TRENDS IN THE USE OF STUDBOOKS IN CAPTIVE BREEDING PROGRAMS OF NEOTROPICAL PRIMATES

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Abstract

Studbooks are databases of individual genealogical records of *ex situ* populations. Since they are an essential tool in management and planning, we conducted a search of studbook reports to explore historical trends in breeding programs of Neotropical primates and implications for *ex situ* conservation. We accessed two databases: one made by the World Association of Zoos and Aquariums (WD) and another one compiled from academic reports and public internet records (PD). WD was comprised of 104 reports (1998-2011) from three habitat and seven non-habitat regions for 44 species. PD consisted of 222 reports for 34 species from two habitat and three non-habitat regions (1973-2019). International studbooks were more frequent in PD (82%), whereas regional reports were more frequent in WD (55.8%). Both databases showed that IUCN levels (LC, NT, VU, EN, CR and DD) with a larger number of species contain a larger number of species with studbooks and a larger number of studbooks. Therefore, there is a bias towards more studbooks on LC (Least Concern) species. Despite limitations in availability and access to studbook records, our results revealed a discrepancy between regions where *in situ* conservation and *ex situ* conservation actions have been made. This underscores the need for international cooperation to strengthen conservation efforts, build infrastructure, increase effective population sizes and ultimately establish viable populations. Finally, we advise assessing opportunities for *ex situ* conservation of threatened or DD (Data Deficient) species whose conservation in the wild is unlikely in the near future.

Key Words: New World primates, Neotropics, *ex situ* population, husbandry, conservation

Resumen

Los studbooks son bases de datos de registros genealógicos individuales en poblaciones *ex situ*. Puesto que son una herramienta esencial en planeación y manejo, realizamos una búsqueda de reportes de studbooks para explorar tendencias históricas en programas de cría de primates neotropicales y sus implicaciones en conservación *ex situ*. Accedimos a dos bases de datos: una construida por La Asociación Mundial de Zoológicos y Acuarios (WD) y otra compilada a partir de registros públicos (PD). WD comprendió 104 reportes (1998-2011) de tres regiones hábitat y siete no hábitat para 44 especies. PD consistió en 222 reportes de 34 especies de dos regiones hábitat y tres no hábitat (1973-2019). Los studbooks internacionales fueron más frecuentes en PD (82%), mientras que los regionales lo fueron en WD (55.8%). Ambas bases de datos mostraron que las categorías de la UICN (LC, NT, VU, EN, CR y DD) con un mayor número de especies contienen un mayor número de especies con studbooks y un mayor número de studbooks. Por lo tanto, existe un sesgo hacia un mayor número de studbooks in especies LC (Preocupación Menor). A pesar de las limitaciones en la disponibilidad y acceso a registros de studbooks, nuestros resultados revelaron una discrepancia entre las regiones donde se han llevado a cabo acciones de conservación *in situ* y de conservación *ex situ*. Esto resalta la necesidad de la cooperación internacional para fortalecer los esfuerzos de conservación, construir infraestructura, incrementar los tamaños efectivos poblacionales y en últimas establecer poblaciones viables. Finalmente, recomendamos evaluar oportunidades de conservación *ex situ* de especies amenazadas DD (Datos Deficientes) cuya conservación en el medio silvestre es improbable en el futuro cercano.

Palabras Clave: Primates del Nuevo Mundo, Neotrópico, poblaciones *ex situ*, cría en cautiverio, conservación

Introduction

Captive breeding of wild species has conferred a remarkable alternative for conservation of threatened species through establishment of populations in controlled environments, and it has been seen as a potential source of specimens for release or reintroduction (Pelletier et al., 2009; Dulloo et al., 2010; Leus, 2011). Such is the emblematic case of the golden lion tamarin (*Leontopithecus rosalia*), whose conservation program achieved a population recovery and status change from Critically Endangered to Endangered (Soorae, 2010; Kierulff et al., 2012). In fact, the International

Union for Conservation of Nature (IUCN) has formulated guidelines to help identify in five steps those cases when *ex situ* management might be an appropriate conservation strategy (IUCN/SSC, 2014). Since the first signatories to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in the 1970s, zoos and animal parks have managed to establish ex situ populations of species whose collection from the wild is no longer permitted (Gippoliti, 2012; Bowkett, 2014; Gilbert et al., 2017; CITES, 2019).

During the transition to CITES, research centers of Neotropical primates mainly in the USA and Europe also established ex situ breeding programs for a variety of purposes including scientific and medical research (Gozalo and Montoya, 1990; Johnsen et al., 2012). Ex situ colonies of New World primates include marmosets, tamarins, squirrel monkeys, owl monkeys, capuchins and titi monkeys (Tardif et al., 2006; Smith, 2012; European Association of Zoos and Aquaria, 2019; NPRC, 2019). These non-conservation-oriented centers have allowed the gathering of relevant information of interest to conservation, in areas related to social behavior, reproductive biology, parasitology, physiology and ecology, but they have also served as a tool for education in conservation, and professional training (Mittermeier et al., 1994; Giovanini, 2002; Weigl, 2005; Nuss and Warneke, 2010; Brito et al., 2010).

Nonetheless, the role of captive breeding programs of wildlife species in conservation has been criticized for: (1) the potential emergence of demographic problems caused by the small size of *ex situ* populations, which makes them prone to rapid loss of genetic diversity (genetic drift) and overall fitness reduction (inbreeding depression) (Thornhill, 1993; Snyder, et al., 1996); (2) the aptitude of captive bred animals for release can also be compromised by their physiological, morphological and behavioral adaption to captive environments. Several traits may include adaptation to confinement, tameness and adaptive response to prevalent parasites in such environments, an effect that increases with the number of generations a species spends in captivity (De Vleeschouwer et al., 2003; O'Regan and Kitchener, 2005; Williams and Hoffman, 2009); (3) limited knowledge of target populations where animals are released (Snyder et al., 1996). Also, political instability and budget constraints have been argued as factors that can hamper the management of *ex situ* populations in the long term.

Despite some criticism of captive breeding programs as a recovery strategy and recognized issues of this practice, effective in situ conservation of primate species, i.e., conservation in their native habitats, may be unrealistic in areas with heavy disturbance or loss of native habitat. Around 40 % of the Neotropical primates (Platyrrhini) are threatened, mainly due to habitat loss and fragmentation (Mittermeier et al., 2009; Dulloo et al., 2010; Laurance et al., 2014; Estrada et al., 2017), and therefore establishment of healthy populations in captivity may no longer be disregarded. Indeed, it has become a sensible or even an unavoidable alternative (Lascuráin et al., 2009; Pelletier et al., 2009; Dulloo et al., 2010; Leus 2011; Soto-Calderón et al., 2015).

An essential tool for successful establishment and management of *ex situ* populations is the studbook (Conway, 1986; Glatston, 1986). It consists of a database with updated individual records for age, sex, location, genealogical relationships, and survival. These records are necessary to estimate demographic and genetic parameters, make management decisions, and ultimately develop viable ex situ populations, while minimizing the risk of inbreeding and erosion of genetic variation (Glatston, 1986, 2001; Valeggia et al.,1999). Unfortunately, studbook databases are frequently restricted to regional communities or experts; thus, identification of trends in species of interest and temporal variation in such cases are hardly traceable.

Given the importance of studbooks as an essential tool in the establishment and management of ex situ populations, we conducted a review of available studbook reports associated with Neotropical primate breeding programs to identify historical emphasis on particular taxa, species of interest for conservation, and level of collaboration between institutions from different regions. We also considered the implications of such trends for future conservation of Neotropical primates.

Methods

A database of Neotropical primate studbooks released between 1998 and 2011 was kindly provided by Laurie Bingaman Lackey (WAZA, the World Association of Zoos and Aquariums) as part of the WAZA Studbook Library (WAZA, 2011); hereafter the WAZA or WD database. We also compiled an alternative database from public sources and peer-reviewed journals (the Public database or PD), consisting of studbook reports starting with the first available studbook record found, continuing up to 2019. To do this, we used "Studbook + *Genus name*" or "Breeding program (in English) + *Genus name*" as key phrases in Google, Google Scholar and Scopus databases. We also retrieved studbook reports from all of the editions of the International Zoo Yearbook and from the list of references in scientific publications. A complete list of records is available from the authors upon request.We classified studbooks in both databases by taxon (subspecies, species or genus), year of publication and country. Studbooks at the genus level with no indication of the species were excluded (*Ateles* spp., *Cebus* spp., *Aotus* spp., and *Callicebus* spp.). We categorized a studbook as regional when target populations were located in zoos or animal parks in a single country; otherwise, we classified it as international. Since records frequently fail to distinguish between new studbooks and updates, we treated every record as an independent report (Supplementary Fig. 1). We followed the taxonomy and Red List categories of The International Union for Conservation of

Nature (IUCN) as of April the 8th 2020 (Supplementary Table 1). These categories are: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD), considering VU, EN, and CR as increasing threat levels for extinction. We used a Spearman-rank correlation (rs) to test the hypothesis that IUCN levels with larger number of species also contain larger numbers of assessed species and studbook reports. We evaluated differences in the number of reports and managed taxa for each threat level between the two databases with Fisher's Exact tests. The authors declare that they have no conflict of interest.

Results

WAZA Database (WD)

We identified 104 studbook reports for 44 Neotropical primate species in the 14-year period spanned by this database (1998-2011) (Supplementary Fig. 2A). This list includes single reports for *Cebus olivaceus* in 2007 and *Cebus albifrons* in 2010, and two reports for *Pithecia pithecia* in 2009 and 2011; each of these taxa were split into several species after the release of such studbooks (Boubli et al., 2012; Marsh, 2014; Lima et al., 2017). Institutions from different locations in three habitat countries (Brazil, Colombia and Costa Rica) and seven non-habitat regions (USA, Europe, New Zealand, Mexico, Colombia, Australia and Japan) compiled these reports through regional efforts or international collaboration in 58 (55.8 %) and 46 cases (44.2 %), respectively. The most productive regions were Europe and the USA, with a total of 79 records (76 %) for 42 of the 44 Neotropical primate taxa in the database. These regions were followed by institutions from Japan and Brazil, each with six studbook reports for a total of 12 different primates (Supplementary Fig. 2A).

Reports from habitat countries included the black lion tamarin (*Leontopithecus chrysopygus*), the crested capuchin (*Sapajus robustus*), the Peruvian spider monkey (*Ateles chamek*), the white-fronted spider monkey (*A. belzebuth*), the black spider monkey (*A. paniscus*) and the white-cheeked spider monkey (*A. marginatus*) in Brazil; the cotton-top tamarin (*Saguinus œdipus*), the white-footed tamarin (*S. leucopus*) and the black-handed spider monkey (*A. geoffroyi*) in Colombia; and the Central American squirrel monkey (*Saimiri œrstedii*) in Costa Rica. Several taxa stand out with five studbook reports, as in the case of *Saguinus œdipus* with three regional (Australia, Colombia and Japan) and two international studbook reports, as well as *A. geoffroyi* with three regional (New Zealand, USA and Colombia) and two international reports from Europe. The genus with the most reports is *Ateles* with 30, followed by *Saguinus* with 17.

Of the 44 Neotropical primate species with at least one studbook report, 24 species (54.5 %) were classified under an increased threat level (VU, EN, or CR), 16 (36.4 %) were categorized as LC, one (2.3 %) as NT and the remaining three (6.8 %) were assigned to other species whose taxonomy changed after the release of their studbooks (*Cebus albifrons*, *Cebus olivaceus* and *Pithecia pithecia*). No reports for DD species were recorded in this database (Table 1). A total of 65 studbooks (62.5 %) were compiled for threatened taxa. Also, 34 reports (32.7 %) corresponded to LC taxa and one (1.0 %) to NT (Table 1). We observed a significant correlation between the total number of species in each IUCN threat level with both the number of managed species ($rs = 0.94$, $p = 0.017$) and the number of studbook reports ($rs = 0.89$, $p = 0.033$).

Table 1. Number of Neotropical primate taxa in the IUCN Red List of Species with their corresponding number of studbook reports, available in the WAZA (WD) and in the Public (PD) databases.

	WD		PD	
	No. Taxa (%)	No. Reports (%)	No. Taxa (%)	No. Reports (%)
LC	16 (36.4)	34 (32.7)	14 (41.2)	71 (32.0)
NT	1 (2.3)	1 (1.0)	1 (2.9)	3 (1.4)
VU	10 (22.7)	21 (20.2)	6 (17.6)	34 (15.3)
EN	9 (20.5)	28 (26.9)	7 (20.6)	65 (29.3)
CR	5 (11.4)	16 (15.4)	5 (14.7)	38 (17.1)
Other *	3 (6.8)	4 (3.8)	1 (2.9)	11 (5.0)
Total	44	104	34	222

LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered. * Species reclassified as two or more species since studbook report.

Of the 104 reports in WD, we had to exclude 23 records with unavailable publication date from yearly statistics. Of the remaining 81, the average annual number of reports was 5.8 (S.D. = 5.9), with the highest number of reports in 2006 and 2010 with 18 reports for each year, followed by 2009 with ten and 2011 with eight (Supplementary Fig. 1A). We found no records for the 1999-2000 period. The first set of reports for Neotropical primates was published in 1998 for spider monkeys (*Ateles chamek*, *A. geoffroyi*, *A. belzebuth* and *A. fusciceps*). The most recent reports were published in 2011 for the pygmy marmoset (*Cebuella pygmaea*), the cotton-top tamarin (*Saguinus œdipus*), the black-headed night monkey (*Aotus nigriceps*), the southern night monkey (*A. azarae*), the grey-legged dourucouli (*A. lemurinus*), the white-faced saki (*Pithecia pithecia*), the white-headed marmoset (*Callithrix geoffroyi*), and the black-handed spider monkey (*Ateles geoffroyi*).

Public Databases (PD)

We found a total of 222 studbook reports produced between 1973 and 2015 for 34 species, including eight studbook reports for *Pithecia pithecia* that were released before this species was divided into two species *P. pithecia* and *P. chrysocephala* more recently (Marsh, 2014). These studbooks were compiled by institutions in three non-habitat

(USA, Europe and Australia) and two habitat regions (Brazil and Colombia) (Supplementary Fig. 2B). Institutions from non-habitat regions, mainly Europe and the USA, have participated in the development of 94.6 % (210) of all reports at both regional and international levels. We identified 182 (82.0 %) international reports for 32 taxa, and 40 (18.0 %) regional reports from habitat and non-habitat countries for 16 taxa (Supplementary Fig. 2B). Only eleven studbook reports were developed in habitat countries, including seven for the black lion tamarin (*Leontopithecus chrysopygus*) endemic to Brazil, along with three for the white-footed tamarin (*Saguinus leucopus*) and one for the brown-headed spider monkey (*Ateles fusciceps*) endemic to Colombia. Two tamarins (*L. rosalia* and *S. œdipus*) and one howler monkey (*Alouatta caraya*) stand out for having the largest number of studbook reports, mostly developed in non-habitat countries. The genus with the most studbook reports was *Leontopithecus* with 40, followed by *Saguinus* with 32.

Among the 34 taxa with at least one studbook report in PD, the Red List category with the largest representation was LC with 14 taxa (41.2 %), followed by 18 species classified under an increased threat level (52.9 %), one NT (2.9 %), and one remaining species with recent taxonomical changes (2.9 %) (Table 1). No DD taxa were present in this database. Threatened taxa were represented by 137 reports (61.7 %), LC by 71 reports (32.0 %), NT by three (1.4 %) and other taxa by 11 reports (5.0 %) (Table 1). The number of studbooks but also the number of managed species in each IUCN level increased with the total number of species in each level, but this relationship was only significant in the second case ($r_s = 0.89$, $p = 0.033$).

The average number of reports per year was 4.63 (S.D. = 6.07) starting in 1973 with a studbook compiled for the golden lion tamarin (*Leontopithecus rosalia*) (Jones, 1973). The most recent reports were released in 2019 for 28 species (Supplementary Fig. 1B). The most productive years were 2016, 2017 and 2019. We found no publications for 1974 and 1975. Only one studbook report in PD was missing the date of release.

Combined databases

We detected no differences between the two databases, neither in the number of reports for species in each Red List category (Fisher´s test, $p = 0.704$) nor in the number of managed species in such categories (Fisher's test, $p = 0.992$). However, a comparison of the two databases for the same time frame (1998-2011) showed that WD was more geographically diverse and covered more taxa than public databases. WD comprised reports from New Zealand, Japan, Mexico, and Costa Rica that were unavailable in PD. Also, WD comprised a larger number of species for this time period, including all the taxa present in PD.

A total of 45 (27.8 %) out of 162 Neotropical primate species recognized in the Red List (after excluding *Cebus albifrons*, *Cebus olivaceus* and *Pithecia pithecia*) had at least one studbook in either of the two databases. LC contains the largest number of species with at least one studbook (17, 37.8 %). A total of 27 threatened species (VU, EN and CR) have studbooks and represent 60.0 % of all managed species. We failed to find active studbooks for three threatened species that had been previously managed (Supplementary Figure 1B). The most concerning case is the Wied's marmoset (*Callithrix kuhlii*), which seems to have a single regional studbook issued in 2003. The two other threatened species are the Geoffroy's spider monkey (*Ateles geoffroyi*) and the common woolly monkey (*Lagothrix lagothricha*), with studbooks issued in 2010 and 2017, respectively. Only five out of 18 CR species have been managed (27.8 %), all with actively updated studbooks in European zoos (Fig. 1 and Supplementary Table 1). The 13 CR species with no record of previous management were the following: the black-faced lion tamarin (*Leontopithecus caissara*), the Ecuadorian capuchin (*Cebus aequatorialis*), the ka'apor capuchin (*C. kaapori*), the Trinidad white-fronted capuchin (*C. trinitatis*), the blond capuchin (*Sapajus flavius*), Barbara brown's titi (*Callicebus barbarabrownae*), the Caqueta titi (*Plecturocebus caquetensis*), the Rio Mayo titi (*P. oenanthe*), the black-bearded saki (*Chiropotes satanas*), the northern muriqui (*Brachyteles hypoxanthus*), the southern muriqui (*B. arachnoides*), the Colombian woolly monkey (*Lagothrix lugens*) and the yellow-tailed woolly monkey (*L. flavicauda*).

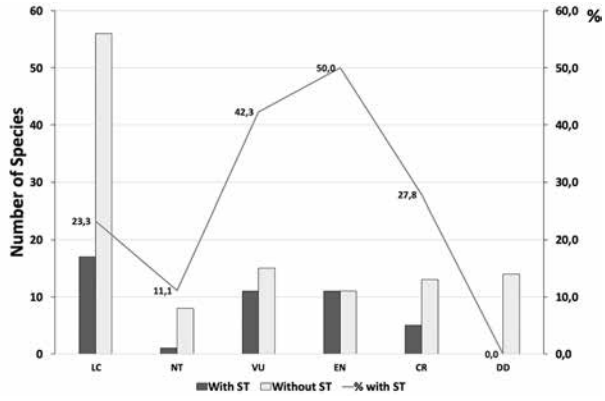

Figure 1. Number of Neotropical primates with presence versus absence of at least one previous studbook (ST), for each IUCN category. The left Y-axis indicates the number of species, and the right Y-axis the proportion of species with at least one studbook for each IUCN category. LC: Least Concern; NT: Nearly Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; DD: Data Deficient.

Discussion

We searched for studbook reports of Neotropical primate species as a means to identify husbandry programs and diagnose their current and/or future use in conservation. We are aware that our results do not reflect the actual number of studbooks but instead, the number of reports of *ex situ* breeding programs of Neotropical primate species based on two independent sources of information. Since studbooks

are not an obligation but a service that institutions provide free of charge to peer institutions (Glatston, 1986), studbook updates are not necessarily reported or accessible and they may not contain comprehensive information regarding studbook keepers or host institutions. This limitation prevented us from distinguishing between novel studbooks and updates of previous studbooks, and there was no unequivocal way to validate simultaneous reports of a given studbook in the two databases; i.e. those present in both PD and WD databases. However, we were able to identify similar trends in both databases, but also compare temporal variations in the number of reports and emphasis made on particular taxa.

Both databases comprised studbook reports exclusively produced by zoos around the world, since studbooks developed by non-zoo institutions were unavailable and therefore out of the scope of this review. This is unfortunate because, despite the relevance of scientific knowledge from research centers in understanding the biological requirements of species for reproduction in captivity and their potential for *in situ* conservation, integration with efforts from zoos and other conservation-oriented institutions seems to be only occasional, if not entirely missing.

Most studbook reports in PD are international, whereas those in WD were mainly regional. The fact that international studbooks require stronger collaboration of stakeholders, and as a consequence, they have more visibility in international journals and other sources available on internet, may account for the high percentage of international studbooks in PD. This contrasts with the higher prevalence of regional studbooks in WD. A similar pattern was found in other monitored taxa in WAZA zoos, where only 15% of studbooks are international (Traylor-Holzer, 2011), indicating that management efforts are mainly conducted at the regional level. Information for specific animal species in zoos around the world is available to the WAZA community through international studbook reports (WAZA, 2018). This may be used to foster integration of efforts from local, regional and international stakeholders to increase effective population sizes through careful metapopulation management, and in so doing improve the genetic and demographic health of established populations and their expected viability to the long term.

Our results showed that institutions from countries in the Neotropics have led only a minority of studbooks, which uncovers a disparity between regions where captive breeding has been stressed and those where *in situ* conservation efforts are required. This is strongly influenced by differences in financial resources and infrastructure between regions, since primate habitats are mostly located in developing countries with less financial capacity, staff and infrastructure (Cuarón, 2005). Also, recent simulations forecast a growing conflict caused by agricultural and human expansion in areas of high primate species richness in the Neotropics, especially in countries such as Brazil, Colombia and Peru (Güneralp and Seto, 2013; Estrada et al., 2017). Once again, cooperation between institutions from habitat and non-habitat countries could be quite advantageous, in this case to integrate *in situ* conservation efforts in the Neotropics with scientific research and infrastructure derived from *ex situ* populations (European Association of Zoos and Aquaria, 2019).

The fact that threatened New World primate species account for 60% of all species with previous studbooks shows that management of *ex situ* populations may have a remarkable impact on conservation of threatened species. However, a previous survey of birds and mammals showed that species in zoos are less threatened than related species not held in zoos (Martin et al., 2014). Among the 18 CR Neotropical primate species, only five have been the target of a studbook because in addition to conservation purposes, other reasons and motivations may guide the decision to whether or not to establish a studbook of a given species (Mendes et al., 2008; Estrada et al., 2017; IUCN, 2017). Some of these include the cost to keep an *ex situ* population in captivity, preference for more charismatic species to attract visitors or restrictions to access species of interest (Bowkett, 2014; Fa et al., 2014). In fact, the two databases compiled in this study revealed that the larger the number of species in a given IUCN level, the larger the number of species with at least one studbook and the larger the number of studbooks. This explains the overrepresentation of studbooks and managed species in LC as compared to other levels, a pattern also seen in other vertebrates (Oberwemmer et al., 2011).

Changes in IUCN categorization and taxonomy also may explain the deficit of studbooks in certain species, and arguably of *ex situ* populations. The genus *Cebus* is a taxon with intricate phylogeography whose taxonomy and systematics has undergone radical changes over the past few years (Boubli et al., 2012; Lima et al., 2017). In particular, a studbook for the capuchin monkey *Cebus olivaceus* was released in 2007, but this taxon is in process of being divided into multiple species including *C. olivaceus, C. brunneus*, *C. castaneus*, and the critically endangered *C. kaapori*, all of which lack a subsequent studbook. Likewise, the capuchin monkeys *Cebus albifrons*, *C. versicolor*, *C. aequatorialis*, *C. cesarae*, *C. trinitatis*, *C. cuscinus* and *C. malitiosus* were all subsumed within *C. albifrons* until recently; a taxonomic change that took place after the release of a studbook for this species in 2010. Similarly, *Pithecia pithecia* was recently split in *P. pithecia* and *P. chrysocephala*, after the release of multiple studbooks between 1989 and 2011 (Marsh, 2014). Following these taxonomic changes, it turned out that several newly named species were classified as threatened, and it is probably too early to have managed the foundation of new *ex situ* populations (e. g., *C. aequatorialis*, *C. malitiosus*, *C. versicolor*, *C. trinitatis*, *C. kaapori*, and *Pithecia chrysocephala*). Similar cases are the critically endangered blond capuchin *Sapajus flavius*, which was recently rediscovered (Oliveira and Langguth, 2006), the

two species of muriqui (*Brachyteles arachnoides* and *B. hypoxanthus*), formerly considered the same species (Groves, 2001; 2005), and lastly the titi monkeys with at least nine new species of *Callicebus* and *Plecturocebus* described since 2010 (Wallace et al., 2006; Defler et al., 2010; Byrne et al., 2016; Boubli et al., 2019; Mittermeier and Rylands, 2020).

We found no studbooks of DD species in our data. Many of these are highly endemic or distributed in relatively remote areas, with limited or untested survival and/or reproductive success in captivity (Müller et al., 2011; Martin et al., 2014a). As a consequence, specimens and *ex situ* populations of these primates are also virtually absent in zoos. Within DD taxa are for instance several species of *Pithecia* and *Plecturocebus* that have been recently described or *Aotus,* such as *A. zonalis* and *A. jorgehernandezi* that have been poorly studied in the field (Defler, 2010; Marsh, 2014; Byrne et al., 2016).

Since habitat loss poses the main threat for conservation of Neotropical primates, it is important to scrutinize the pertinence and viability of prioritizing *ex situ* conservation programs for the most threatened taxa (Estrada et al., 2017). Along with protection of native habitats, *ex situ* conservation may be a plausible conservation alternative for species such as the black-faced lion tamarin (*Leontopithecus caissara*), the blond titi (*Callicebus barbarabrownae*), the Caquetá titi (*Plecturocebus caquetensis*) and other CR species with no studbooks or managed populations, whose estimated population sizes have fallen to critically low numbers with a steady trend to decline (Lorini and Persson, 1994; García et al., 2010; Printes et al., 2011). Should conservation strategies of these species rely on *ex situ* populations in the near future, they will depend on careful prioritization of target species for conservation, identification of *in situ* and *ex situ* strategies, the availability of resources to invest in building infrastructure and research in reproductive biology and creation of collaborative international networks (Martin et al., 2014b).

Acknowledgements

We are grateful to Laurie Bingaman Lackey for granting access to the WAZA Studbook Library of New World primates, and to Jessica W. Lynch for her valuable comments on earlier versions of this manuscript that led to the substantial improvement of its contents. We also thank the Joven Investigador collaborative program of Colciencias and The University of Antioquia (Convocatoria 617, 2014-2015).

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Supplementary Table 1. List of Neotropical primate taxa with at least one studbook record, sorted by IUCN conservation status.

IUCN Status	Taxa with no studbook	Taxa with studbook
CR	*Brachyteles arachnoides*	*Ateles fusciceps*
	Brachyteles hypoxanthus	*Ateles hybridus*
	Callicebus barbarabrownae	*Saguinus bicolor*
	Cebus aequatorialis	*Saguinus œdipus*
	Cebus kaapori	*Sapajus xanthosternos*
	Cebus trinitatis	
	Chiropotes satanas	
	Lagothrix flavicauda	
	Lagothrix lugens	
	Leontopithecus caissara	
	Plecturocebus caquetensis	
	Plecturocebus oenanthe	
	Sapajus flavius	
EN	*Alouatta pigra*	*Ateles belzebuth*
	Alouatta ululata	*Ateles chamek*
	Aotus miconax	*Ateles geoffroyi*
	Callicebus coimbrai	*Ateles marginatus*
	Cebus malitiosus	*Callithrix aurita*
	Cebus versicolor	*Callithrix flaviceps*
	Chiropotes albinasus	*Leontopithecus chrysomelas*
	Chiropotes utahickae	*Leontopithecus chrysopygus*

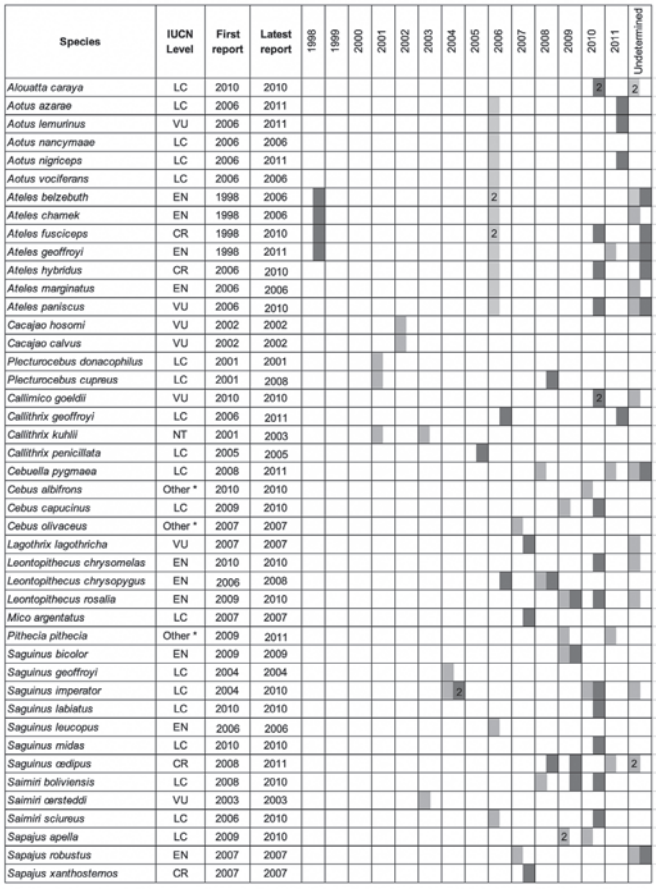
IUCN Status	Taxa with no studbook	Taxa with studbook
LC	*Alouatta arctoidea*	*Alouatta caraya*
	Alouatta guariba	*Aotus azarae*
	Alouatta juara	*Aotus nigriceps*
	Alouatta macconnelli	*Aotus vociferans*
	Alouatta nigerrima	*Callithrix geoffroyi*
	Alouatta palliata	*Callithrix jacchus*
	Alouatta puruensis	*Callithrix penicillata*
	Alouatta sara	*Cebus capucinus*
	Alouatta seniculus	*Mico argentatus*
	Aotus trivirgatus	*Plecturocebus cupreus*
	Cacajao melanocephalus	*Plecturocebus donacophilus*
	Callibella humilis	*Saguinus imperator*
	Cebus brunneus	*Saguinus labiatus*
	Cebus castaneus	*Saguinus midas*
	Cheracebus lucifer	*Saimiri boliviensis*
	Cheracebus lugens	*Saimiri sciureus*
	Cheracebus purinus	*Sapajus apella*
	Cheracebus regulus	
	Cheracebus torquatus	
	Chiropotes chiropotes	
	Leontocebus cruzlimai	

IUCN Status	Taxa with no studbook	Taxa with studbook
EN	*Lagothrix cana*	*Leontopithecus rosalia*
	Plecturocebus modestus	*Saguinus leucopus*
	Plecturocebus olallae	*Sapajus robustus*
VU	*Alouatta belzebul*	*Aotus griseimembra*
	Alouatta discolor	*Aotus lemurinus*
	Aotus brumbacki	*Aotus nancymaae*
	Cacajao ayresi	*Ateles paniscus*
	Callicebus melanochir	*Cacajao calvus*
	Callicebus personatus	*Cacajao hosomi*
	Cebus leucocephalus	*Callimico goeldii*
	Cheracebus medemi	*Callithrix kuhlii*
	Lagothrix poeppigii	*Cebuella pygmaea*
	Mico leucippe	*Lagothrix lagothricha*
	Mico rondoni	*Saimiri ærsteddi*
	Pithecia mittermeieri	
	Plecturocebus ornatus	
	Saguinus niger	
	Saimiri vanzolinii	
NT	*Callicebus nigrifrons*	*Saguinus geoffroyi*
	Cebus cuscinus	
	Leontocebus tripartitus	
	Mico nigriceps	
	Saguinus martinsi	
	Saimiri ustus	
	Sapajus libidinosus	
	Sapajus nigritus	
DD	*Aotus jorgehernandezi*	
	Aotus zonalis	
	Cebus cesarae	
	Mico humeralifer	
	Mico marcai	
	Pithecia cazuzai	
	Pithecia hirsuta	
	Pithecia irrorata	
	Pithecia isabela	
	Pithecia milleri	
	Pithecia pissinattii	
	Pithecia vanzolinii	
	Plecturocebus stephennashi	
	Plecturocebus vieirai	

IUCN Status	Taxa with no studbook	Taxa with studbook
LC	*Leontocebus fuscus*	
	Leontocebus illigeri	
	Leontocebus lagonotus	
	Leontocebus leucogenys	
	Leontocebus nigricollis	
	Mico acariensis	
	Mico chrysoleucos	
	Mico emiliae	
	Mico intermedius	
	Mico mauesi	
	Mico melanurus	
	Mico saterei	
	Pithecia aequatorialis	
	Pithecia albicans	
	Pithecia chrysocephala	
	Pithecia inusta	
	Pithecia monachus	
	Pithecia napensis	
	Plecturocebus aureipalatii	
	Plecturocebus baptista	
	Plecturocebus bernhardi	
	Plecturocebus brunneus	
	Plecturocebus caligatus	
	Plecturocebus cinerascens	
	Plecturocebus discolor	
	Plecturocebus dubius	
	Plecturocebus hoffmannsi	
	Plecturocebus moloch	
	Plecturocebus pallescens	
	Saguinus fuscicollis	
	Saguinus inustus	
	Saguinus melanoleucus	
	Saguinus mystax	
	Sapajus cay	
	Sapajus macrocephalus	
Other *		*Cebus albifrons*
		Cebus olivaceus
		Pithecia pithecia

IUCN status (2020): CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Nearly Threatened), DD (Data Deficient) and LC (Least Concern). * Species reclassified as two or more species since studbook report.

Supplementary Figure 1. Temporal trend in studbook reports of Neotropical primate taxa.



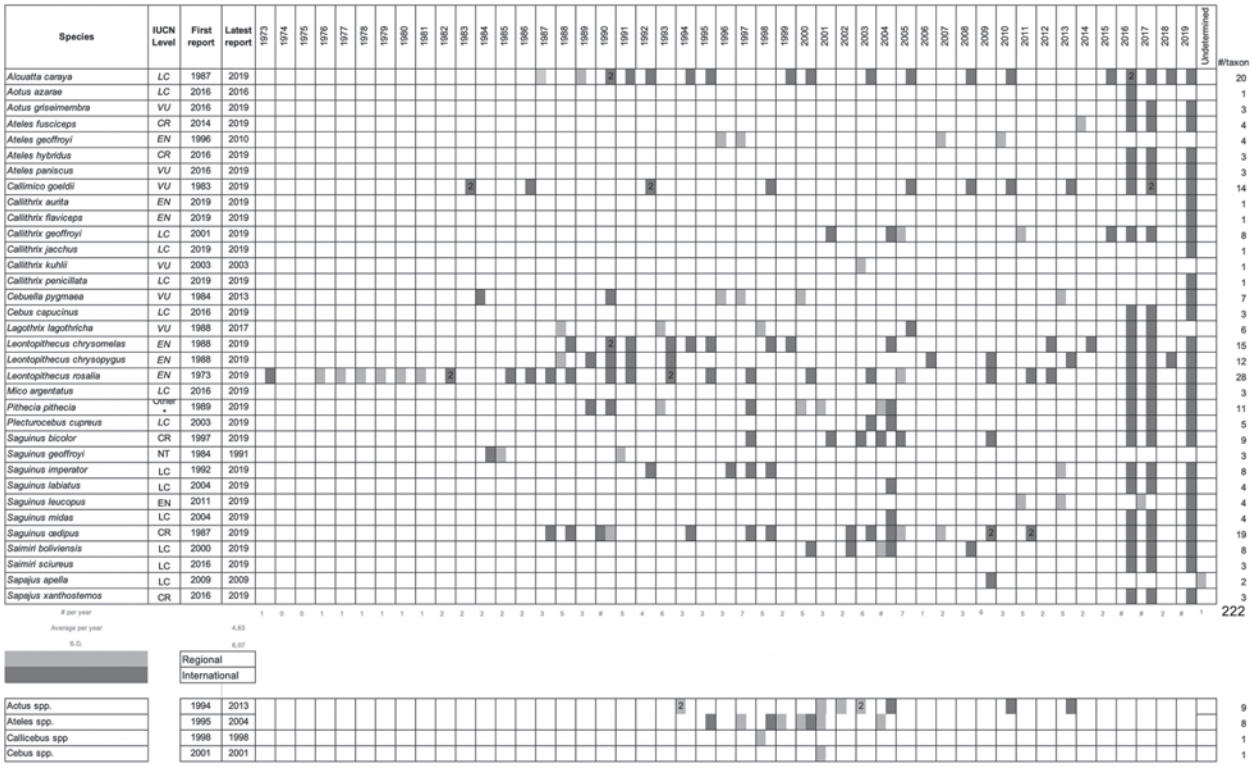
Species	IUCN Level	First report	Latest report	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Undetermined
Alouatta caraya	LC	2010	2010													2		2
Aotus azarae	LC	2006	2011															
Aotus lemurinus	VU	2006	2011															
Aotus nancymaae	LC	2006	2006															
Aotus nigriceps	LC	2006	2011															
Aotus vociferans	LC	2006	2006															
Ateles belzebuth	EN	1998	2006									2						
Ateles chamek	EN	1998	2006															
Ateles fusciceps	CR	1998	2010									2						
Ateles geoffroyi	EN	1998	2011															
Ateles hybridus	CR	2006	2010															
Ateles marginatus	EN	2006	2006															
Ateles paniscus	VU	2006	2010															
Cacajao hosomi	VU	2002	2002															
Cacajao calvus	VU	2002	2002															
Plecturocebus donacophilus	LC	2001	2001															
Plecturocebus cupreus	LC	2001	2008															
Callimico goeldii	VU	2010	2010														2	
Callithrix geoffroyi	LC	2006	2011															
Callithrix kuhlii	NT	2001	2003															
Callithrix penicillata	LC	2005	2005															
Cebuella pygmaea	LC	2008	2011															
Cebus albifrons	Other *	2010	2010															
Cebus capucinus	LC	2009	2010															
Cebus olivaceus	Other *	2007	2007															
Lagothrix lagothricha	VU	2007	2007															
Leontopithecus chrysomelas	EN	2010	2010															
Leontopithecus chrysopygus	EN	2006	2008															
Leontopithecus rosalia	EN	2009	2010															
Mico argentatus	LC	2007	2007															
Pithecia pithecia	Other *	2009	2011															
Saguinus bicolor	EN	2009	2009															
Saguinus geoffroyi	LC	2004	2004															
Saguinus imperator	LC	2004	2010															
Saguinus labiatus	LC	2010	2010															
Saguinus leucopus	EN	2006	2006															
Saguinus midas	LC	2010	2010															
Saguinus œdipus	CR	2008	2011															
Saimiri boliviensis	LC	2008	2010															
Saimiri oersteddi	VU	2003	2003															
Saimiri sciureus	LC	2006	2010															
Sapajus apella	LC	2009	2010															
Sapajus robustus	EN	2007	2007															
Sapajus xanthosternos	CR	2007	2007															

A. Reports in the WAZA (WD) database released between 1998 and 2011.

* Species reclassified as two or more species since studbook report.

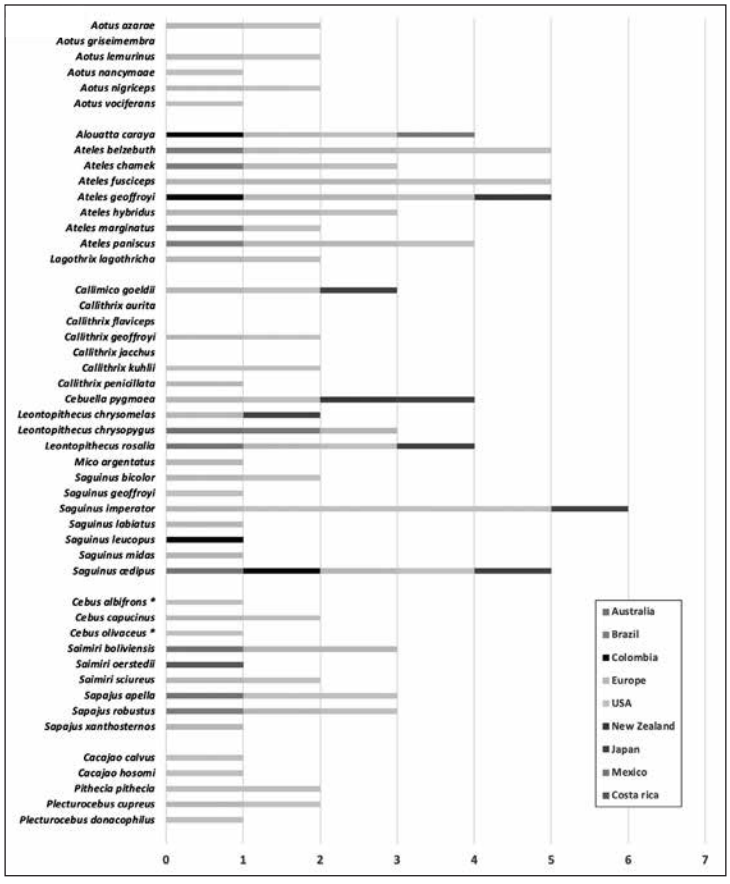
B. Reports in the Public database (PD) released between 1973 and 2019.
Regional (light gray) and international (dark gray) studbooks are categorized according to the species and the year in which they were published. Colored cells indicate single records unless indicated otherwise.

* Studbooks released before split into several species.



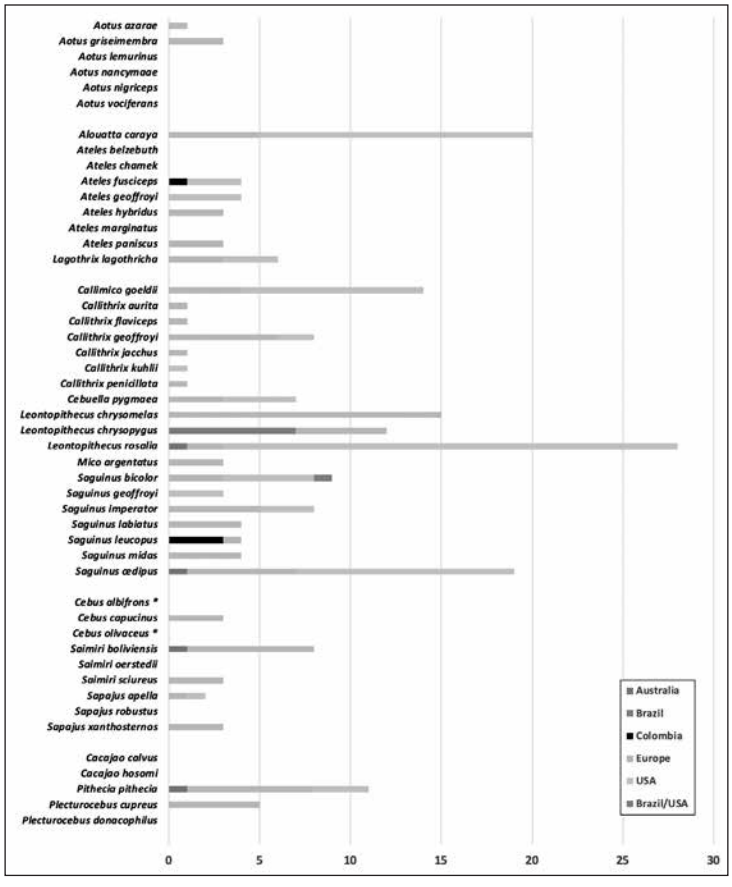
Species	IUCN Level	First report	Latest report	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	Undetermined	#/taxon
Alouatta caraya	LC	1987	2019																		2																															20
Aotus azarae	LC	2016	2016																																																		1
Aotus griseimembra	VU	2016	2019																																																	3
Ateles fusciceps	CR	2014	2019																																																	4
Ateles geoffroyi	EN	1996	2010																																																	4
Ateles hybridus	CR	2016	2019																																																	3
Ateles paniscus	VU	2016	2019																																																	3
Callimico goeldii	VU	1983	2019												2								2																														14
Callithrix aurita	EN	2019	2019																																																	1
Callithrix flaviceps	EN	2019	2019																																																	1
Callithrix geoffroyi	LC	2001	2019																																																	8
Callithrix jacchus	LC	2019	2019																																																	1
Callithrix kuhlii	VU	2003	2003																																																	1
Callithrix penicillata	LC	2019	2019																																																	1
Cebuella pygmaea	VU	1984	2013																																																	7
Cebus capucinus	LC	2016	2019																																																	3
Lagothrix lagothricha	VU	1988	2017																																																	6
Leontopithecus chrysomelas	EN	1988	2019																			2																															15
Leontopithecus chrysopygus	EN	1988	2019																																																		12
Leontopithecus rosalia	EN	1973	2019																																																		28
Mico argentatus	LC	2016	2019																																																		3
Pithecia pithecia	Other *	1989	2019																																																		11
Plecturocebus cupreus	LC	2003	2019																																																		5
Saguinus bicolor	CR	1997	2019																																																		9
Saguinus geoffroyi	NT	1984	1991																																																		3
Saguinus imperator	LC	1992	2019																																																		8
Saguinus labiatus	LC	2004	2019																																																		4
Saguinus leucopus	EN	2011	2019																																																		4
Saguinus midas	LC	2004	2019																																																		4
Saguinus œdipus	CR	1987	2019																																																		19
Saimiri boliviensis	LC	2000	2019																																																		8
Saimiri sciureus	LC	2016	2019																																																		3
Sapajus apella	LC	2009	2009																																																		2
Sapajus xanthosternos	CR	2016	2019																																																		3
# per year				1	0	0	1	1	1	1	1	1	2	2	2	2	2	3	5	3	#	5	4	6	3	3	3	7	5	2	5	3	2	6	#	7	1	2	3	6	3	5	2	5	2	2	#	#	2	#	1	222
Average per year																																																					4,63
S.D.																																																						6,07
Regional																																																								
International																																																									
Actus spp.		1994	2013																							2														2													9
Ateles spp.		1995	2004																																																		8
Callicebus spp		1998	1998																																																		1
Cebus spp.		2001	2001																																																		1

Supplementary Figure 2. Representation of 48 Neotropical primate taxa in studbook reports published across different countries and regions.



A. Records between 1998 and 2011 in the WAZA database (WD).

* Studbooks are categorized by family, taxon and location of the chief organization involved in the development of each studbook.



B. Records between 1973 and 2019 in the Public database (PD).

* Studbooks released before introduction of taxonomic changes.