers to speculate whether such differences might be due to chimerism. Such epigenetic results suggest that it is particularly relevant to examine to what degree chimerism affects epigenetic variation within specific tissues or cell types, because levels of chimerism are known to vary across different marmoset tissues.[4,69,71]

Brain development, evolution, and plasticity is one area of marmoset functional genomics that is being explored. Current work has focused on characterizing candidate gene expression patterns in brain tissues,[86,87] but some research has also assayed candidate gene expression responses following severe psychological perturbations such as parental separation.[88] Interestingly, although most brain regions show conserved levels of candidate gene expression between marmosets and mice, some areas of the brain do show marmoset-specific expression patterns, such as the early visual cortical area and afferent areas of the hippocampus.[86]

Now is a particularly relevant time to pursue functional genomics research, especially in primates,[89] as technologies can characterize whole transcriptomes and epigenomes at both bulk and single-cell resolutions. Already, some comparative cross-species studies that include marmosets have begun utilizing these single-cell methods.[90,91] Further, these technologies can be used on primary tissue samples as well as in vitro cell culture systems. Marmoset cell lines that are readily used include embryonic stem cells (eg,[92]) and induced pluripotent stem cells (eg,[93,94]). Embryonic stem cells and induced pluripotent stem cells are ideal for functional genomics research, especially in the context of disease, because they are immortalized and self-renewing, have the potential to differentiate into cells from any germ layer, and can be readily used in controlled experiments.[92] Another benefit is the relative ease with which these cell lines can be genetically modified.[82]

Finally, consolidating functional genomics data for better access and comparison is essential in these efforts. Larger consortia that compile large -omics datasets for marmosets are being built.[95,96] For instance, functional genomics data from marmoset brain tissues have been collected and incorporated into the NIH Brain initiative.[97] This initiative is of particular relevance because the common marmoset has been identified as an important model organism for neuroscience research that can bridge the gap between mice and humans.[95,98] Such foundational databases have enabled subsequent explorations such as single-cell RNA-seq of *C jacchus* and other mammals have identified primate-specific interneuron subtypes[99] and common and divergent features of preimplantation development.[100]

Callithrix Immunogenetics Although New World primate immunogenetic studies lag behind those of Old World primates, complex immunogene families such as Major Histocompatibility Complex (MHC) Class I and the Natural Killer Complex (NKC) have been sequenced and annotated in *C jacchus*. The MHC, an evolutionary hallmark of enormous genetic variability and genomic diversity, determines immune responsiveness and is associated with many diseases. MHC class I proteins bind pathogen-derived peptides for presentation to specialized cells for immune response initiation.[101] MHC class I proteins also interact with natural killer (NK) cell receptors to prevent NK cell destruction of healthy cells.[102]

The *C jacchus* MHC class I region is composed of 3 segments: *Caja*-B/C segment, the *Caja*-E segment, and the *Caja*-G/F segment.[103,104] In humans, 6 MHC class I loci are known as *HLA* (human leukocyte antigen)-A/B/C/D/E/F/G, and *Caja*-B/C corresponds to *HLA*-B/C[103] and *Caja*-G/F corresponds to the *HLA*-A/G/F region.[103] Shiina et al[104] described *Caja*-B/C as a 1079-kb fragment containing nonclassical (low polymorphism) MHC class I genes, and Kono et al[104] characterized a 854-kb tract of the *Caja*-G/F segment, which harbors classical (polymorphic) MHC class I genes. *Caja*-B/C contains 54 genes, among which are 9 functional MHC genes and 4 MHC pseudogenes.[104] *Caja*-G/F encompasses 6 functional MHC genes as well some non-MHC genes and MHC pseudogenes.[104] The MHC I region maps to chromosome 4 of *C jacchus*[103] (personal observation, Joanna Malukiewicz) and likely evolved by segmental duplication.[103,104]

Interestingly, the human *HLA*-G locus shows limited polymorphism and grants immuno-tolerance between mother and fetus during pregnancy.[105] The homologous *Caja*-G locus instead shows high allelic polymorphism levels, and expression of *Caja*-G/F alleles in various tissues suggests that this locus has taken on the role of classical MHC I function in *C jacchus*.[105] Evidence for genetic conversion in the role of *Caja*-G/F is seen further when comparing exon diversity between *Caja*-G/F and *HLA*-G gene associated with MHC protein binding of pathogen peptides. *Caja*-G/F MHC genes show a high level of polymorphism that sharply contrasts that of *HLA*-G MHC genes.[105]

Using the unpublished *C penicillata* draft genome assembly mentioned earlier, we extracted genomic segments from chromosome 4 between *BAT1* and *CDSN* as the putative *C penicillata* MHC class I B/C (*Cape*-B/C) region and between *RNF39* and *ZFP57* as the putative *C penicillata* MHC class I G/F (*Cape*-G/F) region. The limits chosen for *Callithrix* MHC class I regions followed designations by Shinna et al[104] and Kono et al. [103] Dot plots of *Caja*-B/C:*Cape*-B/C and *Caja*-G/F:*Cape*-G/F (Figure 8) show large tracts that are highly similar or identical between *C penicillata* and *C jacchus*. The 2 *Caja* segments are longer than the 2 *Cape* segments, but given that there are some gaps in the genomic assembly within *Cape* MHC class I segments (personal observation, Joanna Malukiewicz), further sequencing is needed to determine the actual length of these segments for *C penicillata*. Following the annotation methodology of Kono et al[103] and Shinna et al,[104] we identified 7 putative MHC class I loci within *Cape*-G/F and 9 putative MHC class I loci within *Cape*-B/C. Oxford Nanopore long-read targeted sequencing of these putative *C penicillata* MHC class I loci is ongoing to further characterize these genomic regions.

Two structurally unrelated classes of NK cell receptors exist in primates: the killer cell immunoglobulin-like receptors (KIR) encoded by the leukocyte receptor complex (LRC) and killer cell lectin-like receptors encoded by the natural killer complex (NKC).[106] The KIR lineage is present in all simian primates,[102] but in *C jacchus* there are apparently only 2 KIR loci.[65] In *C*
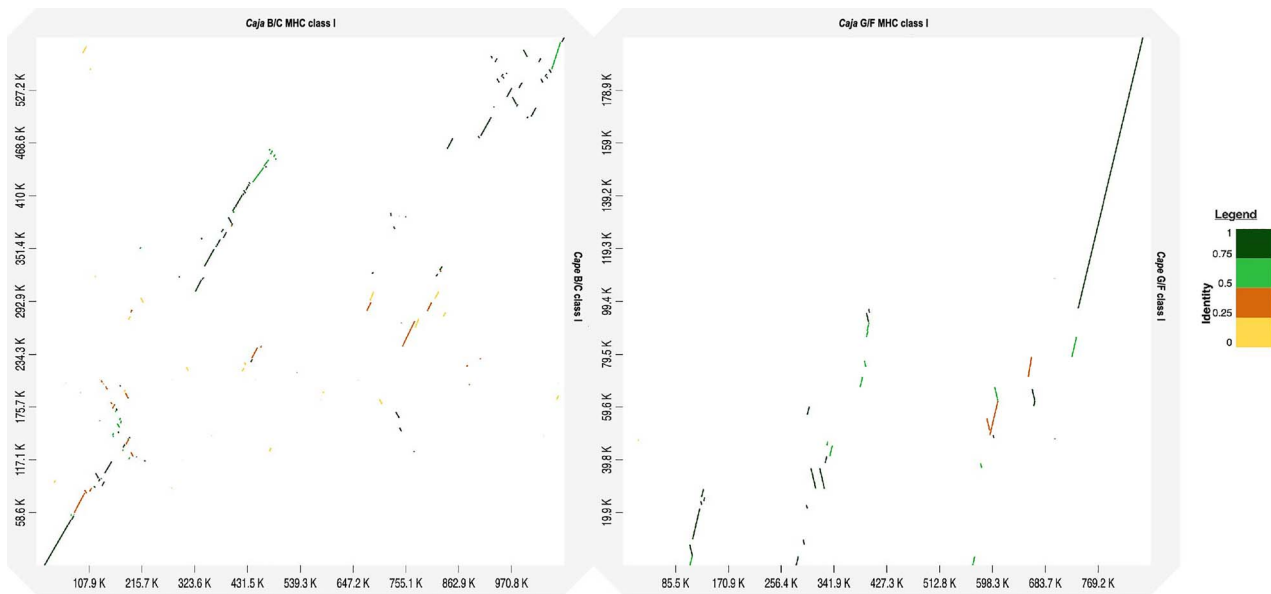
Figure 8: Dot plot between *Caja* B/C and *Cape* B/C MHC Class I segments (left) and *Caja* G/F and *Cape* G/F MHC I segments (right). In both plots, the *C jacchus* segments are represented by the x-axis and *C penicillata* segments are represented by the y-axis. The legend represents color codes that show the percent identity between plotted *C jacchus* and *C penicillata* MHC Class I segments. Two collinear sequences (GenBank accession numbers AB600201 and AB600202) were concatenated to form the *Caja* B/C region in the left plot. Three collinear sequences (GenBank accession numbers AB809558, AB809559, and AB809560) were concatenated to form the *Caja* G/F region in the right plot. The 2 *Cape* regions were extracted from an unpublished *C penicillata* draft genome (personal observation, Joanna Malukiewicz).

jacchus, NKC genes cluster together and are orthologous to humans, but the marmoset NKC segment is 1.5× smaller.[106] Marmoset NKC genes also show moderate polymorphism.[105] Averdam et al[105] found that the *C jacchus* NKC encodes a single inhibitory heterodimer (CD94/NKG2A) and 2 activating NK cell receptors (CD94/NKG2CE and NKG2D). In humans, CD94/NKG2A and CD94/NKG2C are ligands for HLA-E, a nonclassical MHC class I molecule that plays an important function in cell recognition by NK cells,[106] but the role of *Caja*-E remains to be determined.

Callithrix Viruses and the Virosphere

<u>*Callithrix* as Models of Viral Diseases</u> *C jacchus* has served as a model for several aspects of biomedical research related to viruses. In humans, Epstein–Barr virus infection may enhance risk of developing multiple sclerosis, and natural infection of *C jacchus* with the related γ1-herpesvirus CalHV3 has been harnessed to model human autoimmune disease.[107] Additionally, *C jacchus* has been used to model hepatitis A infection.[108] The species was also used for in vitro transformation of 2 permanent and virus-producing lymphoblastoid cell lines with a nasopharyngeal carcinoma–derived Epstein–Barr viral strain.[109] Other viral pathogens that have been explored in *Callithrix* include parainfluenza virus type 1,[110] Flaviviridae-like viruses,[111] Oropouche virus,[112] and Simian foamy virus.[113]

More recently, *Callithrix* is emerging as an infection model of several arthropod borne viruses (arboviruses) of single-stranded RNA viruses from the genus *Flavivirus*. These viruses include dengue virus (DENV), now considered the most prevalent and quickly spreading human arboviral disease, with symptoms ranging from high fever to shock and death.[114] Both *C jacchus* and *C penicillata* are candidate systems to model DENV pathogenesis and for discovery of antiviral drugs and vaccines.[115,116] In *C penicillata*, DENV infection produced marked changes in microglial cells of the central nervous system.[117] Both *Callithrix* species show elevated proinflammatory cytokines from DENV infection,

which may model aspects of human DENV pathogenesis. Another *Flavivirus*, Zika virus (ZIKV), was originally discovered in Uganda[118] but is now the newest *Flavivirus* arrival in the New World. Pregnant women infected with ZIKV are at risk for miscarriage and fetus microcephaly, and adults can develop a neurological condition called Guillain-Barré syndrome.[119] A number of recent studies have found that *C jacchus* replicates many of these human clinical and gestational symptoms.[63,119]

Exposure of Wild *Callithrix* to Pathogenic Arboviruses

Yellow fever virus (YFV), another flavivirus, was anthropogenically introduced to the Americas in the 15th and 16th centuries from Africa and exists in Brazil as part of an established sylvatic cycle.[120] Serological surveys of YFV antibodies in wild primates have shown some positive results in *Callithrix*.[121,122] Retrospective data on surveillance of primate epizootics show that *Callithrix* represented 8.7% of the positive non-human primates (NHPs) for YFV in Brazil between 1996 and 2016, which increased to 17.1% between 2016 and 2019.[122] Since 2016, free-living *Callithrix* infection has been demonstrated in southeastern Brazil during a recent major YFV outbreak, suggesting increasing importance of *Callithrix* for YFV epidemiology in Brazil. Between 2017 and 2018, Mares-Guia et al[123] analyzed 2099 NHP samples from southeastern and northeastern Brazil suspected of YFV. *Callithrix* were among the most frequently YFV-infected NHPs, with 140 (9.3%) *Callithrix* being positive among 1505 tested marmosets. These percentages may be even higher for epizootic diseases, because classification of NHPs in epidemiological data usually does not go beyond the genus level.[124] Cunha et al[125] observed that *Callithrix* found positive for YFV through molecular methods did not necessarily demonstrate any associated histopathological changes or immunohistochemical YFV positivity.

The immunization of NHPs against the yellow fever virus is still the subject of intense debates in the scientific community.

These debates are likely due to the possibility of interfering in the use of these animals as sentinels for the transmission of the virus in the natural environment. Although there are no extensive studies on the safety and effectiveness of the vaccine in NHPs, promising initiatives to test the safety and effectiveness of the vaccine are under development in a partnership between the Institute of Technology in Immunobiologicals (Biomanguinhos/Fiocruz) with the Center of Primatology of Rio de Janeiro.

Callithrix susceptibility has been shown for other arboviruses such as DENV, ZIKV, Mayaro (MAYV), and Chikungunya (CHIKV), all which can potentially establish sylvatic cycles in Brazil and other parts of South America.[126] Currently, only a limited number of studies have looked at arbovirus exposure in wild Brazilian primates, and Moreira-Soto et al[127] found no evidence of exposure to the above arboviruses in urban and peri-urban *jacchus* group marmosets sampled in northeastern Brazil between 2012 and 2017, except 1 *C jacchus* that showed serological CHIKV exposure. Also, Abreu et al[128] found no evidence of ZKV infection in *Callithrix* sampled in southeastern Brazil between 2015 and 2018. On the other hand, evidence for ZKV infection was reported in free-ranging peri-domestic *C jacchus* sampled between 2015 and 2016 in Ceara state.[129] Additionally, Terzian et al[130] found evidence of widespread ZIKV exposure in over 50 *Callithrix* sampled in Minas Gerais and São Paulo states.

For a translocated arbovirus to enzootically establish itself within the neotropics, wildlife exposure, zoonotic infection, and persistent enzootic transmission of the translocated zoonosis need to occur.[131] *Callithrix* characteristics that can facilitate arbovirus transmission include a great adaptability to human environments and frequent interactions with human beings in urban and peri-urban environments also occupied by anthropophilic arbovirus vectors such as *Aedes aegypti* and *A. albopictus*.[123] The persistence of arbovirus transmission is also facilitated by the presence of short-lived, fast-reproducing primates,[131] which are certainly characteristics that define many *Callithrix* species and hybrids.

Exposure of Wild *Callithrix* to Viruses Beyond Arboviruses

Human herpesvirus 1 (HV1) is transmissible from humans to *Callithrix* marmosets, which has resulted in a number of fatal epizootics events.[132,133] Transmission occurs through the close contact these animals have established with humans, facilitated by the human habit of offering food, because the virus can be transmitted through contaminated saliva, aerosols, and fomites. Transmission can also occur spontaneously between marmosets within the same group.[132,134] Affected animals are usually found dead or with severe neurological symptoms, resulting from virus-induced encephalitis.[133] The virus also causes death from meningitis,[133] erosions and ulcers in the oral cavity, and hemorrhages and focal necrosis in several organs.[134]

Rabies is a zoonotic disease caused by lyssaviruses, transmitted through saliva, and infection causes fatal acute encephalomyelitis. The disease is transmissible from animals to humans by bites. *C jacchus* has played an important role in the transmission of rabies in northeastern Brazil, where it maintains a distinct transmission cycle.[135] Infected marmosets often show no clinical signs but rather sudden death preceded by sadness or weakness. A recent case of rabies in *Callithrix* sp. occurred in urban Niterói, Rio de Janeiro state.[136] The proximity of marmosets to urban environments and the practice of capturing and maintaining these animals as pets are 2 factors that greatly increase the risk of marmoset rabies transmission.[137]
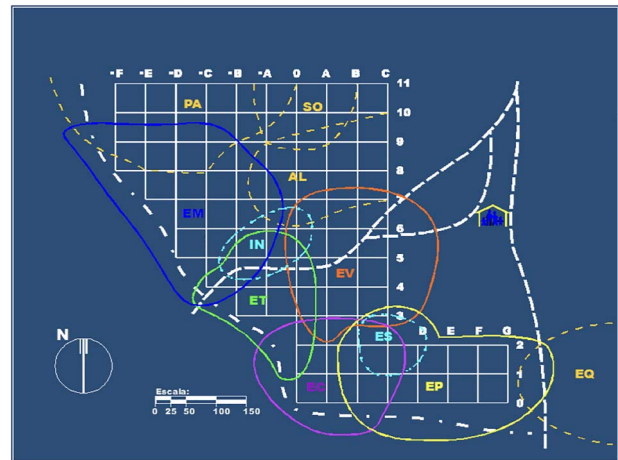

Figure 9: Study area of the Tapacurá Field Station, São Lourenço da Mata, Pernambuco, Brazil, with a 50 m × 50 m grid of trails. Shown are the home ranges of 5 focal *C jacchus* study groups (EC, EM, EP, ET, EV) represented by continuous lines, peripheral groups (orange dotted lines) and temporary groups (pale blue dotted lines) between May 1994 and May 1996.

Callithrix Virome Research

Although the virosphere incorporates the most abundant and diverse group of organisms on Earth, it remains largely neglected, with most attention given to viruses of high biomedical relevance. It is estimated that there are over 500 000 undiscovered animal viruses that are transferable to people.[138] Although *Callithrix* virome work is still in its infancy, 1 pioneering study helped to characterize 2 novel *Papillomavirus* genomes (CpenPV-1 and CpenPV-2) in captive *C penicillata*.[139] Other viral families also have been sequenced in this work but remain to be published. An important future role for *Callithrix* virome studies will be to help understand the capacity of *Callithrix* to be YFV hosts and their susceptibility to YFV disease. Also, virome studies can help to understand if this genus could actually represent a potential risk for a severe urban YFV outbreak[123,125] or even zoonotic virus spillover. Overall, virome studies can greatly enhance our ability to detect known and novel viral sequences and can also help to understand the entire dynamic and interactions of the *Callithrix* virosphere.

Callithrix Social Dynamics

Although long-term studies are still necessary to understand wild *Callithrix* social dynamics, some insight is available from *C jacchus* groups at the Tapacurá Field Station, São Lourenço da Mata, Pernambuco (08⁰ 07' S, 34⁰ 55' W) (Figure 9). A typical Tapacurá *C jacchus* social group may contain 8 individuals: 3 reproductive adults, 2 juveniles, 2 infant twins, and an adult or subadult that may or may not be related to other group members.[140] The 3 breeding adults may include a dominant female and 2 males that take on variable roles in offspring care and group defense. One breeding male will be the principal infant carrier, while the second breeding male aids the breeding female in choosing group feeding, resting, and sleeping sites, and in territorial defense.[140] A breeding female depends on her group's support to maintain dominant status, but the loss of the reproductive position may not result in her departure from the group. There are instances at Tapacurá where breeding females were displaced by 1 or 2 daughters but remained in the group to suckle grandchildren along with the new dominant female(s).[140]
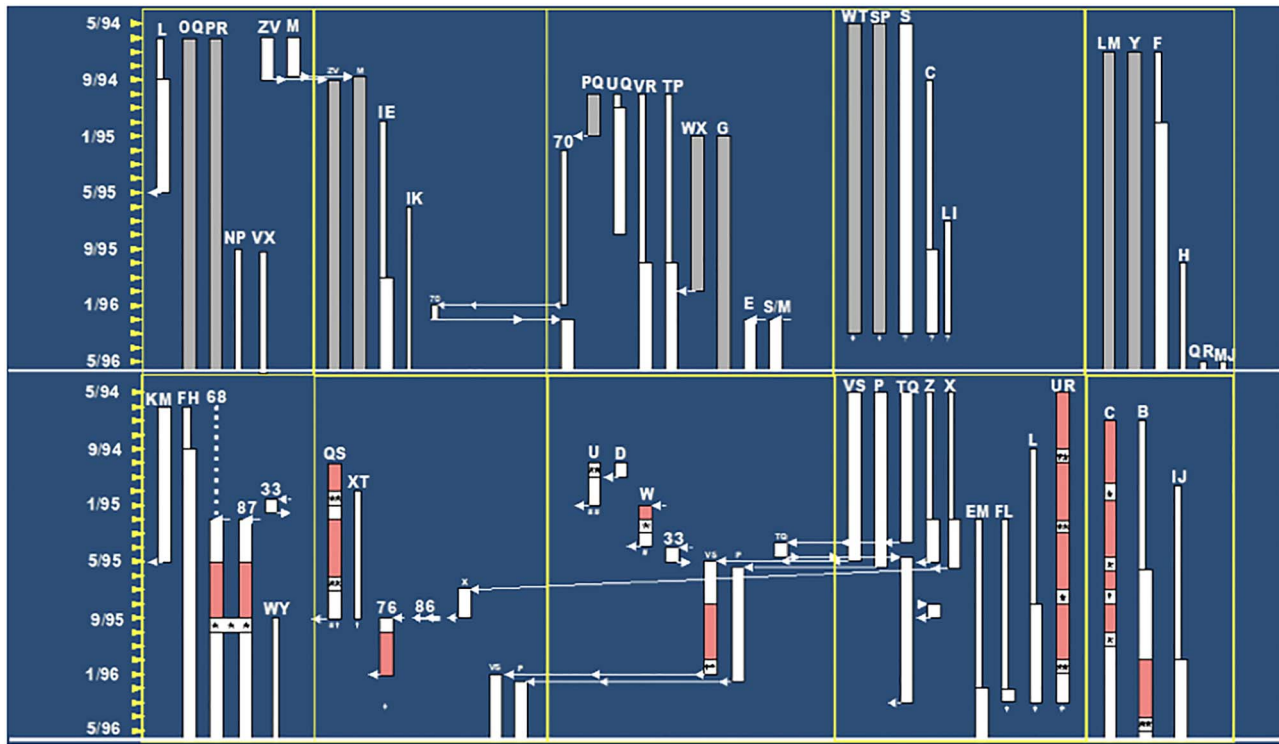
Figure 10: Changes in group composition (males top and females below) of 5 *C jacchus* Tapacurá Field Station focal study groups between May 1994 and May 1996. Each square panel represents a single social group, with male members on top and female members on the bottom. Bars represent individual marmosets and arrows represent their movement between social groups.

Regarding sexual behavior studied at Tapacurá between 1994 and 1996, 52 copulations were observed, of which 16 were intra-group and only 2 involved non-reproductive females. Of 33 extra-group copulations, 17 were between neighboring focal study groups and 16 were between members of a focal group and peripheral groups. To illustrate extra-group copulations, the reproductive female of 1 focal group was seen copulating 7 times with 2 dominant males (2–3 times each) in neighboring groups. In general, sexually mature females take all opportunities to copulate, independent of their phase in the estrous cycle. Females also disperse more than males (Figure 10), leaving their natal groups to increase their chances of breeding.[141]

Interestingly, the strongest social interactions within *C jacchus* groups are between the male caregiver (one of the probable fathers in the group) and infants. The findings help to explain, at least in part, why males disperse less than females, because nutritional provisioning of infants by the male caregiver demands dedication and skill. On 1 occasion, a male carer was seen to dexterously secure the floral pedicel of a cashew fruit with both hands and, while balancing with extended legs, lifted it above his head after biting the hypocarpium several times to allow the infants to lick the juice (Figure 11). During the infant weaning phase, the carer male also teaches infants skills needed to travel, forage, and confront predators and how to recognize, catch, and manipulate food items.[140] The male carer is the last to abandon a dead infant, which illustrates a deep social bond between a marmoset male and marmoset infants.[142]

Anthropogenic Effects on *Callithrix*: Pet Trade, Species Invasions, and Hybridization

Pet Trade   Although it is illegal in Brazil to have native primates as pets[143,144] and in São Paulo state there is a moratorium on captive breeding of marmosets by authorized commercial breeding facilities,[145] there still exists an underground Brazilian illegal pet market.[146] Marmosets, most often *C jacchus* and *C penicillata*, are taken from the wild by several methods, including trapping, killing of adults to take the infants, and rescuing infants after habitat loss, and then either sold locally or transported to large urban areas.[146–148] Confiscated marmosets from animal traffickers are often stressed, malnourished, and dehydrated—conditions that favor the development and transmission of diseases. Transport stress and inadequate hygiene conditions also contribute to the development of infections.

Captured marmosets appear to be trafficked using the same illegal trade routes as other wildlife. In the case of *C penicillata*, construction of roads and increased vehicular traffic between the Cerrado and southeastern Brazil have greatly facilitated illegal trafficking of this species.[17] There are few studies that quantify the pet trade, but *Callithrix* individuals, especially *C jacchus* and *C penicillata*, have been among the top 5 species of mammals confiscated and sent to government triage centers. Between 1999 and 2006, out of 4631 primates received by Brazilian triage centers, 54.2% were from the *Callithrix* genus.[147] However, the actual numbers of marmosets taken from the wild for commercial purposes are likely underestimated, because many confiscated individuals do not go to the triage centers; instead, they are released in the nearest forests by authorities, rural landowners, or dealers/owners. Important consequences of the illegal primate trade include the release of marmosets outside of their natural areas of distribution, anthropogenic hybridization, saturation of captive facilities with hybrids and non-hybrid marmosets, and biological invasions that threaten endangered native *Callithrix* species.[2,149,150]

Figure 11: Illustration of a *C jacchus* breeding male caregiver hydrating marmoset infants with cashew Hypocarpium juice (*Anacardium occidentale*), an act that shows dexterity and skill.

Invasive *Callithrix* Species in the Southeastern Brazilian Atlantic Forest

Allochthonous *Callithrix* species began appearing in portions of the southeastern Brazilian Atlantic forest within approximately the last 20–30 years.[2,151,152] Now, 3 *Callithrix* species, *C geoffroyi*, *C jacchus*, and *C penicillata*, have high invasive potential[60,61] and are spreading throughout the southeastern Atlantic forest due to the legal and illegal pet trades.[17,21,153] As a result, *C jacchus* and *C penicillata* have established several allochthonous populations in southeastern Brazil.[2,17,21,149–154] Mitogenomic data show that source populations of allochthonous *Callithrix* species actually come from across broad geographic origins outside of the southeastern Brazilian Atlantic forest.[2] As discussed below, anthropogenic hybridization between allochthonous marmosets and either other allochthonous or autochthonous congeners occurs widely across southeastern Brazil.[2,4,21,152–154]

Contemporary allochthonous *Callithrix* species are usually found in urban or peri-urban areas of the southeastern Atlantic forest.[17,21,150,151,154–156] Within these contexts, allochthonous *Callithrix* have frequent human contact and exposure and receive anthropogenic food supplementation.[17,54,157] These allochthonous marmosets can also be found within or around natural reserves,[13,17,150,151,154,156] and in some areas, such marmoset populations are larger than those of native, endangered callitrichids (eg,[150]). Such introductions could alter the ecological relationships among taxa,[13,158] because the main threats posed by allochthonous marmosets are competition for food resources, increased predation of native fauna, the introduction and maintenance of disease, and hybridization.[159–161] The threats can become exacerbated when introduced marmosets become abundant in a landscape of small fragments.

Anthropogenic *Callithrix* Hybridization

Due to the legal and illegal pet trades, *C jacchus* and *C penicillata* have established several allochthonous populations in southeastern Brazil that hybridize with allochthonous and autochthonous congeners (Figure 11[19,21,162]). It is highly likely that *C aurita* faces competition, conservation, and genetic threats from allochthonous *jacchus* group species and anthropogenic hybrids.[2,10,153] *C flaviceps* also likely faces similar pressures. Some cases exist of native *C aurita* and *C flaviceps* meeting up and interbreeding with hybrid and allochthonous *Callithrix* at urban fringes (reviewed in[21]). Such interactions likely facilitate gene flow from allochthonous *jacchus* group species into native marmoset populations in southeastern Brazil, with consequences that may include outbreeding depression, admixture, hybrid swamping, or introgressive replacement.[163–165] Indeed, Malukiewicz et al[2] showed for the first time evidence of introgression of mitochondrial DNA from allochthonous *C jacchus* into the genetic background of native *C aurita* from the São Paulo metropolitan area. These data also showed the first genetic evidence for cryptic hybridization within the *aurita* group marmosets. A few anthropogenic *Callithrix* hybrid zones have also been studied using mitochondrial, nuclear, and Y-chromosome markers.[2,4,21,154]

Anthropogenic hybridization with *C jacchus* and/or *C penicillata* also represents a potential risk for genetic extinction of the other 2 *jacchus* group species, *C geoffroyi* and *C kuhlii*, and Silva et al[17] recently showed that *C penicillata* is encroaching on the native range of *C geoffroyi*. Anthropogenic hybridization of *jacchus* group species generally results in the formation of hybrid swarms, admixed populations that lost parental phenotypes and genotypes.[4,21,152] Should large numbers of exotic *C jacchus* or *C penicillata* ever invade native ranges of *C kuhlii* or *C geoffroyi*, the latter 2 species may be threatened with genetic swamping by the former 2 species, a process through which parental lineages are replaced by hybrids that have admixed genetic ancestry.[166] Further, biological invasions by other marmosets present potential conservation risks for *C kuhlii*, which is already considered vulnerable by the IUCN Red List.[167]

Table 4 List and Description of the Main Legal Instruments Related to the Protection and Conservation of *Callithrix* Species

Topics	Legal Instrument	Description	Observations
Protection and conservation of wildlife	Law N° 5.197/1967	Provides for protection of fauna and provides other measures	Art. 1 points out "animals of any species, at any stage of their development and which live naturally outside captivity constituting wild fauna, as well as their nests, shelters and natural breeding grounds, are the property of the State, and their use, pursuit, destruction, hunting, or capture is prohibited"
	Law N° 7.653/1988 - Wildlife Protection Act	Changes wording of articles 18, 27, 33 and 34 of Law No. 5197, of January 3, 1967, which provides for protection of fauna, and provides other measures	Renames, modifies and reenacts LAW No. 5197/1967.
	Federal Constitution of 1988	According to Art. 225: All have the right to an ecologically balanced environment, well of common use of people and essential to the healthy quality of life, imposing on public power and collectivity the duty to defend it and preserve it for present and future generations	Paragraph 1, item VII, points out the burden given to the Public Power to safeguard fauna and flora, being prohibited, in the form of law, practices that endanger their ecological function, that promote the extinction of species or subject animals to cruelty.
	Law No. 9605/1998 - Environmental Crimes Act	Provides for criminal and administrative sanctions resulting from conducts and activities harmful to the environment and provides other measures	Created to be implemented with the participation of federal, district, state and municipal governments, and civil society, considering:
	Decree N° 4.339/2002	Establishes principles and guidelines for implementation of the National Biodiversity Policy	1. The commitments made by Brazil to sign the Convention on Biological Diversity (CBD) during the United Nations Conference on Environment and Development - UNCED in 1992; 2. The provisions of Article 225 of the Constitution, in Law No. 6938, of August 31, 1981, which provides for the National Environment Policy, the Rio Declaration and Agenda 21, both signed by Brazil in 1992, during UNCED, and the other current rules on biodiversity; 3. That the development of national biodiversity strategies, policies, plans and programmes is one of the main commitments made by the member countries of the Convention on Biological Diversity.
	Joint ordinance MMA and ICMBIO N° 316/2009	Applies the following instruments for implementation of the National Biodiversity Policy aimed at conservation and recovery of endangered species: I - Official National Lists of Endangered Species; II—Red Books of Endangered Brazilian Species; II—National Action Plans for the Conservation of Endangered Species	
	Complementary Law No. 140/2011	Lays down rules, pursuant to items III, VI, and VII and the sole paragraph of Art. 23 of the Federal Constitution, for cooperation between the Union, States, Federal District, and Municipalities in administrative actions arising from exercise of common competence relating to protection of notable natural landscapes, protection of the environment, pollution in any of its forms, and preservation of forests, fauna and flora	

Table 4 Continue

Topics	Legal Instrument	Description	Observations
	Ordinance MMA N° 43/2014	Establishes National Program for the Conservation of Endangered Species - Pro-Species, with objective of adopting prevention, conservation, management and management actions, with a view to minimize threats and risk of extinction of species	The instruments of the Pro-Species are: I - Official National Lists of Endangered Species; II—National Action Plans for Conservation of Endangered Species-PAN; III—Databases and information systems aimed at supporting extinction risk assessments, as well as the process of planning actions for conservation.
	Law N° 13.052/2014	Amends Article 25 of Law No. 9605 of February 12, 1998, which provides for criminal and administrative sanctions arising from conduct and activities harmful to the environment and provides other measures to determine that seized animals are released primarily into their habitat and establish conditions necessary for the welfare of these animals	Part § 1 states that "Animals shall be released primarily into their habitat or, if such a measure is not feasible or not recommended for sanitary reasons, delivered to zoos, foundations or similar entities, for custody and care under the responsibility of approved technicians."
	Ordinance MMA N° 444/2014	Recognizes that endangered Brazilian fauna species are those that are part of the "Official National List of Endangered Fauna Species"	*Callithrix aurita* and *C flaviceps* are considered Endangered (EN) by the List.
Conducting research and management activities	Joint normative instruction ICMBio/IBAMA 01/2014	Establishes procedures between ICMBio and IBAMA for management and conservation of Brazilian wildlife species	Art.1 establishes, "within the scope of the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA) and the Chico Mendes Institute for the Biodiversity Conservation, ICMBio, the procedures for the shared use of information and for the complementarity of actions with regard to the management and conservation of wildlife. The shared use of information will cover its use for environmental licensing and control over the resources exercised by IBAMA and for the actions of authorization, monitoring and conservation of biodiversity promoted by ICMBio."
	Normative instruction IBAMA 23/2014	Defines guidelines and procedures for disposal of wild animals seized, rescued by a competent authority, or voluntarily delivered by the population as well as for operation of Wild Animal Triage Centers of IBAMA - CETAS	Art. 21, 22 and 23 state that hybrid and exotic specimens may only be destined for captive management institutions.

(Continued)

(Continued)

Table 4 Continue

Topics	Legal Instrument	Description	Observations
	Normative instruction ICMBio N° 03/2014	Sets standards for use of Authorization and Information System on Biodiversity - SISBio, in the form of the guidelines and conditions provided for in this Normative Instruction, and regulates availability, access, and use of data and information received by Chico Mendes Institute for Biodiversity Conservation through SISBio	Art. 3 sets a standard for the performance of the following activities, "with the purpose of scientific or didactic, in the national territory, on the continental shelf, in the territorial sea and in the exclusive economic zone: I - collection of biological material; II—capture or marking of wild animals in *situ*; III—temporary maintenance of specimens of wild fauna in captivity; IV—transport of biological material; and V—conducting research in federal conservation unit or in underground natural cavity." Activities with didactic purposes are restricted to those performed in the scope of higher education. This normative instruction does not apply to the collection and transportation of material from biological species, domesticated or cultivated, except when related to research carried out in federal conservation units in the public domain, and exotic wild in ex-situ conditions. When the research activities are carried out within state or municipal Conservation Units, in addition to SISBio authorization, it is also necessary to request authorization from the respective competent environmental agencies:—São Paulo: submit a project to the Technical-Scientific Committee of the Forestry Institute (COTEC), in addition to the board of management.—Minas Gerais: follow the standards of the State Forest Institute (IEF), according to Ordinances 130/2017 and 17/2019.—Rio de Janeiro: request the INEA (State Institute of the Environment) based on Ordinance IEF/RJ/PR No. 227/2007.—Espírito Santo: request the IEMA (State Institute of Environment and Water Resources), based on Decree 4.225-N/1998.
Management of hybrids and exotics	Resolution No. 7/2018 OF The National Biodiversity Commission—CONABIO/MMA	Provides National Strategy for Invasive Alien Species	The objective of the Strategy is to guide the implementation of measures to prevent the introduction and dispersion and significantly reduce the impact of invasive alien species on Brazilian biodiversity and ecosystem services, control or eradicate invasive alien species. Exotic species or subspecies are considered as those occurring outside its past or present natural distribution area; including any part, such as gametes, seeds, eggs or propagules that can survive and subsequently reproduce.
	Normativ instruction ICMBio N° 6/2019	Provides for prevention of introductions and control or eradication of exotic or invasive species in federal Conservation Units and their damping zones	Fuidance for the management of invasive alien species in Federal Conservation Units is available in http://www.icmbio.go v.br/cbc/publicacoes, which includes methods already approved by ICMBio and is considered the guiding document for project analysis.

Table 4 Continue

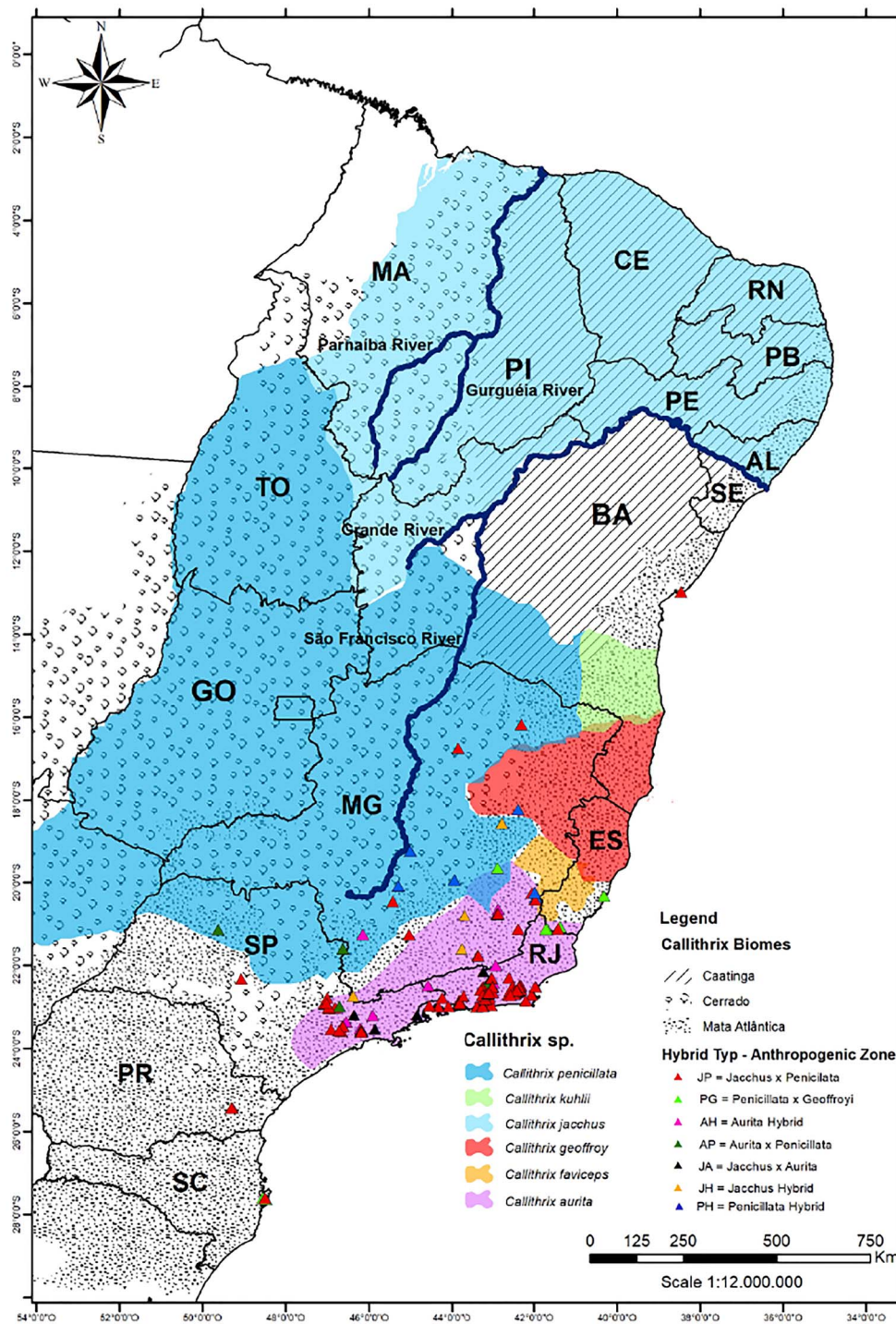| Topics	Legal Instrument	Description	Observations
Conservation research and management (more targeted at endangered *Callithrix* species)	Resolution SMA No. 164/2018 (São Paulo)	Establishes procedures for reproduction of *Callithrix* specimens kept in wildlife enterprises in captivity in State of São Paulo	It prohibits the production of hybrid individuals of the genus *Callithrix* and the reproduction of individuals belonging to the species *C jacchus* and *C penicillata* (exception given only to scientific and commercial breeding sites using these species as matrices, but marketed animals should be sterilized). *Callithrix penicillata* reproduction may be authorized only for individuals of known origin and for conservation, by Zoos and scientific breeding sites for conservation purposes.
	Ordinance ICMBio N° 134/2010	Approves National Action Plan for Conservation of Mammals in central Atlantic Forest	It comprises objectives and actions for the conservation of 23 mammalian taxa, including *Callithrix aurita* and *Callithrix flaviceps*, for a period of 5 years from its date of publication.
	Ordinance ICMBio N° 702/2018	Approves National Action Plan for the Conservation of Atlantic Forest primates and collared sloth—PAN PPMA-contemplating 14 taxa threatened with extinction, establishing their general objective, specific objectives, lead time, scope and forms of implementation and supervision	It covers and establishes priority conservation strategies for 13 primate taxa, including *Callithrix aurita* and *Callithrix flaviceps*, and for the collared sloth for a period of 5 years, from its date of publication.
	Cooperation agreement on process No. 02070.003869/2018-Biodiversity conservation signed between ICMBio and AZAB	This Cooperation Agreement is based on cooperation in the preparation, implementation, maintenance, and coordination of *ex situ* management programs for endangered species in Brazilian zoos and aquariums as detailed in the work plan	*Ex Situ* Conservation Program for *Callithrix aurita*
	Red Book of Endangered Brazilian Fauna (ICMBio/MMA, 2018)	This edition of the Red Book of Endangered Brazilian Fauna brings the result of the process of evaluation of species coordinated by the Chico Mendes Institute, made official by the Ministry of the Environment through Ordinances No. 444 and 445 of 2014	Presents factsheets with information on the species officially categorized as endangered, such as *Callithrix aurita* and *Callithrix flaviceps*, both considered Endangered (EN).
	IUCN Red List of Threatened Species	"The International Union for Conservation of Nature's Red List of Threatened Species has evolved to become the world's most comprehensive information source on the global conservation status of animal, fungi and plant species."	It presents factsheets with information on the species according to the overall assessment. *Callithrix aurita* and *Callithrix flaviceps* were considered Endangered and Critically Endangered, respectively.—Melo, F., Bicca-Marques, J., Ferraz, D. da S., Jerusalinsky, L., Mittermeier, R. A., Oliveira, L. C., Port-Carvalho, M., Ruiz-Miranda, C.R., Valença Montenegro, M., da Cunha, R. and do Valle, R.R. 2020. *Callithrix aurita* (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2020: e.T3570A166617776. https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T3570A166617776.en.—*Callithrix flaviceps*: Ferrari, S., Mendes, S.L. and Rylands, A.B. 2020. *Callithrix flaviceps*. The IUCN Red List of Threatened Species 2020: e.T3571A17936805. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T3571A17936805.en. *Callithrix aurita* and *Callithrix flaviceps* are listed in Appendix I.
	CITES—Convention on International Trade in Endangered Species of Wild Fauna and Flora	"CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) is an international agreement between governments. Its aim is to ensure that international trade in specimens of wild animals and plants does not threaten their survival."	
	THE World's 25 most endangered primates: 2018–2020 (2019)	"The tenth iteration of the biennial listing of a consensus of the 25 primate species considered to be among the most endangered worldwide and the most in need of conservation measures."	*Callithrix aurita* is among the 25 In: C. Schwitzer, R.A. Mittermeier, A.B. Rylands, F. Chiozza, E.A. Williamson, D. Byler, S. Wich, T. Humle, C. Johnson, H. Mynott and G. McCabe (eds.), Primates in Peril: The World's 25 Most Endangered Primates 2018–2020, pp. 24–27. IUCN SSC Primate Specialist Group, International Primatological Society, Global Wildlife Conservation, and Bristol Zoological Society, Washington, DC.

Figure 12: Anthropogenic *Callithrix* hybrid zones. Each natural species range is color-coded as in Figure 1. Hybrid zone locations adapted from da Rosa et al.,[19] Malukiewicz,[21] and Bezerra et al.[168] Hybrid zone. AH = *C aurita* × *Callithrix* Sp.; AP = *C aurita* × *C penicillata*; JA = *C jacchus* × *C aurita*; JH = *C jacchus* × *Callithrix* Sp; JP = *C jacchus* × *C penicillata*; PG = *C geoffroyi* × *C penicillata*; PH = *C penicillata* × *Callithrix* Sp. Abbreviations stand for Brazilian States: AL = Alagoas; BA = Bahia; ES = Espírito Santo; CE = Ceará; GO = Goiás; MA = Maranhão; MG = Minas Gerais; PB = Paraíba; PI = Piauí; PE = Pernambuco; PR = Paraná; RJ = Rio de Janeiro; RN = Rio Grande Do Norte; SE = Sergipe; SP = São Paulo; TO = Tocantins.

Callithrix Population Declines and Conservation

Callithrix Population Declines All *Callithrix* species face population declines across their native ranges as a result of habitat loss and land conversion, principally for urbanization, agriculture,

and livestock production.[10–12,166,168] The estimates of remaining original forest area are 63% for the Cerrado, 47% for the Caatinga, and 11%–28% for the Atlantic forest.[169,170] Furthermore, between 2006 and 2015, the accumulated area of lost natural vegetation of

Brazilian biomes was 300 000 km^2.[171] For arboreal primates, marmosets included, continued deforestation in Brazil is the most serious threat to the persistence of populations and species.[12,172]

The 3 most threatened *Callithrix* species are *C flaviceps*, *C aurita* and *C kuhlii*.[10,11,167] *C aurita* has also been listed among the 25 most threatened primates on the planet.[173] Projections based on forest loss and other anthropic factors predict reductions of over 50% of *C aurita* and *C flaviceps* populations in the next 18 years.[10,11] For instance, forests within the geographical distribution of *C aurita* were reduced by 43% between 1990 and 2008.[174] For *C flaviceps*, agricultural activities have profoundly modified the environment where the species naturally occurs, with cattle breeding and coffee plantation occupying formerly forested areas.[17] The remaining *C flaviceps* sub-populations, estimated at approximately 4440 individuals, are restricted to the margins of riparian forests and steep hillsides unsuitable for raising cattle or planting coffee or eucalyptus.[11] Between 2015 and 2017, the widespread Brazilian YFV epidemic decimated >90% the *C flaviceps* population at RPPN Feliciano Miguel Abdala, a private reserve in Caratinga, Minas Gerais.[175] The virus may have caused other such reductions across the *C flaviceps* range.[11] It is interesting to note that global climate changes could lead to reductions in the distribution area as high as 95% for *C flaviceps* and 27% for *C aurita*.[59] For *C kuhlii*, whose total population is estimated to be >10 000 individuals, a population decline of 30% is expected by 2031 because much of its native habitat is being converted to cattle ranches and agriculture.[172]

The other 3 *Callithrix* species are of "least concern", but nonetheless their populations are declining throughout their native geographic ranges.[166,168,176] These changes are likely driven by the illegal wildlife trade and agricultural/ranching activities. The urban expansion that accompanies agriculture expansion is characterized by activities that limit primate dispersal or increase mortality: building of roads, topographical changes caused by erosion, and the presence of domestic animals such as dogs that enter the forests to hunt.[177] For the 3 "least concern" *jacchus* group species, the human activities that devastated marmoset habitats also drive social groups into urbanized areas, where they are more vulnerable to disease, accidents, and poaching, perhaps making urban *Callithrix* populations less viable.

Nonetheless, marmoset populations manage to persist in urbanized areas[178] (personal observation, Ita de Oliveira e Silva, Joanna Malukiewicz, Luiz CM Pereira, Vanner Boere). The use of urban environments demands plasticity and perhaps adaptations in behavior, diet, metabolism, toxicants, immune defense, and relationships with pathogens. Marmosets are indeed capable of showing adaptive plasticity in social behavior and sleeping site selection in urban, disturbed environments.[179,180]

Callithrix Conservation Legislation, Species Action Plans, and Current Initiatives

The Brazilian constitution grants protection for all wildlife, and Brazil has devised a number of legal instruments related to the protection and conservation of *Callithrix* species (Table 4). The Brazilian National Biodiversity Policy[181] was formulated to comply with the Convention on Biological Diversity of 2002. Three instruments of this policy deal directly with species conservation[182]: the Official National Lists of Endangered Species, the Red Books of Endangered Brazilian Species, and the Conservation of Endangered Species National Action Plans (NAPs). NAPs define both *in situ* and *ex situ* actions for the conservation and recovery of endangered species. Initially, conservation of

Callithrix species came under the Conservation of Mammals in the Central Atlantic Forest NAP.[183] In 2018, *Callithrix* species became part of the NAP for the Conservation of The Primates of the Atlantic Forest and the Collared Sloth.[184] The Saguis-da-serra Conservation Program is an initiative to put into practice the actions foreseen by such NAPs along with the help of several researchers and institutions.

Recently, a studbook was created to track genealogical relationships between individuals of the Brazilian captive *C aurita* population.[153] The *C aurita* studbook keeper, C. Igayara, estimates that there are approximately 33 individuals that make up the current captive population. An important objective in breeding and maintaining a captive *C aurita* population is to maximize genetic diversity individuals.[153,173] Currently, no *C flaviceps* are maintained in captivity (personal observation, Fabiano R de Melo).

Another important *Callithrix* conservation initiative has been the creation of the Center for the Conservation of Saguis-da-serra at the Federal University of Viçosa, Brazil—the first primatology center in the world devoted exclusively to develop both *in situ* and *ex situ* conservation activities (personal observation, Fabiano R de Melo). Among the objectives of the Center for the Conservation of Saguis-da-serra are to develop directives for the management of *in situ* populations of *C aurita* and *C flaviceps* and to help guide researchers in choosing the best management strategies for particular marmoset populations. Additionally, protocols are being developed that aim to standardize data collection for mountain marmosets and prioritize locations for further in situ research (personal observation, Fabiano R de Melo).

In the last decade, regulations for the management of fauna have emerged in Brazil (eg,[185,186]), including, more recently, the management for the control of invasive alien and allochthonous species.[145,187,188] Currently, many confiscated and apprehended animals end up in Brazilian animal triage centers,[189] and these captive facilities do not have further capacity to receive a higher influx of marmosets nor to keep them for long. In addition, most management institutions have no interest in maintaining "common" or non-threatened species. From an ecological perspective, allochthonous marmosets can be considered introduced and potential or *de facto* invasive species. If allochthonous marmoset species are considered exotic, then the proper course of action would be to eradicate them during the early invasion stages or control established populations. Introduced and hybrid marmosets could also be removed from areas in which they pose a direct conservation problem, but the major obstacle for this course of action is resolving the destination of these animals. Ultimately, although these kinds of actions are supported by national Brazilian legislation and NAPs, effective action implementation runs into problems concerning funding and reaching a common consensus for the best plan of action.

CONCLUSION

Marmosets have been the quintessential laboratory primate model for a wide variety of health studies. Currently, with the increased adoption of the concept of One Health and the opportunities afforded by established field sites for several species under a variety of environmental conditions, marmosets can become a model group to study the evolution and ecology of infectious diseases, the relationship between environment, health, aging and genetics, adaptive responses to emerging diseases, immune system genetics, physiology, epidemics, and

other public health topics. These studies can contribute both to the understanding of the dynamics of diseases of concern to humans and to the conservation of several endangered species of marmosets and other primates with which they are sympatric. This scenario offers an unprecedented opportunity for synergy between evolutionary biology, human health, and species conservation concerns. Thus, the stage is set to establish long-term scientific exchange and collaboration among scientists from various disciplines and different countries to address human and non-human primate issues of world-wide importance.[190,191]

Funding

Acknowledgments

References

1. Rylands AB, Coimbra-Filho AF, Mittermeier RA. The systematics and distributions of the marmosets (*Callithrix, Callibella, Cebuella,* and *Mico*) and *Callimico* (*Callimico*) (Callitrichidae, Primates). In: Ford SM, Porter LM, Davis LC, eds. *The Smallest Anthropoids: The Marmoset/Callimico Radiation*. New York: Springer; 2009. p. 25–61.

2. Malukiewicz J, Cartwright RA, Curi NHA, et al. Mitogenomic phylogeny of *Callithrix* with special focus on human transferred taxa. *BMC Genomics* 22, 239 (2021). https://doi.org/10.1186/s12864-021-07533-1.

3. Buckner JC, Lynch-Alfaro JW, Rylands AB et al. Biogeography of the marmosets and tamarins (Callitrichidae). *Mol Phylogenet Evol*. 2015; 82B:413–25. http://doi.org/10.1016/j.ympev.2014.04.031.

4. Malukiewicz J, Boere V, Fuzessy LF et al. Natural and anthropogenic hybridization in two species of eastern Brazilian marmosets (*Callithrix jacchus* and *C. penicillata*). *PLoS One*. 2015; 10(6):e0127268. http://doi.org/10.1371/journal.pone.0127268.

5. Mendes SL. Padrões biogeográficos e vocais em *Callithrix* do grupo jacchus (Primates, Callitrichidae). dissertation. Universidade Estadual de Campinas (UNICAMP), Campinas, Sóo Paulo, Brazil; 1997.

6. Norris D, Rocha-Mendes F, Marques R et al. Density and spatial distribution of buffy-tufted-ear marmosets (*Callithrix aurita*) in a continuous Atlantic Forest. *Int J Primatol*. 2011; 32(4):811–29. http://doi.org/10.1007/s10764-011-9503-1.

7. Ferrari SF, Corre HKM, Coutinho PEG. Ecology of the "southern" marmosets (*Callithrix aurita* and *Callithrix flaviceps*): How different, how similar? In: Norconk MA, Rosenberger AL, Garber PA, eds. *Adaptive Radiations of Neotropical Primates*. New York: Plenum Press; 1996. p. 157–71.

8. Hershkovitz P. *Living New World Monkeys (Platyrrhini) With an Introduction to Primates: Vol 1*. Chicago, IL: Chicago University Press; 1977.

9. Mittermeier RA, Coimbra-Filho AF, Constable ID et al. Conservation of primates in the Atlantic forest region of eastern Brazil. *Int Zoo Yearb*. 1982; 22:2–17.

10. Melo F, Bicca-Marques J, Ferraz DS, et al. (2020) *Callithrix aurita* (amended version of 2019 assessment). The IUCN red list of threatened species 2020: E.T3570A166617776. https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T3570A166617776.en. Accessed July 27, 2020.

11. Ferrari S, Mendes SL, Rylands AB. (2020) *Callithrix flaviceps. The IUCN Red List of Threatened Species 2020: e.T3571A17936805.* https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T3571A17936805.en. Accessed July 27, 2020.

12. Rylands AB, Fonseca GAB, Leite YL et al. Primates of the Atlantic Forest: origin, distribution, endemism, and communities. In: Norconk MA, Rosenberger AL, Garber PA, eds. *Adaptive Radiations of Neotropical Primates*. New York, NY: Plenum Press; 1996. p. 21–51.

13. Oliveira LC, Grelle CEV. Introduced primate species of an Atlantic Forest region in Brazil: present and future implications for the native fauna. *Tropical Conservation Science*. 2012; 5(1):112–20. http://doi.org/10.1177/194008291200500110.

14. Oliver WLR, Santos IB. Threatened endemic mammals of the Atlantic forest region of south-east Brazil. In: *Wildlife Preservation Trust, Special Scientific Report* 4; Jersey Wildlife Preservation Trust. 1991. p. 126.

15. Rylands AB, Spironelo W, Tornisielo VL et al. Primates of the Rio Jequitinhonha valley, Minas Gerais. Brazil. *Primate Conserv*. 1988; 9:100–9.

16. Vivo, M. Taxonomia de *Callithrix* erxleben, 1777 (Callitrichidae, primates). Belo Horizonte: Fundacao Biodiversitas. 1992.

17. Silva FFR, Malukiewicz J, Silva LC et al. A survey of wild and introduced marmosets (*Callithrix*: Callitrichidae) in the southern and eastern portions of the state of Minas Gerais, Brazil. *Primate Conserv*. 2018; 32:1–18.

18. Vale C, Neto LM, Prezoto F. Distribution and invasive potential of the black-tufted marmoset *Callithrix penicillata* in the Brazilian territory. *Scientia Plena*. 2020; 16:1–19. http://doi.org/10.14808/sci.plena.2020.052401.

19. da Rosa CA, Ribeiro BR, Bejarano V. Neotropical alien mammals: a data set of occurrence and abundance of alien mammals in the Neotropics. *Ecology*. 2020; 101(11):e03115. http://doi.org/10.1002/ecy.3115.

20. Ferreira FM, Queiroz LP. Vegetação e flora da Caatinga. *Cienc Cult*. 2018; 70(4):51–6.

21. Malukiewicz J. A review of experimental, natural, and anthropogenic hybridization in *Callithrix* marmosets. *Int J Primatol*. 2019; 40:72–98. http://doi.org/10.21800/2317-66602018000400014.

22. Grelle CEV, Cerqueira R. Determinantes da distribuição geográfica de *Callithrix flaviceps* (Thomas) (Primates, Callitrichidae). *Rev Bras Zool*. 2006; 23:414–20.

23. Ferrari SF, Diego VH. Long-term changes in a wild marmoset group. *Folia Primatol*. 1992; 58(4):215–8.

24. Coutinho PE, Corrêa KM. Polygyny in a free-ranging group of buffy-tufted-ear marmosets. *Callithrix aurita. Folia primatological (Basel)*. 1995; 65(1):25–9.

25. Muskin A. Field notes and geographic distribution of *Callithrix aurita* in eastern Brazil. *Am J Primatol*. 1984; 7:377–80.

26. Cosenza BAP, Melo FR. Primates of the Serra do Brigadeiro State Park, Minas Gerais. Brazil. *Neotropical Primates.* 1998; 86(1):18–20.

27. Costa MD, Fernandes FAB, Hilário RR et al. Densidade, tamanho populacional e conservação de primatas em fragmento de Mata Atlântica no sul do estado de Minas Gerais, Brasil. *Iheringia, Série Zoologia, Porto Alegre.* 2012; 102(1):5–10.

28. Rylands AB, Faria DS. Habitats, feeding ecology, and home range size in the genus *Callithrix*. In: Rylands AB, ed. *Marmosets and Tamarins: Systematics, Behaviour, and Ecology.* Oxford: Oxford University Press; 1993. p. 262–72.

29. Souza VB. *Variação do crânio e da mandíbula em Callithrix Erxleben, 1777 (Platyrrhini, Callitrichidae): resultados de uma abordagem através de morfometria geométrica.* thesis. Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil; 2016.

30. Martins MM, Setz EZF. Diet of buffy tufted-eared marmosets (*Callithrix aurita*) in a forest fragment in southeastern Brazil. *Int J Primatol.* 2000; 21:467–76.

31. Alves MC. Observações sobre o *Callithrix flaviceps* (Thonas, 1903) na Estação Ecológica de Caratinga - EBC/FBCN, Minas Gerais (Callitrichidae, Primates). In: Mello MT, ed. *A primatologica no Brasil - 2.* Brasília: Sociedade Brasileira de Primatologia; 1986:205–206.

32. Ferrari SF. Preliminary report on the field study of *Callithrix flaviceps.* In: Rylands AB, Bernardes AT, eds. *A Primatologia no Brasil - 3.* Belo Horizonte, Brasil: Fundação Biodiversitas e Sociedade Brasileira de Primatologia; 1991. p. 159–71.

33. Guimarães A. *Ecologia, comportamento reprodutivo e marcação de cheiro em um grupo de Callithrix flaviceps (Callitrichidae, Primates), na Estacoa Biologia de Caratinga Minas Gerais.* thesis. Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil; 1998.

34. Hilário RR, Ferrari SF. Feeding ecology of a group of buffy-headed marmosets (*Callithrix flaviceps*): fungi as a preferred resource. *Am J Primatol.* 2010; 72:515–21. http://doi.org/10.1002/ajp.20804.

35. Hilario RR, Ferrari SF. Four breeding females in a free ranging group of buffy-headed marmosets (*Callithrix flaviceps*). *Folia Primatol.* 2010; 81:31–40. http://doi.org/10.1159/000278839.

36. Natori M. Interspecific relationships of *Callithrix* based on the dental characters. *Primates.* 1986; 27:321–36.

37. Ferrari SF. *The ecology and behaviour of the buffy-headed marmoset, Callithrix flaviceps (O. Thomas, 1903).* dissertation. University of London, London, United Kingdom; 1988.

38. Hilário RR, Ferrari SF. Why feed on fungi? The nutritional content of sporocarps consumed by buffy-headed marmosets, *Callithrix flaviceps* (Primates: Callitrichidae), in southeastern Brazil. *J Chem Ecol.* 2011; 37:145–9. http://doi.org/10.1007/s10886-011-9911-x.

39. Passamani M, Rylands AB. Home range of a Geoffroy's marmoset group, *Callithrix geofforyi* (Primates, Callithrichidae) in South-Eastern Brazil. *Rev Brasil Biol.* 2000; 60:275–81. http://doi.org/10.1590/s0034-71082000000200011.

40. Passamani M, Rylands AB. Feeding behavior of Geoffroy's marmoset (*Callithrix geoffroyi*) in an Atlantic Forest fragment of South-Eastern Brazil. *Primates.* 2000; 41:27–38. http://doi.org/10.1007/BF02557459.

41. Chiarello AG. *Mammalian community and forest structure of an Atlantic forest fragment of southeastern Brazil.* dissertation. University of Cambridge, Cambridge, United Kingdom; 1997.

42. Taylor A, Vinyard C. Comparative analysis of masseter fiber architecture in tree-gouging (*Callithrix jacchus*) and nongouging (*Saguinus oedipus*) callitrichids. *J Morphol.* 2004; 261:276–85. http://doi.org/10.1002/jmor.10249.

43. Canton JM, Hill DM, Hume JD et al. The digestive strategy of the common marmoset, *Callithrix jacchus. Comp Biochem Physiol A Physiol.* 1996; 144:1–8. http://doi.org/10.1016/0300-9629(95)02013-6.

44. Garber PA, Caselli CB, McKenney AC et al. Trait variation and trait stability in common marmosets (*Callithrix jacchus*) inhabiting ecologically distinct habitats in northeastern Brazil. *Am J Primatol.* 2019; 81:e23018. http://doi.org/q0.1002/ajp.23018.

45. Castro CSS, Araujo A. Diet and feeding behavior of marmoset. *Callithrix jacchus. Braz J Ecol.* 2007; 7:14–9.

46. Abreu F, De la Fuente MFC, Schiel N et al. Feeding ecology and behavioral adjustments: flexibility of a small neotropical primate (*Callithrix jacchus*) to survive in a semiarid environment. *Mammal Research.* 2016; 61:221–9. http://doi.org/10.1007/s13364-016-0262-4.

47. De la Fuente MFC, Souto A, Sampaio MB et al. Behavioral adjustments by a small neotropical primate (*Callithrix jacchus*) in a semiarid Caatinga environment. *Sci World J.* 2014; 326524:1–8. http://doi.org/10.1155/2014/326524.

48. Streilein KE. Ecology of small mammals in the semiarid Brazilian Caatinga. II. *Water Rel Ann Carnegie Mus.* 1982; 51(6):109–26.

49. Garber PA. Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichidae. *Am J Phys Anthropol.* 1992; 88:469–82. http://doi.org/10.1002/ajpa.1330880404.

50. Tardif SD, Smucny DA, Abbott DH et al. Reproduction in captive common marmosets (*Callithrix jacchus*). *Compar Med.* 2003; 53:364–8.

51. Schiel N, Souto A. The common marmoset: an overview of its natural history, ecology and behavior. *Dev Neurobiol.* 2017; 77(3):244–62. http://doi.org/10.1002/dneu.22458.

52. Raboy BE, Canale GR, Dietz JM. Ecology of *Callithrix kuhlii* and a review of eastern Brazilian marmosets. *Int J Primatol.* 2008; 29:449–67.

53. Rylands AB. Sympatric Brazilian callitrichids: the black-tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin *Leontopithecus chrysomelas. J Hum Evol.* 1989; 18(7):679–695. http://doi.org/10.1016/0047-2484(89)90100-0.

54. Rodrigues NN, Martinez RA. Wildlife in our backyard: interactions between Wied's marmoset *Callithrix kuhlii* (Primates: Callitrichidae) and residents of Ilhéus, Bahia. *Brazil Wildlife Biol.* 2014; 20:91–6. http://doi.org/10.2981/wlb.13057.

55. Fonseca GAB, Lacher TE Jr, Alves C Jr et al. Some ecological aspects of free-living black tufted-ear marmosets (*Callithrix jacchus penicillata*). *Antropologia Contemporâneo.* 1980; 3:197.

56. Miranda GHB, Faria DS. Ecological aspects of black-pincelled marmoset (*Callithrix penicillata*) in the Cerradão and dense Cerrado of the Brazilian central plateau. *Braz J Biol.* 2001; 61(3):397–404. http://doi.org/10.1590/S1519-69842001000300008.

57. Silva IO. *Socialidade e acesso a recursos alimentares por fêmeas de saguis (Callithrix penicillata) em grupos em ambiente natural* dissertation. Universidade de Brasília, Brasília, Federal District, Brazil; 2008.

58. Bicca-Marques J, Jerusalinsky L, Mittermeier RA et al. 2018. *Callithrix penicillata.* The IUCN red list of threatened species 2018: E.T41519A17935797. Available at: https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T41519A17935797.en. Accessed October 11, 2020.

59. Braz AG, Lorini ML, Vale MM. Climate change is likely to affect the distribution but not parapatry of the Brazilian marmoset monkeys (*Callithrix* spp.). *Divers Distrib*. 2019; 25:536–50. http://doi.org/10.1111/ddi.12872.

60. Moraes AM, Vancine MH, Moraes AM et al. Predicting the potential hybridization zones between native and invasive marmosets within neotropical biodiversity hotspots. *Global Ecol Conserv*. 2019; 20:e00706. http://doi.org/10.1016/j.gecco.2019.e00706.

61. Vale CA, Neto LM, Prezoto F. Distribution and invasive potential of the black-tufted marmoset *Callithrix penicillata* in the Brazilian territory. *Sci Plena*. 2020; 052401. http://doi.org/10.14808/sci.plena.2020.052401.

62. Power ML, Ross CN, Schulkin J et al. The development of obesity begins at an early age in captive common marmosets (*Callithrix jacchus*). *Am J Primatol*. 2012; 74:261–9. http://doi.org/10.1002/ajp.21995.

63. Seferovic M, Sánchez-San Martín C, Tardif SD et al. Experimental Zika virus infection in the pregnant common marmoset induces spontaneous fetal loss and neurodevelopmental abnormalities. *Sci Rep*. 2018; 8:6851. http://doi.org/10.1038/s41598-018-25205-1.

64. Rutherford JN, Tardi SD. Placental efficiency and intrauterine resource allocation strategies in the common marmoset pregnancy. *Am J Phys Anthropol*. 2008; 137:60–8. http://doi.org/10.1002/ajpa.20846.

65. Worley K, Warren W, Rogers J et al. The common marmoset genome provides insight into primate biology and evolution. *Nat Genet*. 2014; 46:850–7. http://doi.org/10.1038/ng.3042.

66. Harris RA, Tardif SD, Vinar T et al. Evolutionary genetics and implications of small size and twinning in callitrichine primates. *Proc Natl Acad Sci U S A*. 2014; 111(4):1467–72. http://doi.org/10.1073/pnas.1316037111.

67. Saltzman W, Digby LJ, Abbott DH. Reproductive skew in female common marmosets: what can proximate mechanisms tell us about ultimate causes? *Proc Biol Sci*. 2009; 276:389–99. http://doi.org/10.1098/rspb.2008.1374.

68. Wislocki GB. Observations on twinning in marmosets. *Am J Anat*. 1939; 64:445–83.

69. Ross CN, French JA, Ortí G. Germ-line chimerism and paternal care in marmosets (*Callithrix kuhlii*). *Proc Natl Acad Sci U S A*. 2007; 104:6278–82. http://doi.org/10.1073/pnas.0607426104.

70. Benirschke K, Anderson JM, Brownhill LE. Marrow chimerism in marmosets. *Science*. 1962; 138(3539):513–5.

71. Sweeney CG, Curran E, Westmoreland SV et al. Quantitative molecular assessment of chimerism across tissues in marmosets and tamarins. *BMC Genomics*. 2012; 13:98. http://doi.org/10.1186/1471-2164-13-98.

72. Bell JT, Pai AA, Pickrell JK et al. DNA methylation patterns associate with genetic and gene expression variation in HapMap cell lines. *Genome Biol*. 2011; 12(1):R10. http://doi.org/10.1186/gb-2011-12-1-r10.

73. Feil R, Fraga MF. Epigenetics and the environment: emerging patterns and implications. *Nat Rev Genet*. 2012; 13(2):97–109. http://doi.org/10.1038/nrg3142.

74. Ben-Shlomo R. Invasiveness, chimerism and genetic diversity. *Mol Ecol*. 2017; 26(23):6502–9. http://doi.org/10.1111/mec.14364.

75. Abreu F, Souto A, Schiel N. Wild common marmosets (*Callithrix jacchus*) employ spatial cognitive abilities to improve their food search and consumption: an experimental approach in small-scale space. *Primates*. 2020; 61:807–16. http://doi.org/10.1007/s10329-020-00826-1.

76. Šlipogor V, Gunhold-de Oliveira T, Tadić Z et al. Consistent inter-individual differences in common marmosets (*Callithrix jacchus*) in boldness-shyness, stress activity, and exploration-avoidance. *Am J Primatol*. 2016; 78(9):961–73. http://doi.org/10.1002/ajp.22566.

77. Inoue-Murayama M, Yokoyama C, Yamanashi Y et al. Common marmoset (*Callithrix jacchus*) personality, subjective well-being, hair cortisol level and AVPR1a, OPRM1, and DAT genotypes. *Sci Rep*. 2018; 8(1):10255. http://doi.org/10.1038/s41598-018-28112-7.

78. Šlipogor V, Massen JJM, Schiel N et al. Temporal consistency and ecological validity of personality structure in common marmosets (*Callithrix jacchus*): a unifying field and laboratory approach. *Am J Primatol*. 2021; 83(2):e23229. http://doi.org/10.1002/ajp.23229.

79. del Rosario RC, Rayan NA, Prabhakar S. Noncoding origins of anthropoid traits and a new null model of transposon functionalization. *Genome Res*. 2014; 24(9):1469–84. http://doi.org/10.1101/gr.168963.113.

80. Jayakumar V, Ishii H, Seki M et al. An improved de novo genome assembly of the common marmoset genome yields improved contiguity and increased mapping rates of sequence data. *BMC Genomics*. 2020; 21(Suppl 3):243. http://doi.org/10.1186/s12864-020-6657-2.

81. Yang C, Zhou Y, Marcus S. et al. Evolutionary and biomedical insights from a marmoset diploid genome assembly. *Nature*. 2021 594; 227–233. https://doi.org/10.1038/s41586-021-03535-x.

82. Yoshimatsu S, Sato T, Yamamoto M et al. Generation of a male common marmoset embryonic stem cell line DSY127-BV8VT1 carrying double reporters specific for the germ cell linage using the CRISPR-Cas9 and PiggyBac transposase systems. *Stem Cell Res*. 2020; 44:101740. http://doi.org/10.1016/j.scr.2020.101740.

83. Chin CS, Peluso P, Sedlazeck FJ et al. Phased diploid genome assembly with single-molecule real-time sequencing. *Nat Methods*. 2016; 13(12):1050–4. http://doi.org/10.1038/nmeth.4035.

84. Housman G, Quillen EE, Stone AC. Intraspecific and interspecific investigations of skeletal DNA methylation and femur morphology in primates. *Am J Phys Anthropol*. 2020; 173(1):34–49. http://doi.org/10.1002/ajpa.24041.

85. Narapareddy L, Wildman DE, Armstrong DL et al. Maternal weight affects placental DNA methylation of genes involved in metabolic pathways in the common marmoset monkey (*Callithrix jacchus*). *Am J Primatol*. 2020; 82(3):e23101. http://doi.org/10.1002/ajp.23101.

86. Mashiko H, Yoshida AC, Kikuchi SS et al. Comparative anatomy of marmoset and mouse cortex from genomic expression. *J Neurosci*. 2012; 32(15):5039–53. http://doi.org/10.1523/JNEUROSCI.4788-11.2012.

87. Matsunaga E, Nambu S, Oka M et al. Comparative analysis of developmentally regulated expressions of Gadd45a, Gadd45b, and Gadd45g in the mouse and marmoset cerebral cortex. *Neuroscience*. 2015; 284:566–80. http://doi.org/10.1016/j.neuroscience.2014.10.032.

88. Law AJ, Pei Q, Feldon J et al. Gene expression in the anterior cingulate cortex and amygdala of adolescent marmoset monkeys following parental separations in infancy. *Int J Neuropsychopharmacol*. 2009; 12(6):761–72. http://doi.org/10.1017/S1461145708009723.

89. Housman G, Gilad Y. Prime time for primate functional genomics. *Curr Opin Genet Dev*. 2020; 62:1–7. http://doi.org/10.1016/j.gde.2020.04.007.

90. Bakken TE, Jorstad NL, Hu Q et al. Evolution of cellular diversity in primary motor cortex of human, marmoset monkey, and mouse. *BioRxiv*. 2020; 03(31):016972.

91. Geirsdottir L, David E, Keren-Shaul H et al. Cross-species single-cell analysis reveals divergence of the primate microglia program. *Cell*. 2019; 79(7):1609–1622.e16. http://doi.org/10.1016/j.cell.2019.11.010.

92. Aravalli RN, Steer CJ. Utility of common marmoset (*Callithrix jacchus*) embryonic stem cells in liver disease modeling, tissue engineering and drug metabolism. *Genes (Basel)*. 2020; 11(7):729. http://doi.org/10.3390/genes11070729.

93. Debowski K, Warthemann R, Lentes J et al. Non-viral generation of marmoset monkey iPS cells by a six-factor-in-one-vector approach. *PLoS One*. 2015; 10(3):e0118424. http://doi.org/10.1371/journal.pone.0118424.

94. Vermilyea SC, Guthrie S, Meyer M et al. Induced pluripotent stem cell-derived dopaminergic neurons from adult common marmoset fibroblasts. *Stem Cells Dev*. 2017; 26(17):1225–35. http://doi.org/10.1089/scd.2017.0069.

95. Okano H, Sasaki E, Yamamori T et al. Brain/MINDS: a Japanese national brain project for marmoset neuroscience. *Neuron*. 2016; 92(3):582–90. http://doi.org/10.1016/j.neuron.2016.10.018.

96. Shimogori T, Abe A, Go Y et al. Digital gene atlas of neonate common marmoset brain. *Neurosci Res*. 2018; 128:1–13. http://doi.org/10.1016/j.neures.2017.10.009.

97. Koroshetz W, Gordon J, Adams A et al. The state of the NIH BRAIN initiative. *J Neurosci*. 2018; 38(29):6427–38. http://doi.org/10.1523/JNEUROSCI.3174-17.2018.

98. Kishi N, Sato K, Sasaki E et al. Common marmoset as a new model animal for neuroscience research and genome editing technology. *Develop Growth Differ*. 2014; 56(1):53–62. http://doi.org/10.1111/dgd.12109.

99. Krienen FM, Goldman M, Zhang Q et al. Innovations present in the primate interneuron repertoire. *Nature*. 2020; 586(7828):262–9.

100. Boroviak T, Stirparo GG, Dietmann S et al. Single cell transcriptome analysis of human, marmoset and mouse embryos reveals common and divergent features of preimplantation development. *Development*. 2018; 145(21):dev167833. http://doi.org/10.1242/dev.167833.

101. Klein J, Figueroa F. Evolution of the major histocompatibility complex. *Crit Rev Immunol*. 1986; 6(4):295–386.

102. Walter L. Major histocompatibility complex class-I-interacting natural killer cell receptors of nonhuman primates. *J Innate Immun*. 2011; 3(3):236–41. http://doi.org/10.1159/000323932.

103. Shiina T, Kono A, Westphal N et al. Comparative genome analysis of the major histocompatibility complex (MHC) class I B/C segments in primates elucidated by genomic sequencing in common marmoset (*Callithrix jacchus*). *Immunogenetics*. 2011; 63(8):485–99. http://doi.org/10.1007/s00251-011-0526-8.

104. Kono A, Brameier M, Roos C et al. Genomic sequence analysis of the MHC class I G/F segment in common marmoset (*Callithrix jacchus*). *J Immunol*. 2014; 192(7):3239–46. http://doi.org/10.4049/jimmunol.1302745.

105. van der Wiel MK, Otting N, de Groot NG et al. The repertoire of MHC class I genes in the common marmoset: evidence for functional plasticity. *Immunogenetics*. 2013; 65(12):841–9. http://doi.org/10.1007/s00251-013-0732-7.

106. Averdam A, Petersen B, Rosner C et al. A novel system of polymorphic and diverse NK cell receptors in primates. *PLoS Genet*. 2009; 5(10):e1000688. http://doi.org/10.1371/journal.pgen.1000688.

107. Hart BA, Kap YS. An essential role of virus-infected B cells in the marmoset experimental autoimmune encephalomyelitis model. *Mult Scler J Exp Transl Clin*. 2017; 3(1):2055217317690184. http://doi.org/10.1177/2055217317690184.

108. Pinto MA, Marchevsky RS, Baptista ML et al. Experimental hepatitis a virus (HAV) infection in *Callithrix jacchus*: early detection of HAV antigen and viral fate. *Exp Toxicol Pathol*. 2002; 53(6):413–20. http://doi.org/10.1078/0940-2993-00212.

109. Falk L, Deinhardt F, Wolfe L et al. Epstein-Barr virus: experimental infection of *Callithrix jacchus* marmosets. *Int J Cancer*. 1976; 17(6):785–8. http://doi.org/10.1002/ijc.2910170615.

110. Sutherland SD, Almeida JD, Gardner PS et al. Rapid diagnosis and management of parainfluenza I virus infection in common marmosets (*Callithrix jacchus*). *Lab Anim*. 1986; 20(2):121–6. http://doi.org/10.1258/002367786780865151.

111. Bukh J, Apgar CL. Five new or recently discovered (GBV-A) virus species are indigenous to New World monkeys and may constitute a separate genus of the Flaviviridae. *Virology*. 1997; 229(2):429–36. http://doi.org/10.1006/viro.1997.8461.

112. Tilston-Lunel NL, Hughes J, Acrani GO et al. Genetic analysis of members of the species Oropouche virus and identification of a novel M segment sequence. *J Gen Virol*. 2015; 96(Pt 7):1636–50. http://doi.org/10.1099/vir.0.000108.

113. Muniz CP, Zheng H, Jia H et al. A non-invasive specimen collection method and a novel simian foamy virus (SFV) DNA quantification assay in New World primates reveal aspects of tissue tropism and improved SFV detection. *PLoS One*. 2017; 12(9):e0184251. http://doi.org/10.1371/journal.pone.0184251.

114. Guzman MG, Gubler DJ, Izquierdo A et al. Dengue infection. *Nat Rev Dis Primers*. 2016; 2:16055. http://doi.org/10.1038/nrdp.2016.55.

115. Omatsu T, Moi ML, Takasaki T et al. Changes in hematological and serum biochemical parameters in common marmosets (*Callithrix jacchus*) after inoculation with dengue virus. *J Med Primatol*. 2012; 41(5):289–96. http://doi.org/10.1111/j.1600-0684.2012.00552.x.

116. Ferreira MS, de Castro PH, Silva GA et al. *Callithrix penicillata*: a feasible experimental model for dengue virus infection. *Immunol Lett*. 2014; 158(1–2):126–33. http://doi.org/10.1016/j.imlet.2013.12.008.

117. Vasconcelos BC, Vieira JA, Silva GO et al. Antibody-enhanced dengue disease generates a marked CNS inflammatory response in the black-tufted marmoset *Callithrix penicillata*. *Neuropathology*. 2016; 36(1):3–16. http://doi.org/10.1111/neup.12229.

118. Dick GWA. Zika virus. II. Pathogenicity and physical properties. *Trans Roy Soc Trop Med Hyg*. 1952; 46: 521–534.

119. Chiu CY, Sánchez-San Martín C, Bouquet J et al. Experimental Zika virus inoculation in a New World monkey model reproduces key features of the human infection. *Sci Rep*. 2017; 7(1):17126. http://doi.org/10.1038/s41598-017-17067-w.

120. Chippaux JP, Chippaux A. Yellow fever in Africa and the Americas: a historical and epidemiological perspective. *J Venom Anim Toxins Incl Trop Dis*. 2018; 24:20. http://doi.org/10.1186/s40409-018-0162-y.

121. Freitas ACP, Oviedo-Pastrana ME, da Rocha DA et al. Diagnóstico de animais ilegais recebidos no centro de triagem de animais silvestres de Belo Horizonte, Estado de Minas Gerais, no ano de 2011. *Ciência Rural*. 2015; 45(1):163–70. http://doi.org/10.1590/0103-8478cr20131212.

122. Silva NIO, Sacchetto L, de Rezende IM et al. Recent sylvatic yellow fever virus transmission in Brazil: the news from an old disease. *Virol J*. 2020; 17(1):9. http://doi.org/10.1186/s12985-019-1277-7.

123. Mares-Guia MAMM, Horta MA, Romano A et al. Yellow fever epizootics in non-human primates, southeast and northeast Brazil (2017 and 2018). *Parasit Vectors*. 2020; 13(1):90. http://doi.org/10.1186/s13071-020-3966-x.

124. Cavalcante KRLJ, Tauil PL. Epidemiological characteristics of yellow fever in Brazil, 2000-2012. *Epidemiol Serv Saúde Brasíli*. 2016; 25(1):11–20. http://doi.org/10.5123/s1679-49742016000100002.

125. Cunha MS, da Costa AC, de Azevedo Fernandes NCC et al. Epizootics due to yellow fever virus in São Paulo state, Brazil: viral dissemination to new areas (2016-2017). *Sci Rep*. 2019; 9(1):5474. http://doi.org/10.1038/s41598-019-41950-3.

126. Figueiredo LTM. Emergent arboviruses in Brazil. *Rev Soc Bras Med Trop*. 2007; 40(2):224–9. http://doi.org/10.1590/S0037-86822007000200016.

127. Moreira-Soto A, Torres MC, Lima de Mendonça MC et al. Evidence for multiple sylvatic transmission cycles during the 2016-2017 yellow fever virus outbreak, Brazil. *Clin Microbiol Infect*. 2018; 24(9):1019.e1–4. http://doi.org/10.1016/j.cmi.2018.01.026.

128. Abreu FVS, Ferreira-de-Brito A, Azevedo AS et al. Survey on non-human primates and mosquitoes does not provide evidences of spillover/spillback between the urban and sylvatic cycles of yellow fever and Zika viruses following severe outbreaks in Southeast Brazil. *Viruses*. 2020; 12(4):364. http://doi.org/10.3390/v12040364.

129. Favoretto SR, Araujo DB, Duarte NFH et al. Zika virus in peridomestic neotropical primates. *Northeast Brazil Ecohealth*. 2019; 16(1):61–9. http://doi.org/10.1007/s10393-019-01394-7.

130. Terzian ACB, Zini N, Sacchetto L et al. Evidence of natural Zika virus infection in neotropical non-human primates in Brazil. *Sci Rep*. 2018; 8(1):16034. http://doi.org/10.1038/s41598-018-34423-6.

131. Guth S, Hanley KA, Althouse BM et al. Ecological processes underlying the emergence of novel enzootic cycles: arboviruses in the neotropics as a case study. *PLoS Negl Trop Dis*. 2020; 14(8):e0008338. http://doi.org/10.1371/journal.pntd.0008338.

132. Costa EA, Luppi MM, Malta MC et al. Outbreak of human herpesvirus type 1 infection in nonhuman primates (*Callithrix penicillata*). *J Wildl Dis*. 2011; 47(3):690–3 http://doi.org/10.7589/0090-3558-47.3.690.

133. Longa CS, Bruno SF, Pires AR et al. Human herpesvirus 1 in wild marmosets, Brazil, 2008. *Emerg Infect Dis*. 2011; 17(7):1308–10. http://doi.org/10.3201/eid1707.100333.

134. Mätz-Rensing K, Jentsch KD, Rensing S et al. Fatal herpes simplex infection in a group of common marmosets (*Callithrix jacchus*). *Vet Pathol*. 2003; 40(4):405–11. http://doi.org/10.1354/vp.40-4-405.

135. Kotait I, Oliveira RN, Carrieri ML et al. Non-human primates as a reservoir for rabies virus in Brazil. *Zoonoses Public Health*. 2019; 66(1):47–59. http://doi.org/10.1111/zph.12527.

136. Moutinho FFB, Correa DMS, Marcanth N et al. Surveillance of epizootic diseases in non-human primates in Niterói, RJ. *Brazil Hygeia*. 2020; 16:37–48.

137. Aguiar TDF, Costa EC, Rolim BN et al. Risks of transmitting rabies virus from captive domiciliary common marmoset (*Callithrix jacchus*) to human beings, in the metropolitan region of Fortaleza, state of Ceará, Brazil. *Rev Soc Bras Med Trop*. 2011; 44(3):356–63. http://doi.org/10.1590/S0037-86822011005000031.

138. Carroll D, Daszak P, Wolfe ND et al. The global Virome project. *Science*. 2018; 359(6378):872–4. http://doi.org/10.1126/science.aap7463.

139. D'arc M, Moreira FRR, Dias CA et al. The characterization of two novel neotropical primate papillomaviruses supports the ancient within-species diversity model. *Virus Evol*. 2020; 6(1):veaa036.

140. da Cruz MAO M. *Dinâmica reprodutiva de uma população de saguis-do-Nordeste (Callithrix jacchus) na Estação Ecológica do Tapacurá, PE*. dissertation. São Paulo University, São Paulo, Brasil; 1998.

141. Faulkes CG, Arruda MF, MAOM D C. Genetic structure within and among populations of the common marmoset, *Callithrix jacchus*: implications for cooperative breeding. In: Ford SM, Porter LM, Davis LC, eds. *The Smallest Anthropoids: The Marmoset/Callimico Radiation*. New York, NY: Springer; 2009. p. 103–17.

142. Thompson CL, Hrit R, Melo LCO et al. Callitrichid responses to dead and dying infants: the effects of paternal bonding and cause of death. *Primates*. 2020; 61(5):707–16. http://doi.org/10.1007/s10329-020-00824-3.

143. Brasil. 1967. Lei n° 5.197, de 3 de janeiro de 1967. *Dispõe sobre a proteção à fauna e dá outras providências. Diário Oficial [da] República Federativa do Brasil, Brasília, DF*, 3 Jan. 1967. Available at: http://www.planalto.gov.br/ccivil_03/leis/L5197compilado.htm. Accessed July 27, 2020.

144. Bastos LF, Luz VLF, dos Reis IJ et al. Apreensão de espécimes da fauna silvestre em Goiás–situação e destinação. *Revista De Biologia Neotropical*. 2008; 5(2):51–63.

145. São Paulo (estado). *Secretaria de Estado do Meio Ambiente. Resolução. SMA N° 164, DE 27 DE NOVEMBRO DE 2018. Estabelece procedimentos para reprodução de espécies do gênero Callithrix mantidos em empreendimentos de fauna silvestre em cativeiro no Estado de São Paulo*. Available at: https://smastr16.blob.core.windows.net/legislacao/2018/11/resolucao-sma-164-2018-processo-2029-2016-estabelece-procedimentos-para-reproducao-de-callithrix.pdf. Accessed September 8, 2020.

146. RENCTAS. 2001. 1° Relatório Nacional Sobre o Tráfico de Fauna Silvestre. *RENCTAS, Brasília*. Available at: http://www.renctas.org.br/wp-content/uploads/2014/02/REL_RENCTAS_pt_final.pdf. Accessed September 8, 2020.

147. Levacov D, Jerusalinsky L, Fialho MDS. Levantamento dos primatas recebidos em Centros de Triagem e sua relação com o tráfico de animais silvestres no Brasil. In: Melo FR, Mourthé I, eds. *A Primatologia no Brasil – 11, Belo Horizonte. Belo Horizonte, Brasil: Sociedade Brasileira de Primatologia*; 2011. p. 281–305.

148. Silva NM. *Espécimes recebidos no centro de triagem de animais silvestres de Salvador, BA durante os anos de 2012 a 2014*. Monograph: Federal University of Bahia; 2015.

149. de Morais Jr MM, Ruiz-Miranda CR, Grativol AD et al. Os sagüis, *Callithrix jacchus penicillata*, como espécies invasoras

na região de ocorrência do mico-leão dourado. *Conservação do mico-leão-dourado*. Universidade Estadual do Norte Fluminense Darcy Ribeiro: Campos dos Goytacazes, Rio de Janeiro, Brazil. 2008; 28820:86.

150. Ruiz Miranda CR, De Morais Jr MM, de Paula VR et al. O problema dos saguis introduzidos no Rio de Janeiro: vítimas ou vilões? *Ciência Hoje*. 2011; 48:44–9.

151. Ruiz-Miranda CR, Affonso AG, Martins A et al. Distribuição do sagui (*Callithrix jacchus*) nas areas de ocorrência do mico-leão-dourado (*Leontopithecus rosalia*) no estado do Rio de Janeiro. *Neotropical Primates*. 2000; 8:98–100.

152. Fuzessy LF, Silva IO, Malukiewicz J et al. Morphological variation in wild marmosets (*Callithrix penicillata* and *Callithrix geoffroyi*) and their hybrids. *Evol Biol*. 2014; 41:480–93. http://doi.org/10.1007/s11692-014-9284-5.

153. Carvalho RS, Bergallo HG, Cronemberger C et al. *Callithrix aurita*: a tiny primate on the edge of extinction in the Brazilian Atlantic Forest. *Neotrop Primates*. 2018; 24:1–8.

154. Carvalho RS. Conservação do saguis-da-serra-escuro (*Callithrix aurita* (Primates)) – Analise molecular e colormetrica de populações do gênero *Callithrix* e seus híbridos. dissertation. *Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brasil*. 2015.

155. Secco H, Grilo C, Bager A. Habitat selection by the black-tufted marmoset *Callithrix penicillata* in human disturbed landscapes. *J Trop Ecol*. 2018; 34(02):135–44. http://doi.org/10.1017/S026646741800007X.

156. Detogne N, Ferreguetti AC, Mello JFF et al. Spatial distribution of buffy-tufted-ear (*Callithrix aurita*) and invasive marmosets (*Callithrix* spp.) in a tropical rainforest reserve in southwestern Brazil. *Am J Primatol*. 2017; 79:e22718. http://doi.org/10.1002/ajp.22718.

157. Paula HMG, Távora RS, Almeida MV et al. Estudos preliminares da presença de sagüis no município de Bauru, São Paulo. *Brasil Neotrop Primates*. 2005; 13:6–1. http://doi.org/10.1896/1413-4705.13.3.6.

158. Crispo E, Moore J-S, Lee-Yaw JA et al. Broken barriers: human-induced changes to gene flow and introgression in animals: an examination of the ways in which humans increase genetic exchange among populations and species and the consequences for biodiversity. *BioEssays*. 2011; 33:508–18. http://doi.org/10.1002/bies.201000154.

159. Lyra-Neves RM, Oliveira MAB, Telino-Júnior WR et al. Comportamentos interespecíficos entre *Callithrix jacchus* (Linnaeus) (Primates, Callitrichidae) e algumas aves de Mata Atlântica, Pernambuco, Brasil. *Rev Bras de Zoolo*. 2007; 24(3):709–16 http://doi.org/10.1590/S0101-81752007000300022.

160. Silva IO, Alvarenga ABB, Boere V. Occasional field observations of the predation on mice, dove and ants by black-tufted-ear marmosets (*Callithrix penicillata*). *Neotrop Primates*. 2008; 15(2):59–62. http://doi.org/10.1896/044.015.0209.

161. Sales IS, Ruiz-Miranda CR, Santos CP. Helminths found in marmosets (*Callithrix penicillata* and *Callithrix jacchus*) introduced to the region of occurrence of golden lion tamarins (*Leontopithecus rosalia*) in Brazil. *Vet Parasitol*. 2010; 171(1–2):123–9. http://doi.org/10.1016/j.vetpar.2010.02.044.

162. Silva FFR. *Distribuição do gênero Callithrix no estado de Minas Gerais: introdução de espécies e hibridação*. thesis. Federal University of Viçosa, Viçosa, Minas Gerais, Brazil; 2014.

163. Rhymer JM, Simberloff D. Extinction by hybridization and introgression. *Annu Rev Ecol Syst*. 1996; 27:83–109. http://doi.org/10.1146/annurev.ecolsys.27.1.83.

164. McFarlane SE, Pemberton JM. Detecting the true extent of introgression during anthropogenic hybridization. *Trends Ecol Evol*. 2019; 34(4):315–26. http://doi.org/10.1016/j.tree.2018.12.013.

165. Allendorf F, Leary R, Spruell P et al. The problems with hybrids: setting conservation guidelines. *TREE*. 2001; 16:613–22.

166. Bicca-Marques J, Jerusalinsky L, Mittermeier RA, et al. (2018) *Callithrix penicillata. The IUCN Red List of Threatened Species 2018: e.T41519A17935797*. Available at: http://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T41519A17935797.en. Accessed July 27, 2020.

167. Nieves L, Bicca-Marques J, Jerusalinsky L et al. *Callithrix kuhlii. The IUCN red list of threatened species 2019: E.T3575A17936243*. 2019. http://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T3575A17936243.en Accessed July 27, 2020.

168. Bezerra B, Bicca-Marques J, Miranda J, et al. (2018) *Callithrix jacchus. The IUCN Red List of Threatened Species 2018: e.T41518A17936001*. Available at: http://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T41518A17936001.en. Accessed July 27, 2020

169. Beuchle R, Grecchi RC, Shimabukuro Y et al. Land cover changes in the Brazilian Cerrado and Caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. *Appl Geogr*. 2015; 2015(58):116–27. http://doi.org/10.1016/j.apgeog.2015.01.017.

170. Rezende C, Scarano LFR, Assad ED et al. From hotspot to hopespot: an opportunity for the Brazilian Atlantic Forest. *PECON*. 2018; 16:208–14. http://doi.org/10.1016/j.pecon.2018.10.002.

171. Crouzeilles R, Ferreira MS, Chazdon RL et al. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Sci Adv*. 2017; 3(11):e1701345. http://doi.org/10.1126/sciadv.1701345.

172. Jerusalinsky L, Melo FR. Conservação de primatas no Brasil: perspectivas e desafios. In: Urbani B, Kowalewski M, Cunha RGT et al, editors. *La primatología en Latinoamérica 2 – A primatologia na America Latina 2. Tomo I Argentina-Colombia. Ediciones IVIC. Caracas: Instituto Venezolano de Investigaciones Científicas (IVIC)*. 2018:161–186.

173. Carvalho RS, Fransen SJ, Valença-Montenegro MM et al. Buffy-tufted-ear marmoset *Callithrix aurita* É. Geoffroy Saint-Hilaire, 1812, Brazil. In: Schwitzer C, Mittermeier RA, Rylands AB et al., eds. *Primates in Peril: The world's 25 most endangered primates 2018–2020*. Washington, DC: IUCN SSC Primate Specialist Group, International Primatological Society, Global Wildlife Conservation, and Bristol Zoological Society; 2019. p. 79–81.

174. Bechara IM. *Abordagens metodológicas em Biogeografia da Conservação para avaliar risco de extinção de espécies: um estudo de caso com Callithrix aurita (Primates: Callitrichidae)*. thesis. Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil; 2012.

175. Possamai CB, Mendes SL, Strier KB. *Decline of a primate community following a yellow fever outbreak in the Brazilian Atlantic Forest*. https://www.asp.org/meetings/abstractDisplay.cfm?AccesabstractID=13328&expand=true&confEventID=10544&parenteventid=10467 Accessed February 9, 2021.

176. Rylands AB, Mendes SL. Callithrix geoffroyi. *The IUCN Red List of Threatened Species*; 2018: e.T3572A17936610. Available at: http://doi.org/10.2305 IUCN.UK.2018-2.RLTS.T3572A17936610.en. Accessed February 9, 2021.

177. Estrada A, Garber PA, Mittermeier RA et al. Primates in peril: the significance of Brazil, Madagascar. *Indonesia and the Democratic Republic of the Congo for global primate conservation. Peer J.* 2018; 6:e4869. http://doi.org/10.7717/peerj.4869.

178. Teixeira B, Hirsch A, Goulart VDLR et al. Good neighbours: distribution of black-tufted marmoset (*Callithrix penicillata*) in an urban environment. *Wildl Res.* 2015; 42:579–89. http://doi.org/10.1071/WR14148.

179. Duarte MHL, Young RJ. Sleeping site selection by urban marmosets (*Callithrix penicillata*) under conditions of exceptionally high predator density. *I J Primatol.* 2011; 32:29–334. https:doi.org/10.1007/s10764-010-9468-5.

180. Goulart VDLR, Teixeira CP, Young RJ. Analysis of callouts made in relation to wild urban marmosets (*Callithrix penicillata*) and their implications for urban species management. *Eur J of Wildl Res.* 2010; 56(4):641–9. http://doi.org/10.1007/s10344-009-0362-4.

181. http://www.planalto.gov.br/ccivil_03/decreto/2002/d4339.htm. Accessed July 27, 2020.

182. Brasil. 2009. Portaria Conjunta MMA/ICMBIO n° 316, de 09 de setembro de 2009. *Dispõe sobre os instrumentos de implementação da Política Nacional da Biodiversidade voltados para a conservação e recuperação de espécies ameaçadas de extinção. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 10 set.* 2009. Available at: https://www.mma.gov.br/estruturas/179/_arquivos/portaria_316_mma_icmbio_179.pdf. Accessed July 27, 2020.

183. Brasil. 2010. Portaria ICMBio n° 134 de 23 de dezembro de 2010. *Aprova o Plano de Ação Nacional para a Conservação dos Mamíferos da Mata Atlântica Central. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 24 dez.* 2010. Available at: https://www.icmbio.gov.br/portal/images/stories/docs-pan/pan-mamac/1-ciclo/pan-mamac-portaria-aprovacao.pdf. Accessed July 27, 2020.

184. Brasil. 2018. Portaria ICMBio n° 702 de 21 de março de 2018. *Aprova o Plano de Ação Nacional para a Conservação dos Primatas da Mata Atlântica e da Preguiça-de-coleira. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 22 mar.* 2018. Available at: https://www.in.gov.br/web/guest/materia/-/asset_publisher/Kujrw0TZC2Mb/content/id/7526450/do1-2018-03-22-portaria-n-702-de-21-de-marco-de-2018-7526446. Accessed July 27, 2020.

185. Brasil. 2014. Instrução Normativa ICMBio/IBAMA n°01, de 08 de dezembro de 2014. *Estabelece procedimentos entre o ICMBio e o IBAMA para o manejo e a conservação de espécies da fauna silvestre brasileira. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 19 dez.* 2014. Available at: https://www.icmbio.gov.br/cepsul/images/stories/legislacao/Instrucao_normativa/2014/in_icmbio_ibama_01_2014_procedimentos_entre_icmbio_ibama_manejo_conserva%C3%A7%C3%A3o_fauna_br.pdf. Accessed July 27, 2020.

186. Brasil. 2014. Instrução Normativa IBAMA n°23, de 31 de dezembro de 2014. *Define as diretrizes e os procedimentos para a destinação de animais silvestres apreendidos, resgatados por autoridade competente ou entregues voluntariamente pela população, bem como para o funcionamento dos Centros de Triagem de Animais Silvestres do IBAMA - CETAS. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 2 jan.* 2015. Available at: https://www.in.gov.br/materia/-/asset_publisher/Kujrw0TZC2Mb/content/id/32094529/do1-2015-01-02-instrucao-normativa-n-23-de-31-de-dezembro-de-2014-32094512.

187. Brasil. 2018. Resolução da Comissão Nacional de Biodiversidade – CONABIO/MMA n° 7, de 29 de maio de 2018. *Aprova a Estratégia Nacional para Espécies Exóticas Invasoras. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 13 jun.* 2018. Available at: https://www.in.gov.br/en/web/dou/-/instrucao-normativa-n-6-de-25-de-julho-de-2019-211213911#:~:text=Regulamenta%20o%20inciso%20XX%20do,e%20suas%20zonas%20de%20amortecimento. Accessed July 27, 2020.

188. Brasil. 2019. Instrução Normativa ICMBio n° 6, de 25 de julho de 2019. *Regulamenta o inciso XX do artigo 2° do Anexo I do Decreto 8.974, de 24 de janeiro de 2017, que dispõe sobre a prevenção de introduções e o controle ou erradicação de espécies exóticas ou invasoras em Unidades de Conservação federais e suas zonas de amortecimento. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 19 ago.* 2019. Available at: https://www.in.gov.br/en/web/dou/-/instrucao-normativa-n-6-de-25-de-julho-de-2019-211213911#:~:text=Regulamenta%20o%20inciso%20XX%20do,e%20suas%20zonas%20de%20amortecimento. Accessed July 27, 2020.

189. Brasil. 2018. *Define as categorias de atividades ou empreendimentos e estabelece critérios gerais para a autorização de uso e manejo, em cativeiro, da fauna silvestre e da fauna exótica. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 29 out.* Resolução CONAMA n°489, de 26 de outubro de 2018. Available at: https://www.in.gov.br/materia/-/asset_publisher/Kujrw0TZC2Mb/content/id/47542644/do1-2018-10-29-resolucao-n-489-de-26-de-outubro-de-2018-47542603. Accessed July 27, 2020.

190. Todesco M, Pascual MA, Owens GL et al. Hybridization and extinction. *Evol Appl.* 2016; 9:892–908. http://doi.org/10.1111/eva.12367.

191. Estrada A, Garber PA, Rylands AB et al. Impending extinction crisis of the world's primates: why primates matter. *Sci Adv.* 2017; 3(1):e1600946. http://doi.org/10.1126/sciadv.1600946.