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 two 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 into them. Due to their small size and fast life history, marmosets are prized biomedical models. As a result, there are increasingly sophisticated genomic *Callithrix* resources available and burgeoning marmoset functional, immuno-, and epi- genomic 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.

Keywords: marmoset, Neotropical, Brazil, biomedical, arbovirus, conservation, hybridization, biological invasion

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 chapter, we first give a general overview of the six *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 chapter 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 chapter by identifying new avenues for research with wild and captive *Callithrix.*

AN OVERVIEW of the *CALLITHRIX* GENUS

CALLITHRIX BIOGEOGRAPHY and EVOLUTIONARY HISTORY

The *Callithrix* genus is composed of six 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 two 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
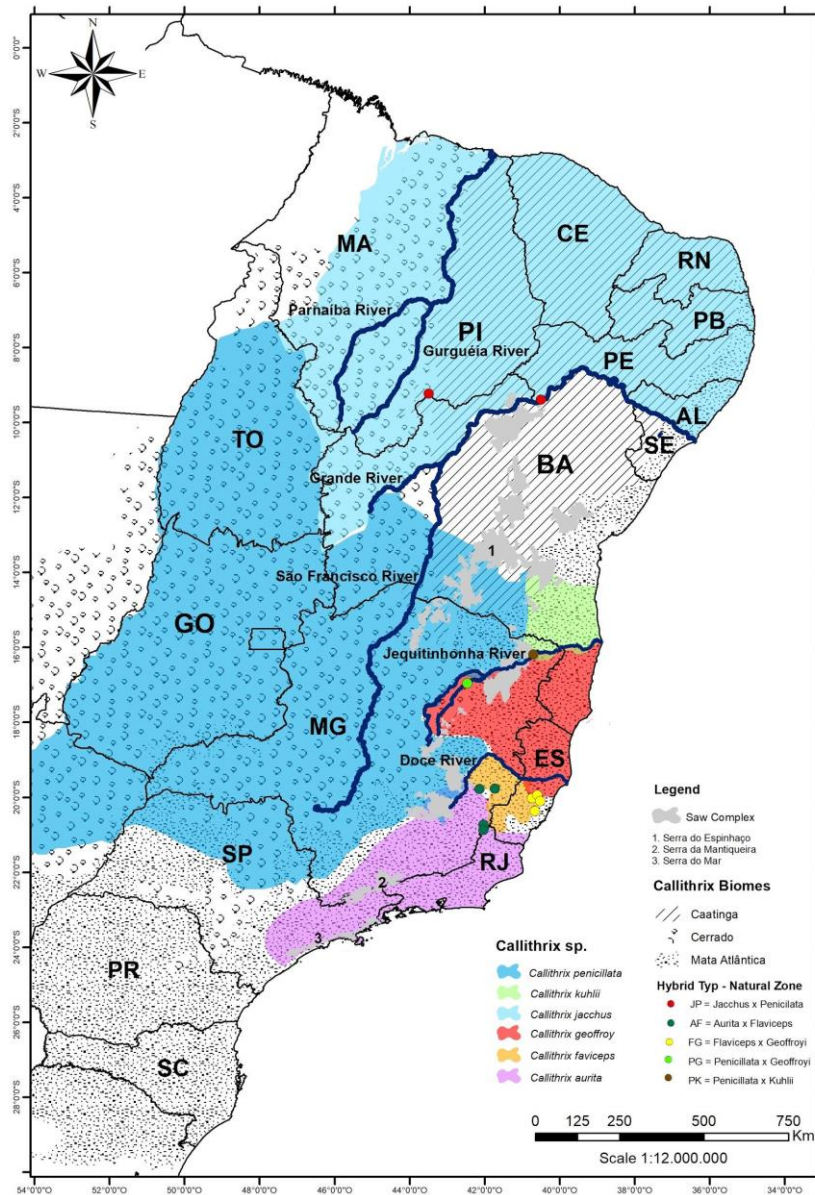
Figure 1. Maps of natural Brazilian *Callithrix* ranges following [1], and natural hybrid zones [21].

Each range is color-coded by species and respective hybrid zones are shown as points. Abbreviations

are 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

abbreviations: JP: *C. jacchus* x *C. penicillata*; AF: *C. aurita* x *C. flaviceps*; FG: *C. flaviceps* x *C.

geoffroyi*; PG: *C. geoffroyi* x *C. penicillata*; PK: *C. penicillata* x *C. kuhlii*.
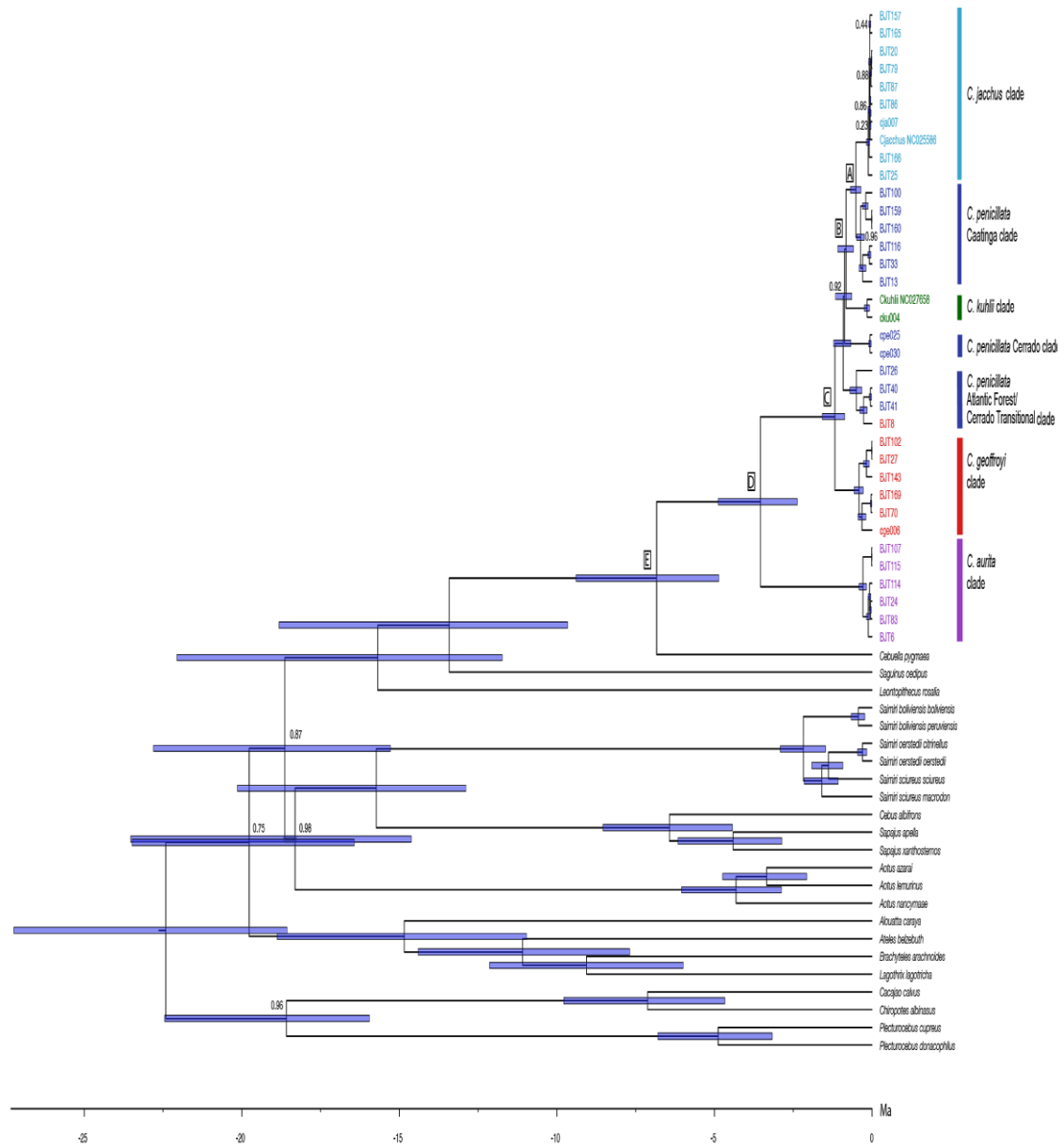
Figure 2. BEAST Bayesian phylogeny showing divergence patterns and temporal divergence estimates between *Callithrix* mitogenomic lineages, modified from [2]. Boxed letters represent major divergence nodes among *Callithrix* clades. 'Ma' refers to millions of years.

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]. *Callithrix jacchus* can be found in the Atlantic Forest and the semi-arid Caatinga biome of northeastern Brazil [1]. *Callithrix penicillata* mostly occurs in the semi-arid Cerrado of central and central-western Brazil [1], but also is found in the Caatinga [4, pers obs. JM, LCP].

CALLITHRIX NATURAL GEOGRAPHIC RANGES

Callithrix 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, [9] noted that the species also inhabits the region north of the Rio Doce State Park, MG, but does not exceed the northern limits of the Doce river. The southern limit of *C. aurita*'s range is undefined, but may occur at the intersection of the Tietê and Piracicaba rivers in São Paulo state [10].

With a geographical distribution of 30,815 km², *Callithrix 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 at altitudes up to at least 1,200 m [11]. Its range begins south of the Doce River [5] and continues into the Serra da Mantiqueira 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 *Callithrix flaviceps* occurrence was reported in the municipality of Varre-Sai, northern Rio de Janeiro state [13].

The northern distribution limit of *Callithrix 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 Rio de Contas, in the region of Valença, Bahia [12], and within the vicinity of Todos os Santos Bay, Bahia [14, pers. obs. VB and IOS]. 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].

Callithrix 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]. *Callithrix geoffroyi* occurrences have also been recorded in the Espinhaço Mountains, Minas Gerais (see Figure 1), which are located 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* is introduced there [15,17]. While *C. geoffroyi* is considered a lowland species, it has beens 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 [pers. obs., JM].

Callithrix penicillata, or the black-tufted marmoset, has the widest *Callithrix* geographic distribution, with an area of about 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 to be 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, north of the Tietê and
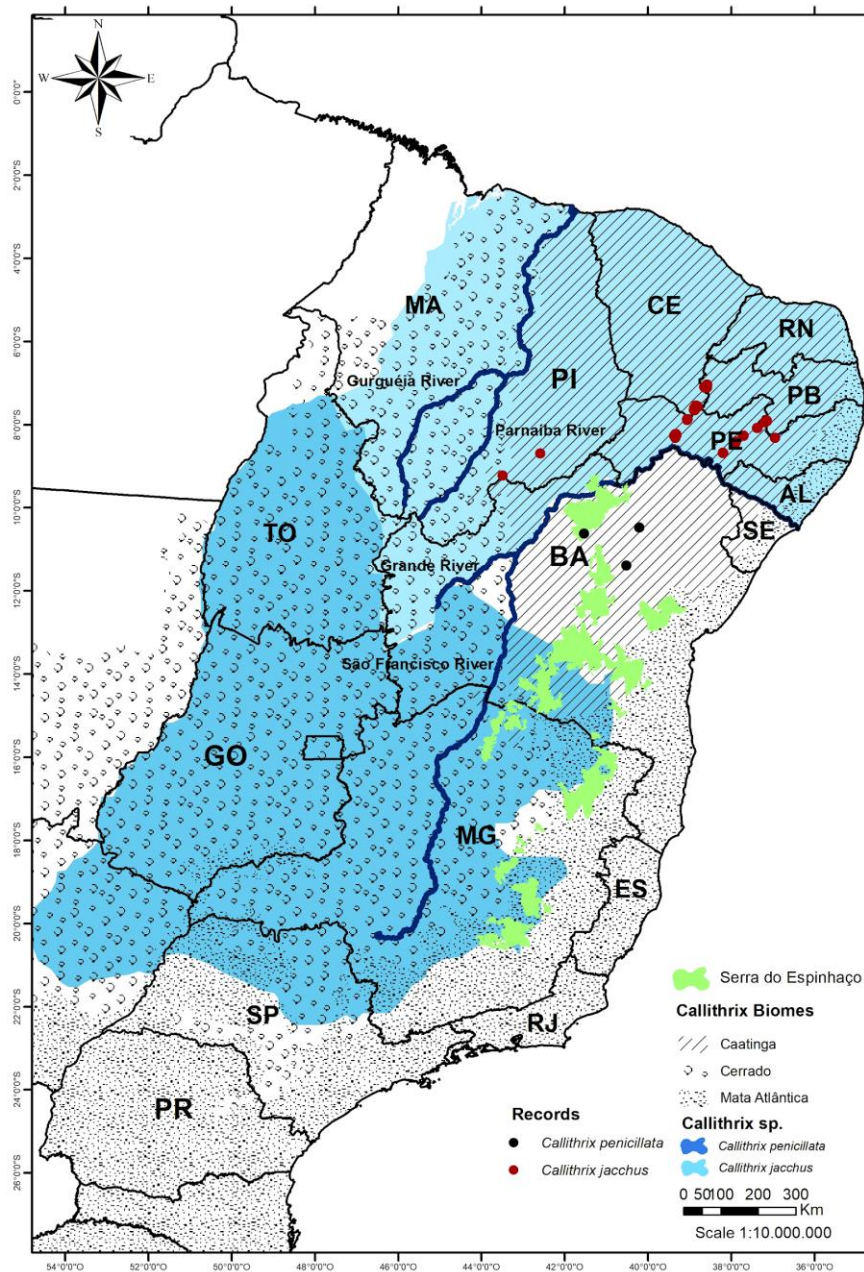
Figure 3. Light blue and darker blue regions respectively represent natural *C. jacchus* and *C. penicillata* ranges [1]. Maroon and black dots respectively represent unpublished *C. jacchus* and *C. penicillata* occurrences observed by LCMP and JM. State abbreviations follow Figure 1.

Piracicaba rivers [8], as well as eastern Minas Gerais and southern Bahia, 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 [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) (pers. obs. LCMP and JM). The dataset of [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 about 15-10 years ago MYA [20]. Further the *C. penicillata* Caatinga clade and the *C. jacchus* clades represent the two youngest clades within the phylogeny shown in Figure 2 [2]. Thus, these occurrences of *C. penicillata* in the Caatinga may be part of a natural expansion from the Cerrado and into the Caatinga.

Callithrix 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 [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 [1].

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]. *Callithrix 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 (pers. obs., LCMP). Natural hybrids between the two 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 (pers. obs. LCMP).

CHARACTERISTICS and DIFFERENCES between *CALLITHRIX* SPECIES

CALLITHRIX AURITA

The total population size adult *C. aurita* (Figure 4) is estimated to be10,000 individuals, and the species is currently listed as endangered [10]. *Callithrix 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 5-11 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, [6] estimated a general population of 1892 individuals in an 250.7 km^2 area of Atlantic Forest in southern São Paulo state.

Several morphological differences distinguish *C. aurita* from other *Callithrix* species. *Callithrix aurita* is perhaps the largest *Callithrix* species considering body weight and overall body (Figure 5 and Table 1). *Callithrix aurita* shares morphological similarities with *C. flaviceps* [e.g., 29], likely due to the close evolutionary relationship between them [5]. For example, [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, *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].

CALLITHRIX FLAVICEPS

Callithrix flaviceps (Figure 6) is one of the least studied *Callithrix* taxa. The species is listed as critically endangered [11], as 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 to 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 per day, but food scarcity during the dry season likely causes the species to have longer daily travel than in the rainy season [7]. The size *C. flaviceps* social groups is between 3-15 members [31]. Although social groups tend to have one reproductive female, there occasionally are two or more reproductive females and several adult helpers that care for offspring [35].
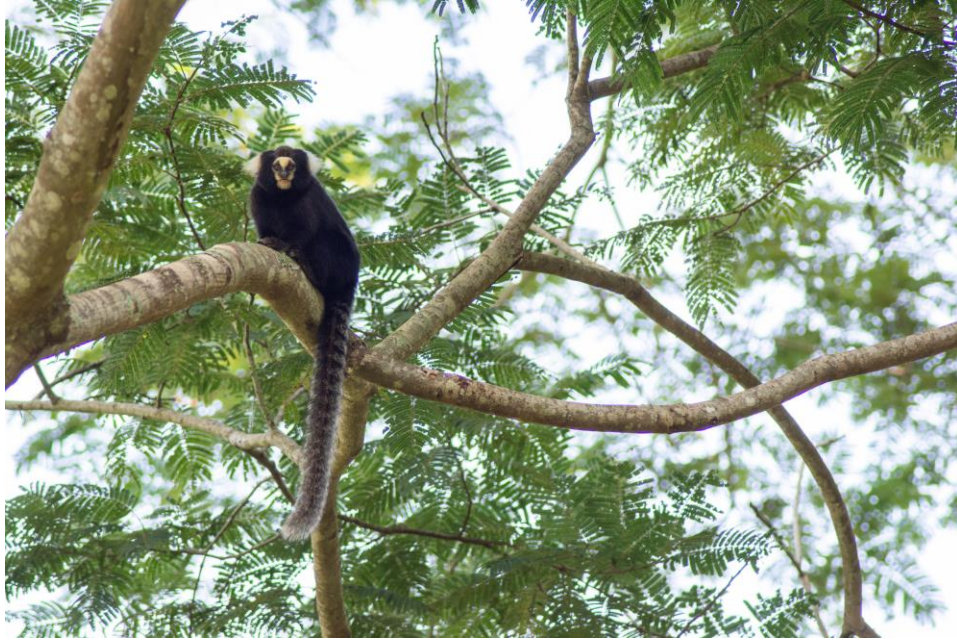
Figure 4. Image of *C. aurita*. Photo credit: Orlando Vital.
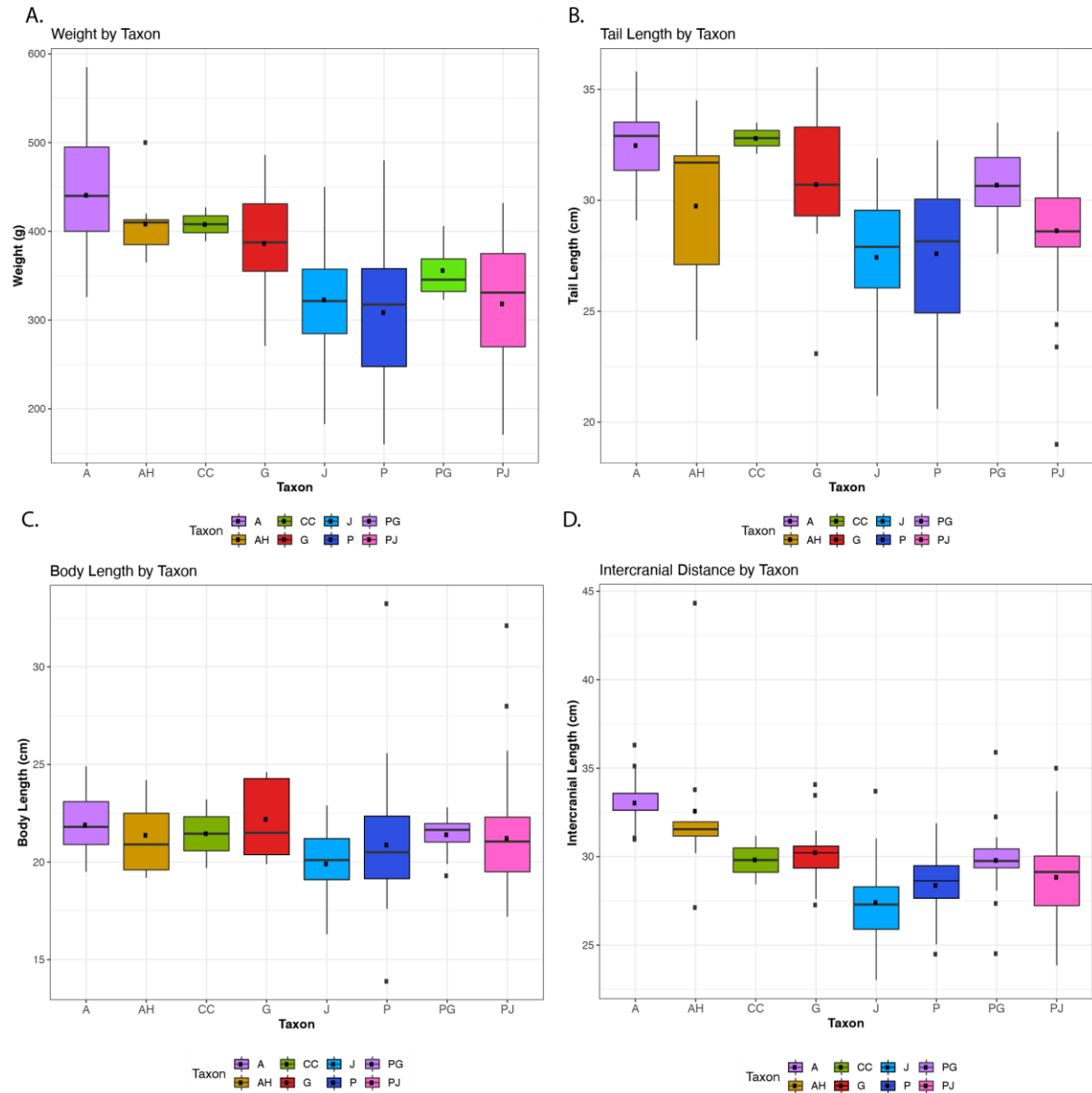
Figure 5. Boxplots of body weight (A), tail length (B), body length (C), and intercranial length for select *Callithrix* species and hybrid types. Taxa abbreviations are A=*C. aurita*, CC= unidentified hybrid, J=*C. jacchus*, PG= *C. penicillata* x *C. geoffroyi* hybrid, AH=*C. aurita* hybrid, G= *C. geoffroyi*, G=*C. geoffroyi*, P=*C. penicillata*, PJ=*C. penicillata* x *C. jacchus* hybrid. Modified from Malukiewicz et al. (unpublished data).

Table 1. Means of thirteen morphometric measures. Numbers in parentheses represent the number of samples for a given measure. Measure abbreviations are as follows: IC=intercranial distance, FO=cranial frontal-occipital distance, Zyg=distance between zygomatic arches, jaw= intermandibular distance. Taxa abbreviations follow Figure 4. Modified from Malukiewicz et al. (unpublished data). Taxon abbreviations follow Figure 5.

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. (54)2
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 (540	6.7 (54)	54.4 (54)

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]. *Callithrix flaviceps* uses a "scan and pouce" 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, as this species exploits

gums from tree holes made by wood-digging insects [7].

CALLITHRIX GEOFFROYI

Callithrix 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 and Table

1). One *C. geoffroyi* social group in an Atlantic Forest patch was composed of a single female, two

males, and two 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

meters [39]. In a 110 ha forest fragment in Espírito Santo, major food categories for one

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

upon insects, arachnids, gastropods, lizards, and frogs [41]. Population densities for *C. geoffroyi* in

northern Espírito Santo ranged from 0.7 groups/km^2 (Putiri) 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

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

CALLITHRIX JACCHUS

Callithrix jacchus (Figure 7) is one of the smallest *Callithrix* species (Table 1, Figure 5), and several of its biological traits seem associate 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, [29] attributed the compressed brain case and protruding zygomatic arches of the *jacchus* group as tree gouging adaptations. *Callithrix jacchus* and its sister species, *C. penicillata,* also share derived dentition patterns [36], that also likely represent exudivory adaptations.

Few *Callithrix* species have home ranges as small as those of *Callithrix.* In comparing Atlantic Forest living marmosets and Caatinga living marmosets, the former had a mean group composition of 8.3 individuals while Caatinga mean group size was 5.9 [44]. When comparing the animals' home range between these two 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 were negatively related and influenced by seasonality. In contrast, [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 like 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 that facilitates exudate extraction [49]. Having a cooperative breeding system and production of two litters per year [50] coupled with complex cognitive abilities [51] certainly contribute to *C. jacchus* ecological success. However, behavioural adjustments might be the key factor for navigating the challenges of the
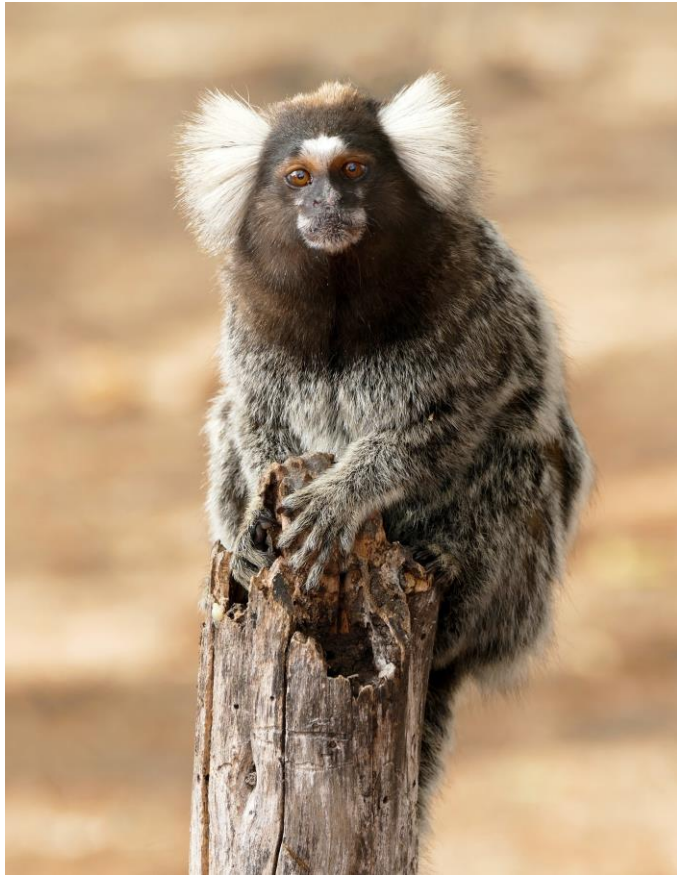
Figure 7. Image of *C. jacchus.* Photo Credit: Antonio Souto.

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]. Added to that Caatinga marmosets eat cactus, which requires cognitive skills to access the resource while avoiding injury [46].

CALLITHRIX 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, considered the longest daily 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 two species [52].

Callithrix kuhlii utilizes various habitats that include restinga forest, riverside forests, secondary forests, mangroves, fruit groves, 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 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].

CALLITHRIX 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] to 18.5 ha [56], and social groups are composed of 2-19 individuals [28, 57]. *Callithrix 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 give a great advantage 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 [58]. 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 [58, 59, pers obs. JM, VB, IOS]. Mathematical models predict that the expansion of *C. penicillata* may be greater than expected, and that this species may even replace the species of marmosets native to areas of the Atlantic Forest [59-61].

While 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 [62]. 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 (e.g., pediatric obesity [63]; Zika infection during pregnancy [64], 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 humans [65]. Understanding this difference is extremely important to ensuring appropriate use of the species to model pregnancy and development [64]).

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* [66,67]. Further, *Callithrix* growth patterns are likely tied to selection in marmosets for routine ovulation of multiple ova that leads to dizygotic twinning [68]. Altered placental and fetal growth patterns in marmosets may provide protection against discordant growth and placental pathologies of gestating litters in a simplex uterus [67]. The four positively selected genes with a likely role in regulating ova number and multiple gestations in *C. jacchus* are *GDF9*, *BMP15*, *BMP4*, and *WFIKKN1* [67].

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 one 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 [68]. 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 [69]. Fusion of the chorionic membranes during embryonic development may allow blastocyst stem and precocial cells to cross the anastomoses, rendering littermates chimeric [70]. Marmosets are therefore hematopoietic chimeras with blood derived tissues containing cells of the individual as well as their littermates [71]. However the selection pressures that may have led to this trait remain obscure.

Benirshke et al. [71] 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 [70]. Accordingly, [70] showed that blood-derived tissues from deceased and living *C. kuhlii* being between approximately 50%-100% chimeric. Malukiewicz et al. [4] found similar results for *C. jacchus* when comparing blood and skin tissues via microsatellite genotyping. In another chimerism tissue analysis based on the SRY gene concluded that germ line cells were not chimeric and only hematopoietic lineages were [72]. 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 [73,74]. 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 [75]. However, while 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 versus 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 five 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 [76]. Studies like this, 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 [e.g., 77] and behavioural observations [e.g., 78]. In particular, marmosets exhibit short-term and long-term consistency of non-social and social personality traits [79]. Personality structure under captive and wild conditions is rather similar [79]. Inoue-Murayama et al. [78] 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 [77], possibly as a product of shared social environment, genetics or social facilitation. Future studies are needed to further explore links between inter-individual behavioural 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 ultimate published sequence (designated CalJac3 in the NCBI genomics database) consisted of 2.26 billion base pairs covering all *Callithrix* chromosomes [66]. 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 [66, 67], and detection of primate-specific constrained elements [80].

Tables 2 and 3 list several genomic assemblies now available for *C. jacchus*, some which

Table 2. Marmoset genome assemblies from short-read next-generation sequencing.

Genbank Accession	Submitter	Date	Sequencing Technology	Contig N50 (Kb)	Scaffold N50 (Mb)	Number contigs	Number 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)	Number contigs	Num Scaffolds
GCA_013373975.1 (**CJA1912RKC**)	Keio University / RIKEN	2020/06/03	PacBio RSII	24,828.9	132.3	3,719	1,872
GCA_009663435.2 (**cj1700_1.1**)	McDonnell Genome Institute at Washington University	2020/05/22	PacBio, Illumina	25,227.1	98.2	1,336	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	8,609.0	146.9	1,284	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	1,124	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	1,312	353
GCA_009811775.1 (CJ2019)	Keio University	2019/12/13	PacBio RSII	6,375.4	143.9	1,812	65

have been published [e.g., 81]. One unpublished *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 [82]. The most

recent assembly is designated cj1700_1.1, which has now replaced calJac3 as the *C. jacchus*

reference genome. Cj1700_1.1 has a contig N50 (defined as the length of an individual contig for

which 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.

More accurate and (largely) complete reference genome sequences for marmosets are opening

tremendous opportunities for novel research. For example, CRISPR/Cas9 gene knock-in [83]

generated transgenic marmosets to model human disease. Further, the newer *Callithrix* genomic

assembles contain less 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 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 [84].

CALLITHRIX *FUNCTIONAL GENOMICS and EPIGENOMICS*

Marmoset epigenetics studies have examined DNA methylation patterns in a wide sampling of

tissues like bone [85] and placental tissue [86]. 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 [86]. Interestingly, [85] found that DNA methylation variation in marmosets

is not strongly associated with variation in static traits like bone morphology. This study also noted

higher levels of DNA methylation heterogeneity as compared to 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, as levels of chimerism are known to vary

across different marmoset tissues [4,70,72].

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 [87,88], but some research has also assayed candidate gene expression responses following severe psychological perturbations such as parental separation [89]. Interestingly, while 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 [87].

Now is a particularly relevant time to pursue functional genomics research, especially in primates [90], 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 [91,92]. 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 (ESCs) [eg., 93] and induced pluripotent stem cells (iPSCs) [e.g., 94,95]. ESCs and iPSCs are ideal for functional genomics research, especially in the context of disease, as 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 [93]. Another benefit is the relative ease with which these cell lines can be genetically modified [83].

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 [96,97]. For instance, functional genomics data from marmoset brain tissues have been collected and incorporated into the NIH Brain initiative [98]. This is of particular relevance as the common marmoset has been identified as an important model organism for neuroscience research that can bridge the gap between mice and humans [96,99]. 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 [100] and common and divergent features of preimplantation development [101].

CALLITHRIX *IMMUNOGENETICS*

Although New World primate immunogenetic studies lags behind that of Old World primates, complex immunogene families like 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 [102]. MHC class I proteins also interact with natural killer (NK) cell receptors to prevent NK cell destruction of healthy cells [103].

The *C. jacchus* MHC class I region is composed of three segments- *Caja*-B/C segment, the *Caja*-E segment, and the *Caja*-G/F segment [104,105]. In humans, six 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 [104] and *Caja*-G/F corresponds to the HLA-A/G/F region [104]. Shiina [105] described *Caja*-B/C as a 1,079 kb fragment containing nonclassical (low polymorphism) MHC class I genes and [105] 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 there are nine functional MHC genes and four MHC pseudogenes [105]. *Caja*-G/F encompasses six functional MHC genes as well some non-MHC genes and MHC pseudogenes [105]. These MHC I regions likely evolved by segmental duplication [104,105].

Interestingly, the human HLA-G locus shows limited polymorphism and grants immuno-tolerance between mother and fetus during pregnancy [106]. 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* [106]. 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 [106].

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) [107]. The KIR lineage is present in all simian primates [103], but in *C. jacchus* there are apparently only two KIR loci [66]. In marmosets, NKC genes cluster together and are orthologous to humans, but the marmoset NKC segment is 1.5x smaller [107]. Marmoset NKC genes also show moderate polymorphism [106]. Averdam et al. [106] found that the *C. jacchus* NKC encodes a single inhibitory heterodimer (CD94/NKG2A) and two 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 [107], but the role of *Caja*-E remains to be determined.

CALLITHRIX VIRUSES and the VIROSPHERE

CALLITHRIX *as MODELS of VIRAL DISEASES and VACCINE DEVELOPMENT*

Callithrix 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 [108]. Additionally, *Callithrix jacchus* has been used to model hepatitis A infection [109]. The species was also used for *in vitro* transformation of two permanent and virus producing lymphoblastoid cell lines with a nasopharyngeal carcinoma derived Epstein-Barr viral strain [110]. Other viral pathogens that have been explored in *Callithrix* include parainfluenza virus type 1 [111], Flaviviridae-like viruses [112], Oropouche virus [113], and Simian foamy virus [114].

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 [115]. DENV infection causes disease in humans that ranges from high fever and joint pain to shock and death (https://www.cdc.gov/dengue/index.html). Both *C. jacchus* and *C. penicillata* are candidate systems to model DENV pathogenesis and for discovery of antiviral drugs and vaccines [116,117]. In

C. penicillata, DENV infection produced marked changes in microglial cells of the central nervous system [118]. Both *Callithrix* species show elevated proinflammatory cytokines upon DENV infection, which may model aspects of human DENV pathogenesis. Another *Flavivirus,* Zika virus (ZIKV) was originally discovered in Uganda [119], 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 neurological condition like Guillain-Barré syndrome [120]. A number of recent studies have found that *C. jacchus* replicates many of these human clinical and gestational symptoms [64,120].

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 [121]. Serological surveys of YFV antibodies in wild primates have shown some positive results in *Callithrix* [122,123]. Retrospective data on surveillance of primate epizootics shows 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 to 2019 [123]. 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, [124] analyzed 2,099 NHP samples from southeastern and northeastern Brazil suspected of YFV. *Callithrix* were among the most frequently infected YFV- infect NHPs, with 140 (9.3%) *Callithrix* being positive among 1505 tested marmosets. These percentages may be even higher for epizootic diseases, as classification of NHPs in epidemiological data usually doesn't go beyond the genus level [125]. Cunha et al. [126] 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 like DENV, ZIKV, Mayaro (MAYV), and Chikungunya (CHIKV), all which can potentially establish sylvatic cycles in Brazil and other parts of South America [127]. Currently, only a limited number of studies have looked at arbovirus exposure in wild Brazilian primates, and [128] found no exposure evidence to the above arboviruses in urban and peri-urban *jacchus* group marmosets sampled in northeastern Brazil between 2012 and 2017, except one *C. jacchus* that showed serological CHIKV exposure. Also, [129] 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 [130]. Additionally, [131] found evidence of widespread ZIKV exposure in over 50 *Callithrix* sampled Minas Gerais and São Paulo states.

In order 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 [132]. *Callithrix* characteristics that can facilitate arbovirus transmission include a great adaptability to human environments, frequent interactions with human beings in urban and peri-urban environments also occupied by anthropophilic arbovirus vectors such as *Aedes aegypti* and *A. albopictus* [124]. The presence of short-lived, fast reproducing primates also facilitates the persistence arbovirus transmission [132], which are certainly characteristics that define many *Callithrix* species and hybrids.

OTHER PATHOGENS of CALLITHRIX

Human herpesvirus 1 (HV1) is transmissible from humans to *Callithrix* marmosets, which has resulted in a number of fatal epizootics events [133,134]. Transmission occurs through the close contact that these animals have developed with humans, facilitated by the habit of offering food, since the virus can be transmitted through contaminated saliva, aerosols and fomites. Transmission can also occur spontaneously between marmosets within the same group [133,135]. Affected animals are usually found dead or with severe neurological symptoms, resulting from virus-induced encephalitis [134]. The virus also causes death from meningitis [134], erosions and ulcers in the oral cavity, in addition to hemorrhages and focal necrosis in several organs [135].

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. *Callithrix jacchus,* has played an important role in the transmission of rabies in northeastern Brazil, where it maintains a distinct transmission cycle [136]. 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, Brazil [137]. The proximity of marmosets to urban environments and the practice of capturing and maintaining these animals as pets are two factors that greatly increase the risk of marmoset rabies transmission [138].

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 [139]. Although *Callithrix* virome work is still at an infancy, one pioneering study helped to characterize two novel *Papillomavirus* genomes (CpenPV-1 and CpenPV-2) in captive *C. penicillata* [140]. 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 disease reservoirs and further understand why infected *Callithrix* show relatively low YFV viral loads. Also, virome studies can help to understand if this genus could actually represent a potential risk for a severe urban YFV outbreak [124,126] and even unknown 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

While 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 (08° 07' S, 34 55' W, Figure 8). A typical Tapacurá *C. jacchus* social group may contain eight individuals- three reproductive adults, two juveniles, two infant co-twins, and an adult or subadult that may or may not be related to other group members [141]. The three breeding adults may include a dominant female and two 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 aidsthe breeding female in choosing group feeding, resting, and sleeping sites, and in territorial defense [141]. 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. There are instances at Tapacurá where breeding females were displaced by one or two daughters, but remained in the group to suckle grandchildren along with the new dominant female(s) [141].
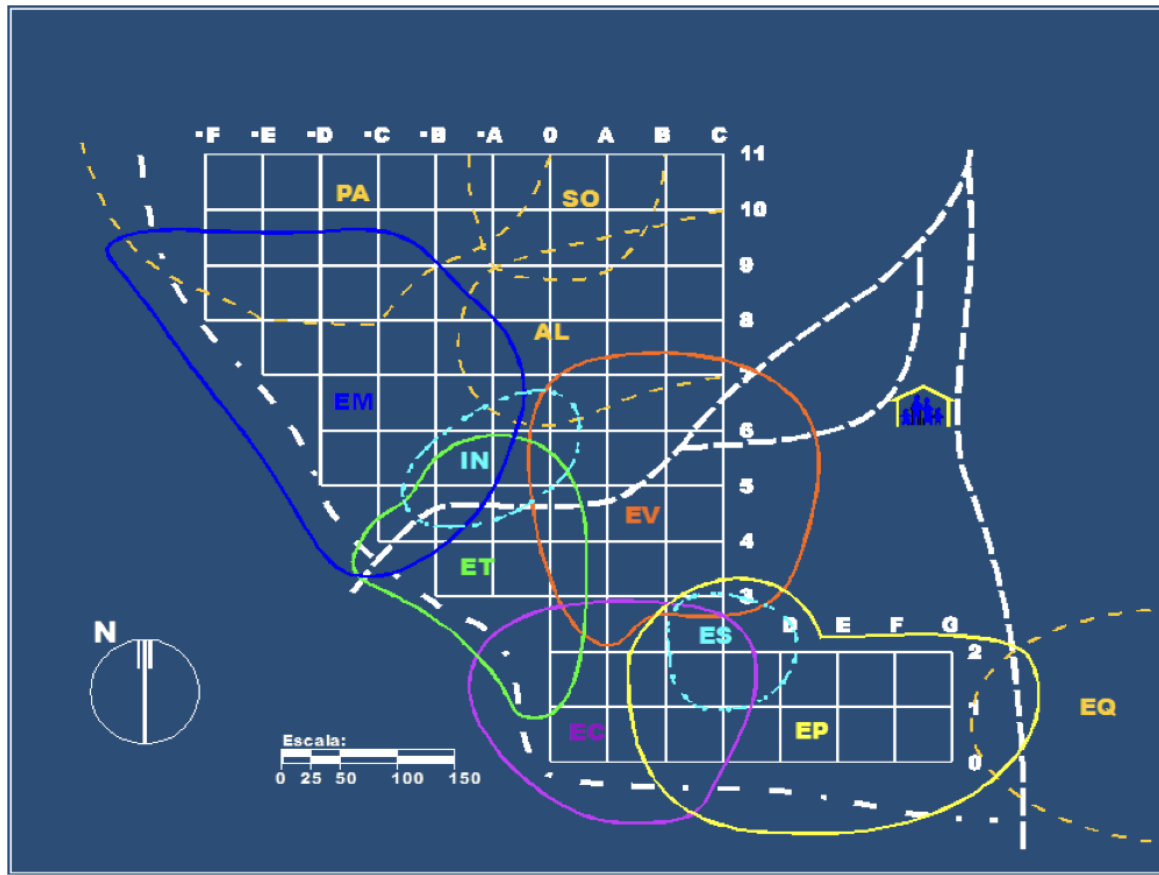
Figure 8. Study area of the Tapacurá Field Station, São Lourenço da Mata, Pernambuco, Brazil, with a
50m × 50m grid of trails. Shown are the home ranges of five focal *C. jacchus* study groups (EC, EM,
EP, ET, EV) represented by continuous lines, peripheral groups (orange dotted lines) and temporary
groups (pale blue dotted lines) between May 1994 and May 1996.

In regards to sexual behavior studied at Tapacurá, between 1994-1996, 52 copulations were observed, of which 16 were intra-group, and only two 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 one focal group was seen copulating seven times with two dominant males (2 to 3 times each) in neighboring groups. In general, sexually mature females take all opportunities to copulate, independent of their phase in the estrus cycle. Females also disperse more than males (Figure 9), leaving their natal groups to increase their chances of breeding [142].

Interestingly, the strongest social interactions within *C. jacchus* groups are between the male care-giver (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, as nutritional provisioning of infants by the male caregiver demands dedication and skill. On one 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, lifting it above his head after biting the hypocarpium several times to allow the infants to lick the juice (Figure 10). During the infant weaning phase, the carer male also teaches infants skills needed to travel, forage, confront predators, and how to recognize and catch and manipulate food items [141]. The male carer is the last to abandon a dead infant, which illustrates a deep social bond between a marmoset male and infants [143].

ANTHROPOGENIC EFFECTS on *CALLITHRIX:* PET TRADE, SPECIES INVASIONS, and HYBRIDIZATION

PET TRADE

While it is illegal in Brazil to have native primates as pets [144,145] and in São Paulo state there is a moratorium on captive breeding of marmosets by authorized commercial breeding
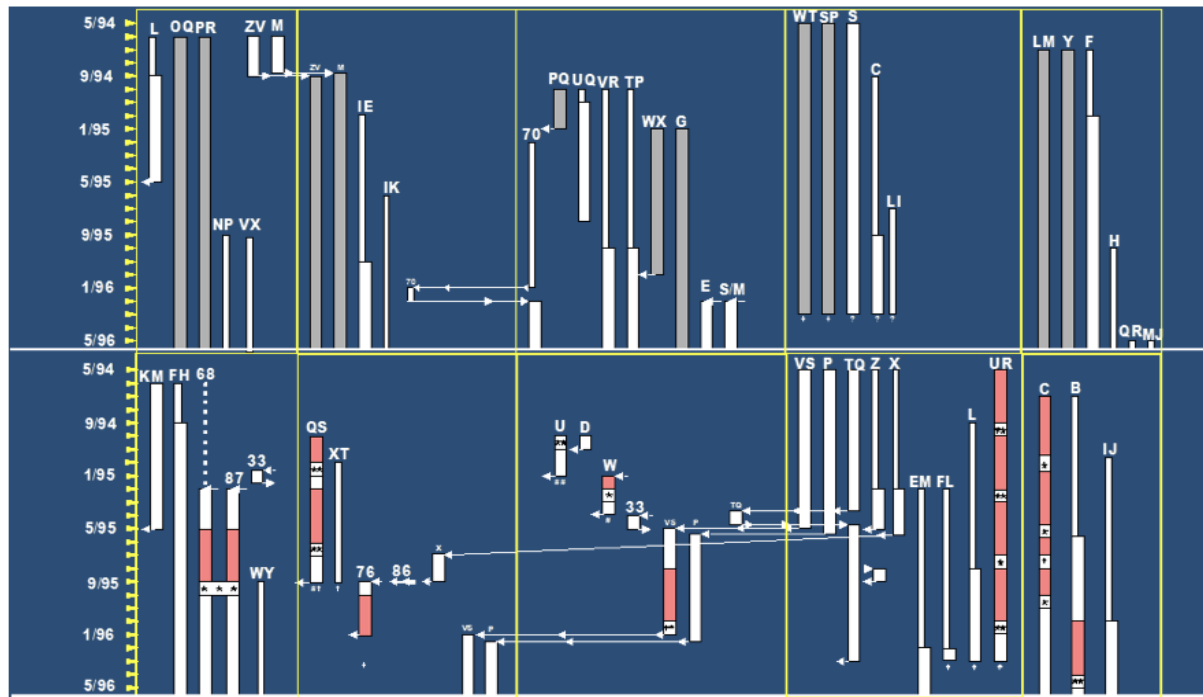
Figure 9. Changes in group composition (males in the top and females below) of five *C. jacchus* Tapacurá Field Station focal study groups between May 1994 and May 1996. Each square panel represents a single social group, with male members on top and female members on the bottom. Bars represent individual marmosets and arrows represent their movement between social groups.

Figure 10. Illustration of a *C. jacchus* breeding male caregiver hydrating marmoset infants with cashew hypocarpium juice (*Anacardium occidentale*), an act which shows dexterity and skill.

facilities [146], there still exists an underground Brazilian, illegal pet market [147]. 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, rescue of infants after habitat loss, and then either sold locally or transported to large urban areas [147-149]. 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 wildlife trade routes as other wildlife. In the case of *C. penicillata,* construction of roads and increased vehicular traffic between the Cerrado and southeastern Brazil, has greatly facilitated illegal trafficking of this species [58]. There are few studies that quantify the pet trade, but *Callithrix* individuals, especially *C. jacchus* and *C. penicillata*, have been among the top five 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 [148]. However, the actual numbers of marmosets taken from the wild for commercial purposes are likely underestimated, as 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 [2,150,151].

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 [2,152,153]. Now, three *Callithrix* species, *C. geoffroyi*, *C. jacchus*, and *C. penicillata*, have high invasive potential [61,62], and are spreading

throughout the southeastern Atlantic Forest due to the legal and illegal pet trades [21,58,154]. As a result, *Callithrix jacchus* and *C. penicillata* have established several allochthonous populations in southeastern Brazil [2,21,58,150-155]. Mitogenomic data shows 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 within the southeastern Brazilian Atlantic Forest [2,4,21,153-155].

Contemporary allochthonous *Callithrix* species are usually found in urban or peri-urban areas of the southeastern Brazilian Atlantic Forest [21, 58,151,152,155-157]. Within these contexts, allochthonous *Callithrix* have frequent human contact and exposure, and receive anthropogenic food supplementation [54, 58,158]. These allochthonous marmosets can also be found within or around natural reserves [13,58,151,152,155, 157], and in some areas, such marmoset populations are larger than those of native, endangered callitrichids [e.g., 151]. Such introductions could alter the ecological relationships among taxa [13, 159], as 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 [160-162]. 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; [19,21,163]). It is highly likely that *C. aurita* faces competition, conservation, and genetic threats from allochthonous *jacchus* group species and anthropogenic hybrids [2,10,154]. *Callithrix 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 [164-166]. Indeed, [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 [2,4,21,155, https://tede.ufrrj.br/jspui/handle/jspui/3009].

Anthropogenic hybridization with *C. jacchus* and/or *C. penicillata* also represents a potential risk for genetic extinction of the other two *jacchus* group species, *C. geoffroyi* and *C. kuhlii*, and [58] 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 [4,21,153]. Should large numbers of exotic *C. jacchus* or *C. penicillata* ever invade native ranges of *C. kuhlii* or *C. geoffroyi*, the latter two species may be threatened with genetic swamping by the former two species, a process through which parental lineages are replaced by hybrids that have admixed genetic ancestry [169]. Further, biological invasions by other marmosets present potential conservation risks for *C. kuhlii*, which is already considered vulnerable.

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 [11, 10, 12,168,169]. The estimates of remaining original forest area are 63% for the Cerrado, 47% for the Caatinga, and 11-28% for the Atlantic forest [170,171]. Furthermore, between 2006 and 2015, the accumulated area of lost natural vegetation of Brazilian biomes was 300,000 km² [172].
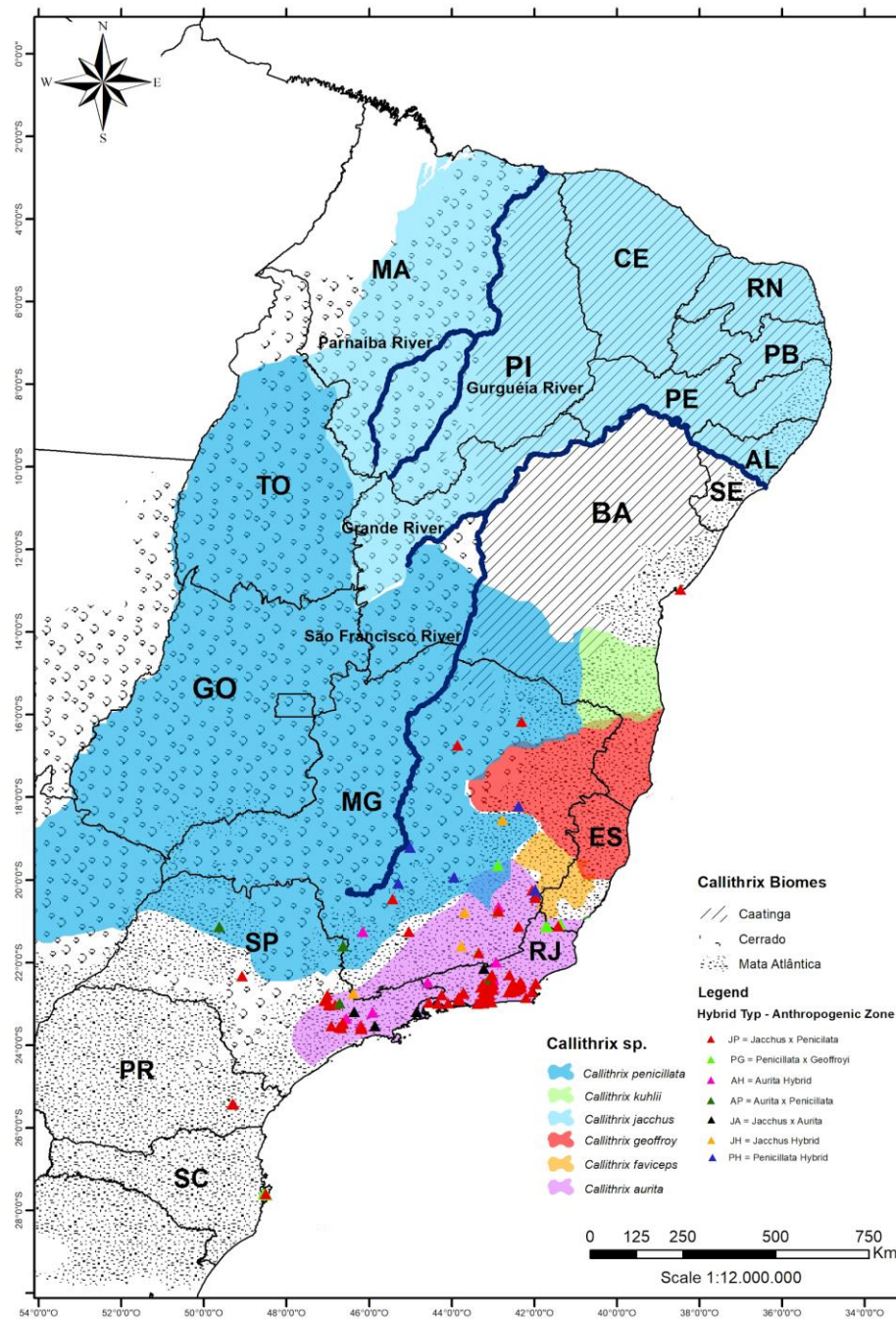
Figure 11. Anthropogenic *Callithrix* hybrid zones. Each natural species range is color-coded as in

Figure 1. Abbreviations of Brazilian states follow Figure 1. Hybrid zone abbreviations: JP: *C. jacchus*

x *C. penicillata;* PG: *C. geoffroyi* x *C. penicillata*; AH: *C. aurita* x *Callithrix* sp.; AP: *C. aurita* x *C.*

penicillata; JA: *C. jacchus* x *C. aurita*; JH: *C. jacchus* x *Callithrix* sp; PH: *C. penicillata* x *Callithrix*

sp. Hybrid zone locations adapted from [19,21,168]

For arboreal primates, marmosets included, continued deforestation in Brazil is the most serious threat to the persistence of populations and species [12,173].

The three most threatened *Callithrix* species are *C. flaviceps, C. aurita* and *C. kuhlii;* with the first considered "critically endangered" [11], the second listed as "endangered" [10], and the third considered "vulnerable" [174]. *Callithrix aurita* has also been listed among the 25 most threatened primates on the planet [175]. 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 to 2008 [176]. For *C. flaviceps*, agricultural activities have profoundly modified the environment where the species naturally occurs, with cattle breeding and coffee plantation occupy formerly forested areas [58]. The remaining *C. flaviceps* sub-populations, estimated at ~4,440 individuals, are restricted to the margins of riparian forests, and steep hillsides unsuitable for raising cattle, or planting coffee or eucalyptus [11]. Between 2015-2017, the wide-spread Brazilian YFV epidemic decimated > 90% the *C. flaviceps* population at RPPN Feliciano Miguel Abdala, a private reserve in Caratinga, Minas Gerais [177]. The virus may have caused other such reductions across the *C. flaviceps* range [11]. It is interesting to note that the global climate changes that are happening could lead to reductions in the distribution area as high as 95% for *C. flaviceps* and 27% for *C. aurita* [60]. 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 [174].

The other three *Callithrix* species are of "least concern", nonetheless their populations are declining throughout their native geographic ranges [168,169,178]. 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 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 for hunting [180]. For the three "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 [181, pers. obs. IOS, JM, LCMP, VB]. 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 [182,183].

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 [184] was formulated to comply with the Convention on Biological Diversity of 2002. Three instruments of this policy deal directly with species conservation [185]: 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 [186]. In 2018, *Callithrix* species became part of the NAP for the Conservation of The Primates of the Atlantic Forest and the Collared Sloth [187]. The Saguis-da-serra Conservation Program (PCSS) 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 [154]. 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 [154,175]. Currently, no *C. flaviceps* are maintained in captivity (pers obs., FR 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 (CCSS-UFV) - the first primatology center in the world devoted exclusively to develop both *in situ* and *ex situ* conservation activities (pers obs., FR de Melo). Among objectives of the CCSS-UFV 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 prioritizing locations for further *in situ* research (pers obs., FR de Melo).

In the last decade, regulations for the management of fauna have emerged in Brazil [e.g., 188,189] including, more recently, the management for the control of invasive alien and allochthonous species [146,190,191]. Currently, many confiscated and apprehended animals end up in Brazilian animal triage centers [192], 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 be also 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. Nowadays, with the increased adoption of the concept of OneHealth, 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 relationships among environment, health, ageing 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 human concern 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. The stage is prime to establish long term scientific exchange and collaboration among scientists from various disciplines and different countries to address issues of world-wide importance.

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	It provides for the protection of fauna and provides other measures	"Art. 1° Os animais de qualquer espécie, em qualquer fase do seu desenvolvimento e que vivem naturalmente fora do cativeiro constituindo a fauna silvestre, bem como seus ninhos, abrigos e criadouros naturais, são propriedade do Estado, sendo proibida a sua utilização, perseguição, destruição, caça ou apanha"
	Law Nº 7.653/1988 - Wildlife Protection Act	Altera a redação dos arts. 18, 27, 33 e 34 da Lei nº 5.197, de 3 de janeiro de 1967, que dispõe sobre a proteção à fauna, e dá outras providências.	renames, modifies and reenacts LAW No. 5,197/1967.

	FEDERAL CONSTITUTION of 1988	Art. 225. All have the right to the ecologically balanced environment, well of common use of the people and essential to the healthy quality of life, imposing on the public power and the collectivity the duty to defend it and preserve it for the 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. 9,605/1998 - Environmental Crimes Act	Dispõe sobre as sanções penais e administrativas derivadas de condutas e atividades lesivas ao meio ambiente, e dá outras providências.	

| | | DECREE Nº 4.339/2002 | Establishes principles and guidelines for the implementation of the National Biodiversity Policy | Created to be implemented with the participation of federal, district, state and municipal governments, and civil society, considering: 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. 6,938, 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; And 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 Nº 316/2009 | Apply the following instruments for the implementation of the National Biodiversity Policy aimed at the 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	It lays down rules, pursuant to item III, VI and VII of the caput and the sole paragraph of Art. 23 of the Federal Constitution, for cooperation between the Union, the States, the Federal District and the Municipalities in administrative actions arising from the exercise of common competence relating to the protection of notable natural landscapes, the protection of the environment, the protection of pollution in any of its forms and the preservation of forests , fauna and flora.	

	Ordinance MMA Nº 43/2014	Establish the National Program for the Conservation of Endangered Species - Pro-Species, with the objective of adopting prevention, conservation, management and management actions, with a view to minimizing threats and the 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 Nº 13.052/2014.	It amends Article 25 of Law No. 9,605 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.	"§ 1º 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 technicians habilitados."
	Ordinance MMA N°444/2014	Recognize as endangered brazilian fauna species those constant "Official National List of Endangered	*Callithrix* aurita *and C. flaviceps* are considered endangered (EN) in the List.

		Fauna Species".	
Conducting Research and Management Activities	JOINT NORMATIVE INSTRUCTION ICMBio/IBAMA 01/2014	It establishes procedures between ICMBio and IBAMA for the management and conservation of Brazilian wildlife species.	"Art.1º Establish, within the scope of the Brazilian Institute of the Environment and Renewable Natural Resources - IBAMA and the Chico Mendes Institute for 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. Single paragraph. 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	It defines the guidelines and procedures for the disposal of wild animals seized, rescued by a competent authority or voluntarily delivered by the population, as well as for the operation of the Wild Animal Triage Centers of IBAMA - CETAS.	Os espécimes híbridos e exóticos apenas poderão ser destinados para instituições de manejo em cativeiro (Artigos 21, 22 e 23).

	NORMATIVE INSTRUCTION ICMBio Nº 03/2014	It sets standards for the use of the Authorization and Information System on Biodiversity - SISBio, in the form of the guidelines and conditions provided for in this Normative Instruction, and regulates the availability, access and use of data and information received by the Chico Mendes Institute for Biodiversity Conservation through SISBio.	"Art. 3. Fix a standard on 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. § 1 - The activities with didactic purposes provided for in the caput are restricted to those performed in the scope of higher education. § 2 - This Normative Instruction does not apply to the collection and transportation of material biological species: I - domesticated or cultivated, except when related to research carried out in federal conservation units in the public domain; And II - exotic wild in ex situ condition." 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 on the National Strategy for Invasive Alien Species	Objective of the Strategy: 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 - species, subspecies or upper hierarchy is occurring outside its past or present natural distribution area; includes any part, such as gametes, seeds, eggs or propagules that can survive and subsequently reproduce.
	INSTRUÇÃO NORMATIVA ICMBio Nº 6/2019	It provides for the prevention of introductions and the control or eradication of exotic or invasive species in federal Conservation Units and their damping zones.	"Art. 2º The Guidance guide for the management of invasive alien species in Federal Conservation Units is established, available in http://www.icmbio.gov.br/cbc/publicacoes, which includes methods already approved by ICMBio and is considered the guiding document for project analysis."

	RESOLUTION SMA No. 164/2018 (São Paulo)	It establishes procedures for reproduction of specimens of the *genus Callithrix* kept in wildlife enterprises in captivity in the State of São Paulo.	It prohibits the production of hybrid individuals of the *genus Callithrix* and the reproduction *of individuals belonging to the species Callithrix jacchus* and *Callithrix penicillata* (exception given only to scientific and commercial breeding sites using these species as matrices, but marketed animals should be sterilized). To C. *penicillata* reproduction may be authorised only for individuals of known origin and within the programme of conservação, by Zoos and scientific breeding sites for conservation purposes.
Conservation Research and Management (more targeted at endangered *Callithrix* species)	ORDINANCE ICMBio N° 134/2010	Approve the National Action Plan for the Conservation of Mammals in the Central Atlantic Forest	It comprises objectives and actions for the conservation of 23 mammalian dollar sons, *including Callithrix aurita and Callithrix flaviceps,* for a period of five years from its date of publication.

| | ORDINANCE ICMBio N° 702/2018 | Approves the National Action Plan for the Conservation of Atlantic Forest primates and collared sloth - PAN PPMA, contemplating fourteen taxons 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 (thirteen) primate sums and for collared sloth, considered endangered, listed in the National List (MMA Ordinance No. 444/2014), including *Callithrix aurita* and *Callithrix flaviceps,* for a period of five 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).

| | THE 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* e *and Callithrix flaviceps* were considered Endangered and Critically Endangered (CR), respectively.
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	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."	*Callithrix aurita* and *Callithrix flaviceps* are listed in Appendix I.

| | 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.

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