American Journal of Primatology

REVIEW ARTICLE

Capuchin Monkey Research Priorities and Urgent Issues

JESSICA W. LYNCH ALFARO[1,2]*, PATRICIA IZAR[3], AND RENATA G. FERREIRA[4]
[1]Institute for Society and Genetics, University of California, Los Angeles, California
[2]Department of Anthropology, University of California, Los Angeles, California
[3]Department of Experimental Psychology, University of São Paulo, São Paulo, Brazil
[4]Psychobiology Graduate Program, Department of Physiology, Rio Grande do Norte Federal University, Natal, Brazil

The "Capuchin research community roundtable: working together towards a comparative biology of *Cebus* and *Sapajus*" was held at the International Primatological Society Congress in Cancún, Mexico, August 2012. Goals of the roundtable were to strengthen interactions among the capuchin research community, and to prioritize and coordinate research and training in a more systematic and interactive way in light of increasing conservation urgency. New phylogenetic and biogeographic evidence highlights the distinct evolutionary histories of the two radiations of capuchin monkeys, *Cebus* (untufted or gracile capuchins) and *Sapajus* (tufted or robust capuchins), that were formerly lumped under *Cebus*, and points to a higher number of species, or Evolutionarily Significant Units, in each compared to past capuchin taxonomies. Many of the lesser-known species face increasing fragmentation and destruction of habitat, and most populations of still non-threatened species face encroachment from human settlements. Here, we present capuchin research priorities and urgent issues based on the discussion by capuchin researchers in the roundtable. These include a call for the immediate end to the use of the name *Cebus apella* and the employment of the term *Sapajus* spp. instead for captive robust capuchins of unknown origin; for the implementation of rapid assessments for previously unstudied capuchin species or populations in biomes of interest; for the development of standardized methods to allow for comparative analyses across capuchin field sites; and for the creation and maintenance of an open-access website for capuchin monkey data. Finally, we planned the creation of an international Capuchin Action Network, to help disseminate research information; to work as a research community in a more efficient, collaborative manner; to help prioritize research and conservation goals as a community of experts; and to strengthen our political voice. Am. J. Primatol. © 2014 Wiley Periodicals, Inc.

Key words: *Sapajus*; *Cebus*; conservation; research community; outreach

INTRODUCTION

On August 17, 2012, at the International Primatological Society Congress in Cancún, Mexico, we held a session titled "Capuchin research community roundtable: working together towards a comparative biology of *Cebus* and *Sapajus*," led by Jessica Lynch Alfaro, Patrícia Izar, and Renata Ferreira. Participants at the meeting included: Mary Baker, Marcelo F. Bolanos, Janet C. Buckner, Nicolas Claudiere, Irene Delval, Mariana Dutra Fogaca, Mariana Edaes, Yonat Eshchar, Dorothy M. Fragaszy, Camila Galheigo Coelho, Katharine Jack, Charles Janson, Mariana Mascarenhas Winandy, Emily Messer, Antônio Moura, Maria Adélia B. de Oliveira, Lucas Peternelli-dos-Santos, Emannuelle Ponydebat, Andrea Presotto, Adelina Schutt, Marcos Tokuda, Barth Wright and Kristin Wright. Online contributors included: Luke J. Matthews and Susan Perry.

The goals of the roundtable were to: (1) strengthen interactions among the capuchin research community; (2) prioritize and coordinate research and community actions in a more systematic and interactive way in light of increasing conservation urgency; and (3) form an international Capuchin Action Network (CAN).

This article is a product of the roundtable and ongoing discussions with the capuchin research

Contract grant sponsor: National Science Foundation; contract grant number: BCS 0833375; contract grant sponsor: FAPESP and CNPq; contract grant sponsor: CNPq and FAPERN

*Correspondence to: Jessica Lynch Alfaro, Institute for Society and Genetics, UCLA, 1321 Rolfe Hall, Los Angeles, CA 90095. E-mail: jlynchalfaro@ucla.edu

Received 10 November 2013; revised 28 January 2014; revision accepted 3 February 2014

DOI: 10.1002/ajp.22269
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

community, especially with Dorothy M. Fragaszy, Anthony B. Rylands, and José de Sousa e Silva Jr.

BACKGROUND

In 1996, Linda Fedigan, Alfred Rosenberger, Sue Boinski, Marilyn Norconk, and Paul Garber wrote an article, "Critical issues in cebine evolution and behavior." Their first concern was the taxonomic status of capuchin monkeys. At that time, the taxonomic position of capuchin monkeys was unclear in relation to other neotropical primate genera [Fedigan et al., 1996]. They suggested in the article that capuchins were the sister group to squirrel monkeys (*Saimiri*), as now confirmed by numerous genetic studies [Canavez et al., 1998; Opazo et al., 2006; Perelman et al., 2011; Schneider et al., 1996, 2001]. Since the publication of that article, it also has become clear that capuchins and squirrel monkeys together form the sister group to the clade of marmosets and tamarins (Callitrichidae) and to the owl monkeys (Aotidae) [Perelman et al., 2011; Schneider & Sampaio, 2013]. It has taken longer to resolve the taxonomic relationships among extant capuchin monkey species, and this work is ongoing.

Traditionally capuchin monkeys have been lumped into one genus, *Cebus* Erxleben, 1777. Hershkovitz [1949, 1955] recognized four species, *C. albifrons*, *C. olivaceus*, *C. capucinus*, and *C. apella*, a taxonomy that dominated the capuchin literature for about 50 years. Recent morphological, genetic, and biogeographic studies, however, suggest that capuchin monkeys diversified into two clades about 6 million years ago and are distinct enough to be distinguished at the genus level: the gracile or untufted capuchins, *Cebus*, and the robust or tufted capuchins, *Sapajus*[1] [Lynch Alfaro et al., 2012a,c; Rylands et al., 2013; Silva, 2001]. Each genus contains more species than previously recognized, due to the discovery of *Cebus kaapori* [Queiroz, 1992], the rediscovery of *Sapajus flavius* Schreber, 1774 [Oliveira & de Langguth, 2006], and the accumulation of more detailed morphological and genetic evidence for known capuchins [Boubli et al., 2012; Lynch Alfaro et al., 2012a,c; Ruiz-García et al., 2010, 2012a,b; Silva, 2001] that has resulted in the resurrection of species previously considered synonyms. Biogeographic evidence suggests two very distinct evolutionary histories for the group, with gracile *Cebus* radiating rapidly through the Andes and the Amazon, the Guianas, northern Colombia, Venezuela and Central America, and the robust *Sapajus* diversifying first in Brazil's Atlantic coastal forest and only recently invading the Cerrado and Caatinga, and the Amazon where it entered into sympatry with *Cebus* [Lynch Alfaro et al., 2012a]. The split between *Cebus* and *Sapajus* is estimated to have occurred 5–7 million years ago, around the same time as that between humans (*Homo*) and chimpanzees (*Pan*) [Lynch Alfaro et al., 2012a; Perelman et al., 2011].

Overall, the distinct evolutionary and ecological histories based on genetic and biogeographic evidence, the divergent morphological and behavioral patterns (Table I), and the extreme overlap in sympatry of *Cebus* and *Sapajus* throughout the Amazon provide strong support for the split of these two sister groups into separate genera [Lynch Alfaro et al., 2012a,c; Rylands and Mittermeier, 2013; Rylands et al., 2013; Schneider & Sampaio, 2013; Silva, 2001]. In some research areas, such as cytogenetics; however, the division is not so clear; for example, Amaral et al. [2008] found that in a phylogeny based on chromosome painting and karyotype characters, *Sapajus robustus*, *Sapajus cay*, and *Sapajus* sp. formed a monophyletic clade, but that *C. olivaceus* was more similar to the robust capuchins than to the other gracile capuchins in the study; and Nieves et al. [2011] found a capuchin-specific heterochromatin within neotropical primates, but with highly variable patterns across capuchin species. At least one expert in neotropical primate morphology has argued that it is more convenient to continue to consider all capuchins congeneric as before [Rosenberger, 2012]. At the IPS roundtable, in light of all the available evidence, the researchers were unanimous in support of the taxonomic split of *Sapajus* and *Cebus*.

The capuchin phylogeny provides an evolutionary framework or backbone on which to map behavioral and morphological variation across populations and species; see Lynch Alfaro et al. [2012b] for anointing behaviors, Matthews [2012] for sexual and courtship behavior, and Wright et al. [2012] for morphology. This framework clarifies several significant differences between *Sapajus* and *Cebus*, across a range of research domains, at least from what we know so far of the diversity in these two genera (see Table I for some examples). We believe this phylogenetic evolutionary framework provides new research questions and opportunities, and our aim was to use the meeting to brainstorm together about the future for capuchin work in the following areas: priorities for captive research; priorities for field research; methods and research foci for comparative cross-site studies, including priorities for genetic research; conservation challenges and community outreach; and the establishment of an international CAN to facilitate interaction among the capuchin research community.

[1] The genus *Sapajus* Kerr, 1792 has been registered on Zoobank under urn:lsid:zoobank.org:act:3AAFD645-6B09-4C88-B243-652316B55918.

TABLE I. Comparison Between *Cebus* and *Sapajus* in Different Domains

Domain/research area	*Cebus*	*Sapajus*
Tool use	15% of studies (captivity/wild)[1]	75% of studies (captivity/wild)
	In wild populations:	In wild populations:
	No stone tool use	Habitual nut cracking with stones[4]
	Use of branches for defense[2]	Stone banging as defense[5]
	Leaves to absorb liquid[3]	Probing with sticks[6]
Anointing behavior	Relatively frequent behavior in several populations[7]	Rare behavior[7]
	Most common with plants[7,8]	Most common with insects[7,8]
Behavioral traditions	Several social conventions[9]	No social conventions yet reported
	Interspecific interactions[10]	Interspecific interactions[11]
	No variation in tool use for feeding	Tool use for feeding[4]
Sexual behavior	No obvious female choice and lack of proceptive behaviors[12,13]	Female choice with rich proceptive courtship display[12,13]
	Female behavior consistent with strategy of paternity confusion[13]	Female behavior consistent with strategy of paternity concentration[13]
Fission-fusion dynamics	Low degree in populations studied so far	Increased evidence for high degree in some populations[14]
Dispersal	Male biased, multiple male dispersals[15]	Male biased
	Occasional female transfer related to risk of infanticide[16]	In some populations, frequent female transfer related to food competition[17]
Functional morphology	Ripe fruit specialists[18]	Adaptations to durophagy[19]

Note: [1]Reviewed in Fragaszy et al. [2004a, b]; [2]Boinski [1988]; [3]Phillips [1998]; [4]Review of reports in Ottoni and Izar [2008]; [5]Moura [2007]; [6]Mannu and Ottoni [2008]; [7]Lynch Alfaro et al. [2012b]; [8]Leca et al. [2007]; [9]Perry et al. [2003]; [10]Rose et al. [2003]; [11]Resende et al. [2004]; [12]Matthews [2012]; [13]Izar et al. [2009]; [14]Lynch Alfaro [2007] and Nakai [2007]; [15]Fedigan and Jack [2004]; [16]Jack and Fedigan [2009]; [17]Izar et al. [2012] and Tokuda et al. [2011]; [18]Fragaszy et al. [2004a]; [19]Wright et al. [2009].

DISCUSSION

Priorities and Issues for Captive Research

Nomenclature

Our discussion of captive research focused on the need to shift from the umbrella term *C. apella*, long used to describe most captive (laboratory and zoo) colonies of robust capuchin monkeys of unknown or mixed provenance. We strongly advocate for an end to the use of *C. apella* and for the immediate adoption of the term *Sapajus* spp. in studies when the species of *Sapajus* is unknown, or known to be a hybrid or mixed colony in captivity, or semi-captivity (such as the Tietê Ecological Park population in the city of São Paulo [Ottoni & Mannu, 2001]) as well as for likely introduced wild isolates, such as the *Sapajus* group studied in an urban fragment in Foz do Iguaçu, Paraná, Brazil [Back et al., 2013]. The term *Sapajus apella* (or *S. apella apella*, considering that the population on the island of Margarita, Venezuela, may be a distinct subspecies *S. apella margaritae*) should be restricted for use only for individuals that are of known provenance from the eastern Amazon [Rylands et al., 2013]. We advocate the use of the term *Sapajus* spp. because it indicates that the captive group or individuals are robust capuchins, providing more information than the blanket use of *Cebus* spp., a term that could be interpreted by researchers as specifically signifying gracile capuchins. There is currently a divide in the literature in which most field researchers working with robust capuchins publish their work as *Sapajus* in concert with the species and sometimes subspecies for the given location [e.g., Falotico & Ottoni, 2014; Fragaszy et al., 2013; Scarry, 2013] while captive researchers publish work with any captive robust capuchin monkey populations or medical research subjects variously as *C. apella* [Addessi et al., 2013; Phillips & Thompson, 2013; Wheeler et al., 2013], *S. apella* [Brito et al., 2013; Morton et al., 2013; Rimpley & Buchanan-Smith, 2013], *Sapajus* spp. [Goulart et al., 2013], or *S.* (*C.*) *apella* [Wilson et al., 2014]. This last construction, while evidently trying to indicate that *S. apella* was formerly in the genus *Cebus*, is unfortunate in that this is the nomenclatural syntax that indicates that *Cebus* is a subgenus of *Sapajus*, and there is no evidence that this is so.

We stress the importance of accurately ascribing the taxon in relation to behavioral, morphological, and medical research findings. The use of *C. apella* for all the robust capuchins has obfuscated differences between species and even among their populations (now *Sapajus*) over several decades. A growing number of field studies and morphological analyses of specimens from known origin makes it clear that there are significant differences among the different *Sapajus* species. Uncertainty of the species' identity can invalidate the interpretation and validity of experimental results. We advocate that laboratory colonies have their animals genotyped to identify the species and check for hybrids. These capuchins breed well in captivity and many colonies are likely to contain, or consist entirely of, hybrids. In the short term, mitochondrial markers are a first step to determining maternal lineage of origin (see Lynch Alfaro et al., 2012a supplementary material for 12s and cytochrome *b* primers, and Boubli et al., 2012 for DLoop primers). Advances in genomics are making it more feasible to do a detailed "fingerprint" for pinpointing where captive populations fit in a capuchin phylogeny. If interested, please contact the first author, Jessica Lynch Alfaro, with questions about genotyping colonies.

Captive *C. albifrons*, like captive *Sapajus*, is a problematic group. While morphological assessments have named up to 13 subspecies of *C. albifrons* [Hershkovitz, 1949], captive *C. albifrons* populations are almost always managed at the "species" level [Littlefield, 2009]. Recent genetic studies suggest that *C. albifrons* is paraphyletic [Boubli et al., 2012; Lynch Alfaro et al., 2012a], and the most recent taxonomic review for capuchin monkeys splits *C. albifrons* into nine different species [Rylands et al., 2013; see Table II]. This suggests the need for more care in documenting the origin of captive gracile *Cebus* and avoiding hybridization among different species or populations.

We suggest the following guidelines for researchers, authors, and reviewers for academic journals with regard to the use of taxonomic names for capuchins, to help in the standardization of names, with the understanding that the reassessment of capuchin diversity is in its early stages, and the taxonomy is likely to continue to change: (1) include locality or provenance whenever possible; (2) make clear that the animals are hybrid and/or of unknown origin if this is the case; and (3) include subspecies (or when commonly used that way, raised to species level, at the preference of author) for all *Sapajus* and *Cebus*. The current assessment of taxa or potential Evolutionarily Significant Units for *Cebus* and *Sapajus* [Rylands et al., 2013] is listed in Table II. This list is "conservative" in the sense of preferring to err on the side of splitting taxa into too many different species/subspecies [contra Rosenberger, 2012], following IUCN's guidelines for dealing with uncertainty in taxonomic assessment. We do not know enough about capuchin monkeys to know yet how many species there are. This is an important area for further study.

Hybridization and health

Problems related to captive capuchins and hybridization are especially complex in habitat countries. In Brazil, for example, there is a high influx of robust capuchin pets that are abandoned or

TABLE II. Provisional Capuchin Monkey Taxonomy and Distributions [Based on Boubli et al., 2012; Groves, 2001; Rylands et al., 2013]

GENUS *SAPAJUS* Kerr, 1792
Sapajus apella apella Guianan Brown Capuchin—eastern and central Amazon in Brazil, Colombian border, French Guiana, Guyana, Suriname, Venezuela; and *S. apella margaritae*—Margarita Island, Venezuela
Sapajus macrocephalus Large-headed Capuchin—western Amazon in Bolivia, Brazil, Ecuador, Peru, Colombia
Sapajus flavius Blond Capuchin —extreme northeast Brazil
Sapajus libidinosus Bearded Capuchin—Brazilian Caatinga and Cerrado
Sapajus cay Hooded Capuchin—Mato Grosso do Sul in Brazil, Bolivia, Paraguay
Sapajus xanthosternos Yellow-Breasted Capuchin—Bahia, Atlantic Forest, Brazil
Sapajus robustus Crested Capuchin—Espírito Santo and Minas Gerais, Atlantic Forest, Brazil
Sapajus nigritus nigritus Black Horned Capuchin—Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Brazil [Groves, 2001]; and *S. nigritus cucullatus*—Santa Catarina, Rio Grande do Sul, Brazil; Iguazu, Argentina [Groves, 2001]
GENUS *CEBUS* Erxleben, 1777
Cebus capucinus Colombian White-faced Capuchin—eastern Panama, Colombia
Cebus imitator Panamanian White-faced Capuchin —western Panama, Costa Rica, Nicaragua
Cebus leucocephalus Sierra de Perijá White-fronted Capuchin (provisionally includes *C. adustus*)—eastern Andes, northern Venezuela, Colombia border
Cebus cesarae (includes *C. pleei*) Río Cesar White-fronted Capuchin—northwest Andes in Colombia and Venezuela
Cebus versicolor Varied White-fronted Capuchin—Intra-Andes valley, Colombia
Cebus aequatorialis Ecuadorian White-fronted Capuchin—Ecuador and far northern Peru, west of the Andes
Cebus albifrons Humboldt's White-fronted Capuchin—northern Amazon, north of Rio Branco to Venezuela
Cebus yuracus Marañón White-fronted Capuchin —western Amazon, Ecuador, Peru
Cebus cuscinus Shock-headed Capuchin—southern Amazon, Peru, Brazil, Bolivia south of Rio Purus
Cebus unicolor Spix's White-fronted Capuchin—Amazon Basin, south of the Rio Amazonas (or south of Rio Negro [Boubli et al., 2012])
Cebus malitiosus Santa Marta White-fronted Capuchin—Sierra Nevada de Santa Marta, Colombia
Cebus brunneus (provisionally includes the form *trinitatis*) Venezuelan Brown Capuchin—extreme eastern Andes in Venezuela and Trinidad
Cebus olivaceus olivaceus Guianan Weeper Capuchin—Venezuela, western Guianas south to Roraima, Brazil; and *C. olivaceus castaneus*—eastern Guianas
Cebus kaapori Ka'apor Capuchin—eastern Amazon, in Pará and Maranhão, possibly Ilha do Marajó

seized by the authorities; these individuals are usually of unknown origin and tend to be kept together in zoos or government holding facilities, where they hybridize. There is a long history in Brazil of releasing capuchins of unknown origin into the wild as well, both at the outskirts of rural towns and in more continuous forest. We suggest the practice of identifying the origin of capuchin monkeys (through interviews as well as morphological and genetic means) and keeping different species separate in captivity. This may be especially important for endangered species such as the blond capuchin *Sapajus flavius* and the yellow-breasted capuchin *S. xanthosternos*. The many captive hybrids of both with *Sapajus libidinosus* and *S. apella* cannot contribute to ex situ conservation programs. Fortunately, captive breeding programs have been established for *S. xanthosternos* in Brazilian zoos and abroad [Lernould et al., 2012].

We should consider what opportunities for research arise from having such a large number of capuchin hybrids in captivity. If we can identify hybrids and ascribe parentage, and collect data on both the parents and offspring, then there may be several interesting avenues for research—for example, how do genetics and environment affect vocal learning? Are the vocalizations of hybrids the same as those of one of the parents, intermediate, or most similar to other individuals with whom they interact? Similar questions could be asked about tool use acquisition.

Another important area of captive research is the development of behavioral health assessment protocols and captive enrichment protocols as tools to ensure ex situ conservation of species. Protocols are also needed for behavioral training and reintroduction of animals to the wild, as well as the publication of examples of successful and unsuccessful attempts at reintroduction.

Field Research Priorities

An area of urgent concern among capuchin researchers is how field research funding should be prioritized. What are the costs and benefits of the focus on long-term field sites versus new short-term sites for unstudied or understudied populations or species? What about the need for rapid assessments across the range of capuchins?

Rapid assessment and short-term field studies on unstudied or understudied populations

There was consensus among researchers at the roundtable regarding urgent need for an assessment of the populations of capuchin monkeys across habitat types in areas where little is known of capuchin ecology or behavior. This is particularly important for habitat types that have until now been poorly studied, for populations living in areas subjected to increasing fragmentation and urbanization, and in areas predicted to be affected by global climate change.

As pointed out by Janson [2000] more than a decade ago, humans continue to invade and destroy the habitats of wild primate populations, and we need to study them before we lose the natural context of their adaptations. This is essential for the advancement of behavioral sciences, as well as for the conservation of these primates [Caro & Sherman, 2011]. Although capuchin monkeys are considered a widespread and hardy animal, there are very few data points in the Amazon and around the Andes to confirm their current presence across much of their hypothetical ranges (J. Lynch Alfaro, personal observation). As pointed out by Luke Matthews, "because capuchins are a hugely variable group and we have still sampled relatively little of them," new sites have the potential to produce a different and complementary kind of knowledge to that from long-term established studies, about the breadth and dimensions of capuchin diversity across habitat types.

An important area for the focus of field research is "*C. albifrons*." As traditionally configured, *C. albifrons* has a disjunct distribution, with four separate ranges, in the northern Andes, the west coast of Ecuador and Peru, the Amazon, and Trinidad. Preliminary evidence suggests that the population in Trinidad may be more closely related to a population of *C. olivaceus* or *Cebus brunneus* in western coastal Venezuela [Boubli et al., 2012]—this needs more research. There are also several distinct subspecies or species of *Cebus* in the Andes, each isolated from one another by the various mountain ridges. These Andean forests of Colombia are already severely fragmented, and the isolated populations have small ranges and are at high risk of extinction. *C. albifrons* from the Amazon (which may include at least four distinct taxa: *C. albifrons*, *C. unicolor*, *C. yuracus*, *C. cuscinus*) has been the subject of behavioral ecological studies at only three field sites (see Fig. 1, Table III): Manu National Park, Peru [*C. cuscinus*: Janson, 1986a; Terborgh, 1983], El Tuparro National Park, Colombia [*C. albifrons*: Defler, 1979a, b, 1985], and Tiputini Biodiversity Station, Ecuador [*C. yuracus*: Matthews, 2009]. There are no behavior ecology studies of the *C. albifrons* group in Brazil, the country that includes the largest part of its range.

At the other end of the spectrum, the white-faced capuchin in Costa Rica and Panama, now classified as *Cebus imitator*, is the most studied of wild capuchin monkeys, with both short-term and long-term field sites [Baldwin & Baldwin, 1997; Fedigan & Jack, 2012; Garber & Brown, 2006; Oppenheimer, 1969; Perry et al., 2012; Rose et al., 2003; see also Fig. 1 and Table III]. *C. capucinus* in Colombia, on the other hand, has never been studied in the field. It may have diverged from *C. imitator* up to 2 million years ago

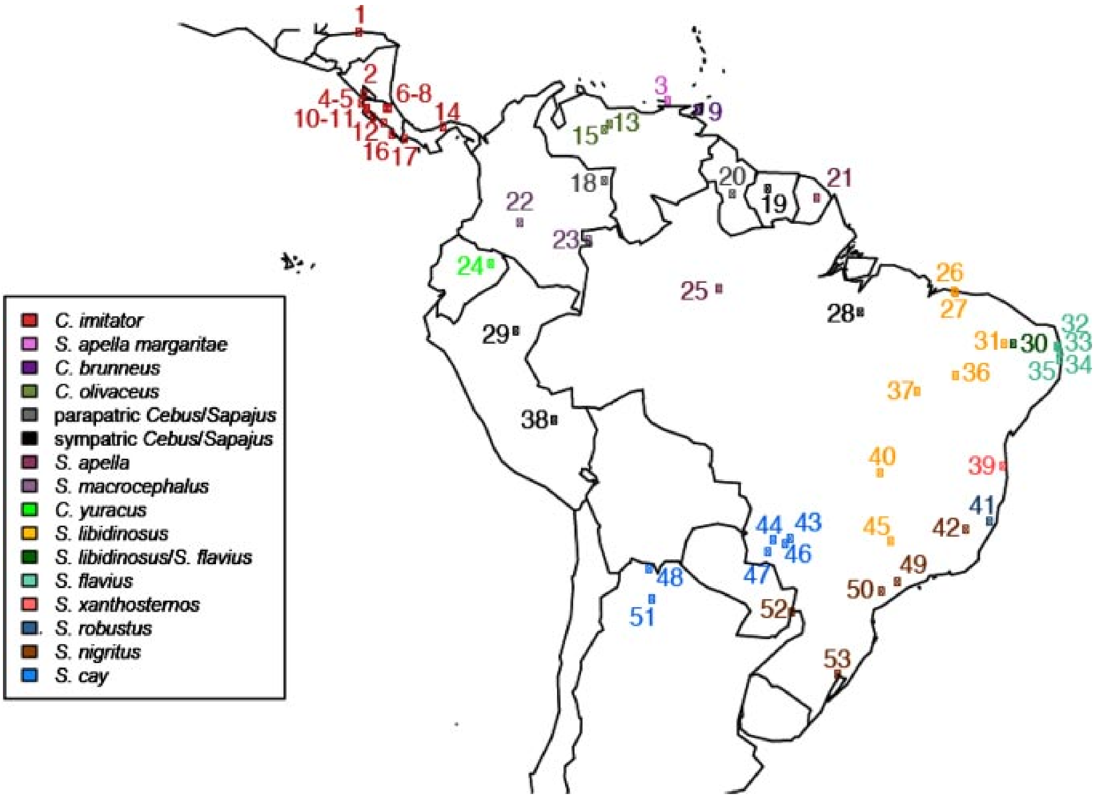

Fig. 1. Map of locations of past and present field research sites for *Cebus* and *Sapajus* behavior and ecology. See Table III for key to field site names.

[Boubli et al., 2012]. *C. olivaceus* appears to be a very recent successful radiation, expanding over the Llanos and northern Amazon in the last 500 ky [Boubli et al., 2012]. *C. olivaceus* has been the subject of long-term data collection at only two field sites, both in the wetland savanna, the Llanos [Miller, 1998; Robinson, 1986, 1988], but has never been studied in the Amazon. Finally, *C. kaapori*, first described in 1992 from south of the lower Rio Amazonas, has begun to be studied only at one field site [Oliveira et al., this issue]. This endemic species is listed as Critically Endangered on the Brazilian List of Threatened Species, and is currently considered to be one of the world's 25 Most Endangered Primates. It is naturally scarce and there has been widespread deforestation in its range in the eastern Amazon; its forests are now severely fragmented and degraded.

In contrast to *Cebus*, there are more available data and ongoing research projects for *Sapajus*, at least in the Atlantic Forest, and more recently in the Caatinga and Cerrado. *Sapajus nigritus* in the southern Atlantic Forest has been studied in Brazil at Carlos Botelho State Park, São Paulo [Izar et al., 2012] and in Caratinga Biological Station (now RPPN Feliciano Miguel Abdala), Minas Gerais [Lynch Alfaro, 2007], as well as Iguazú Falls, Argentina [Janson et al., 2011]. The first research project on wild *S. robustus* was carried out at the Reserva Natural Vale, Espírito Santo, Brazil [Martins, 2010]. *S. xanthosternos* has been studied at Una Biological Reserve in Bahia [Kierulff et al., 2005], and there are several new field sites for *S. flavius* in the extreme northeast of Brazil [Montenegro, 2011]. The first field sites for *S. cay* are in Mato Grosso do Sul [Cazzadore, 2007; Pinto, 2006; Rímoli et al., 2002, 2005, 2009]. A handful of dry Cerrado and Caatinga field sites have produced several studies of tool use in *S. libidinosus*, *S. xanthosternos*, and indicated tool use in *S. flavius* [Emidio & Ferreira, 2012; Fragaszy et al., 2004a,b; Mannu & Ottoni, 2008; Moura, 2007; Moura & Lee, 2004; Ottoni & Izar, 2008]. Broader surveys of Cerrado and Caatinga have yielded ample evidence for even more widespread capuchin stone tool use [Canale et al., 2009; Ferreira et al., 2009], but motivating researchers to set up long-term sites and conduct behavioral observations in these extreme environments is difficult.

In comparison, the behavioral and ecological research study sites on wild Amazonian *Sapajus* are relatively few. Research has been carried out by Izawa [1979, 1980, 1999] in La Macarena, Colombia; Terborgh [1983] and Janson [1984, 1985, 1986b, 1990a,b] in Manu National Park, Peru; Spironello

TABLE III. Past and Present Field Sites for Capuchin Monkey Behavior and Ecology

Map code	Species	Latitude	Longitude	Country	Site name
1	*C. imitator*	15.92	−85.95	Honduras	Trujillo
2	*C. imitator*	11.5	−85.58	Nicaragua	Isla de Ometepe
3	*S. apella margaritae*	11	−63.54	Venezuela	Isla Margarita
4	*C. imitator*	10.85	−85.78	Costa Rica	Santa Rosa National Park
5	*C. imitator*	10.51	−85.38	Costa Rica	Lomas Barbudal Reserve
6	*C. imitator*	10.46	−83.95	Costa Rica	Refugio de Vida Silvestre Privado Nogal, Sarapiquí, Heredia
7	*C. imitator*	10.44	−83.77	Costa Rica	La Suerte Biological Research Station
8	*C. imitator*	10.43	−83.98	Costa Rica	La Selva Biological Station
9	*C. brunneus* (or *c. albifrons trinitatis*, see text)	10.39	−61.3	Trinidad	Bush Bush Sanctuary
10	*C. imitator*	10.35	−85.35	Costa Rica	Palo Verde, Estación MINAE
11	*C. imitator*	9.78	−84.93	Costa Rica	Curú National Wildlife Refuge
12	*C. imitator*	9.45	−84.15	Costa Rica	Manuel Antonio National Park, Quepos
13	*C. olivaceus*	9.38	−67.7	Venezuela	Hato Masaguaral
14	*C. imitator*	9.15	−79.85	Panama	Barro Colorado
15	*C. olivaceus*	8.95	−68.08	Venezuela	Hato Piñero
16	*C. imitator*	8.55	−83.58	Costa Rica	Corcovado National Park
17	*C. imitator*	8.32	−82.63	Panama	Barqueta
18	Sympatric *C. albifrons* and *S. macrocephalus*	5.28	−68.07	Colombia	El Tuparro National Natural Park
19	Sympatric *C. olivaceus* and *S. apella apella*	4.72	−56.2	Suriname	Raleighvallen
20	Parapatric *C. olivaceus* and *S. apella apella*	4.35	−58.75	Guyana	Turtle Mountain, Iwokrama Reserve
21	*S. apella apella*	4.08	−52.67	French Guiana	Noragues Field Station
22	*S. macrocephalus*	2.25	−74.25	Colombia	La Macarena
23	*S. macrocephalus*	1.04	−69.3	Colombia	Estación Biológica Mosiro Itajura-Caparú
24	*C. yuracus*	−0.7	−76.35	Ecuador	Tiputini, Yasuni National Park
25	*S. apella apella*	−2.45	−59.77	Brazil	DBFF, north of Manaus, Amazonas
26	*S. libidinosus*	−2.62	−42.69	Brazil	Estuario do Rio Preguiças, Maranhão
27	*S. libidinosus*	−2.71	−42.53	Brazil	Estuario do Rio Novo, Maranhão
28	Sympatric *C. kaapori* and *S. apella apella*	−4.14	−49.51	Brazil	Tucuruí Dam area of influence, Pará
29	Sympatric *C. yuracus* and *S. macrocephalus*	−5.43	−74.57	Peru	Pacaya-Samiria National Reserve
30	*S. libidinosus* or *S. flavius* (contested)	−6.21	−37.04	Brazil	Serra do Estreito, Jurucutu, Rio Grande do Norte
31	*S. libidinosus*	−6.4	−38.39	Brazil	Luis Gomes, Rio Grande do Norte
32	*S. flavius*	−6.56	−35.13	Brazil	Mamanguape, Paraíba
33	*S. flavius*	−6.6	−35.05	Brazil	Est. Experimental de Camaratuba, Mataraca, Paraíba
34	*S. flavius*	−7.11	−34.98	Brazil	Reserva do Patr. Natural Engenho Gargaú, Santa Rita, Paraíba
35	*S. flavius*	−7.51	−34.97	Brazil	Córrego das Borboletas, Pernambuco
36	*S. libidinosus*	−8.67	−42.55	Brazil	Parque Nacional Serra da Capivara, Piauí
37	*S. libidinosus*	−9.84	−45.35	Brazil	Fazenda Boa Vista, Gilbués, Piauí
38	Sympatric *C. cuscinus* and *S. macrocephalus*	−11.86	−71.72	Peru	Manu National Park
39	*S. xanthosternos*	−15.17	−39.13	Brazil	Reserva Biológica de Una, Bahia
40	*S. libidinosus*	−15.67	−48	Brazil	Parque Nacional de Brasília, Brasília
41	*S. robustus*	−19.14	−40.07	Brazil	Reserva Natural Vale em Linhares, Espírito Santo
42	*S. nigritus*	−19.73	−41.82	Brazil	RPPN Feliciano Miguel Abdala (Caratinga), Minas Gerais
43	*S. cay*	−20.39	−54.59	Brazil	Matas do Corrego do Segredo, Mato Grosso do Sul

(Continued)

TABLE III. (Continued)

Map code	Species	Latitude	Longitude	Country	Site name
44	*S. cay*	−20.47	−55.79	Brazil	Aquidauana, Mato Grosso do Sul
45	*S. libidinosus*	−20.52	−47.3	Brazil	Ribeirão dos Correias, São Paulo
46	*S. cay*	−20.73	−54.92	Brazil	RPPNNQ-Fazendas Nova Querência e Nova Esperança, MS
47	*S. cay*	−21.36	−56.16	Brazil	Fazenda São Marcos, Município de Guias Lopes da Laguna, MS
48	*S. cay*	−22.566	−64.8	Argentina	Baritú National Park
49	*S. nigritus*	−23.46	−46.77	Brazil	Parque Estadual do Jaragui, São Paulo
50	*S. nigritus*	−24.13	−47.95	Brazil	Carlos Botelho, São Paulo
51	*S. cay*	−24.7	−64.63	Argentina	El Rey National Park
52	*S. nigritus*	−25.7	−54.44	Argentina	Iguazú Falls
53	*S. nigritus*	−30.05	−51.11	Brazil	Porto Alegre, Rio Grande do Sul

Note: Key to Capuchin field sites from Figure 1. Species names follow Rylands et al. [2013].

[1991, 2001] in the central Amazon; Sampaio and Ferrari [2005] in Pará, Brazil; Zhang [1995] in French Guiana; and Boinski and colleagues [Boinski et al., 2000; Gunst et al., 2008, 2010] in Raleighvallen-Voltzberg, Suriname. Most capuchin monkeys in the enormous area of sympatry between *Cebus* and *Sapajus*, however, remain unstudied, except censuses of primate communities [e.g., Haugaasen & Peres, 2005]. A review of *Cebus* population densities at sites with and without *Sapajus* shows they are often lower in the presence of *Sapajus*, but the reverse is not true [see Lynch Alfaro et al., 2012c]. For some gracile capuchin populations, such those of *C. kaapori*, competition with *Sapajus* may interact with anthropogenic changes to increase extinction risk [Oliveira et al., this issue]. Understanding these cross-capuchin dynamics and their ecological and behavioral causes will be key in conservation planning.

We agreed that it would be useful to develop a protocol for rapid assessment, and its dissemination and use in a standardized way across sites and countries. This protocol is currently being developed, and will include the following types of data collection:

1. Demographic data: number of animals in groups, age, and sex class structure. These data are essential for evaluation of conservation status. For example, a low proportion of juveniles and infants could suggest reproductive problems in the population. Demographic information is also important for understanding ecological factors that affect primate social organization.
2. General behavioral data: foods eaten to document dietary flexibility and preferences of different species; reaction to humans (information to indicate the degree of human alteration of natural behavior); recording of vocalizations (useful data for phylogenetic studies); recording of tool use based on direct or indirect observation.
3. Opportunistically collected fecal samples for genetic assessment, allowing for the evaluation of the health and conservation status of a given population (based on the degree of inbreeding) and for comparative study. Fecal samples can also be analyzed for parasites, the microbiome, and seed dispersal.
4. When darting of animals is feasible and appropriate, morphological measurements and health indicators (i.e., blood analysis) for live individuals.
5. Skeletal material: another key request for people working at field sites, or with captive individuals of known provenance, is to keep the skeletons if animals die. The information is invaluable to morphologists, and is especially difficult to come by for capuchin monkeys because most *Sapajus* museum specimens are only identified as "*C. apella*" without provenance; in fact, there are few post-cranial specimens available for either *Cebus* or *Sapajus*.
6. Data relevant to conservation status assessment, such as population density and home range size estimations based on census surveys.

One example of a wide-scale rapid assessment is that carried out for *Cebus aequatorialis* in western Ecuador [Jack & Campos, 2012]. This research identified known localities for species (and also many areas of extirpation), and followed up with distribution modeling to create a conservation plan for this Critically Endangered species [Campos & Jack, 2013]. This shows one way by which a rapid assessment can contribute to conservation implementation.

Finally, we discussed the importance of publishing descriptive short-term studies in scientific journals, as well as encouraging the publication of theses and dissertations (many already conducted but yet unpublished) to help disseminate information. We agree that the collection of basic data at new field sites is needed as a first step, and publications are

Fig. 2. Locations of capuchin monkey research from Figure 1, superimposed on habitat type in the area of capuchin monkey distribution. Map created in DataBasin, 2013. Blue dots correspond to presently active long-term field sites described in the text. Red dots correspond to all other past and present sites for behavioral and ecological research on wild capuchin monkeys.

required in order to get further research funded, so we urge editors to view basic data favorably for publication.

Long-term field sites

We emphasize the importance and necessity of long-term behavioral field studies [Clutton-Brock & Sheldon, 2010; Kappeler et al., 2012]. As Charles Janson pointed out in our meeting, some types of events only occur every 5 or 10 years, and these can be crucial to understanding group dynamics and life history. This is especially true for animals that can live up to 50 years in captivity. Field studies have not been of sufficient duration to even know what the maximum lifespan might be in the wild, although Perry et al. [2012] can quantify alpha male tenure at a maximum of 18 years from long-term research at Lomas Barbudal. We need long-term data to understand demographic dynamics in wild populations. For example, in a 4-year period of a long-term study at Carlos Botelho State Park, the capuchin groups were divided into subgroups with rapidly and constantly changing membership, but in another 4-year period, the group traveled as an entity 100% of the time [Izar & Nakai, 2006; Nakai, 2007]. A short-term study could easily have captured only one of the states of group fluidity (constant dynamic subgrouping vs. cohesive groups). The few ongoing long-term field studies are at risk due to loss of funding, with reviewers espousing a view that "everything has already been learned there." This is short sighted, as these sites continue to be powerhouses of research production and are the only places that many kinds of questions can be answered in coming years, precisely because of the tremendous databases already in place.

See Figure 1 and Table III for short- and long-term study sites that have produced behavioral and ecological research focusing on capuchin monkeys. The long-term field sites currently active in capuchin behavioral research include: Boa Vista, Piauí, Brazil; Serra da Capivara, Piauí, Brazil; Carlos Botelho State Park, São Paulo, Brazil; Una Biological Reserve, Bahia, Brazil; Iguazú Falls, Argentina; Lomas Barbudal, Costa Rica; and Santa Rosa, Costa Rica (these sites are represented as blue circles in Fig. 2). Other long-term field sites that are currently inactive for capuchin monkey research include: La Macarena, Colombia; Caratinga Biological Station (RPPN Feliciano Miguel Abdala), Minas Gerais, Brazil; Manu National Park, Peru; Corcovado National Park, Costa Rica; Barro Colorado, Panama; Hato Masuagaral, Venezuela; and Hato Piñero, Venezuela.

Cross-Site Comparative Studies

Detailed comparative intra-specific studies are available only for *C. imitator* (formerly *C. capucinus* or *C. capucinus imitator*), with a rich literature on variation in social and foraging behavior across populations [Manson et al., 1997, 1999; Perry, 2011;

Perry et al., 2003; Rose et al., 2003]. Miller [1998] compared diet between *C. olivaceus* at two field sites. Terborgh [1983] and Janson [1986a] gave the first detailed comparisons of *Sapajus macrocephalus* (formerly *C. apella*) and *C. cuscinus* (formerly *C. albifrons*) in sympatry at Manu National Park, and Defler [1982, 1985, 2012] compared parapatric *C. albifrons* and *S. macrocephalus* at El Tuparro. Izar et al. [2012] recently provided a detailed cross-species comparison for *S. libidinosus* and *S. nigritus* (both formerly considered subspecies of *C. apella*). Here, we consider some priorities for comparative studies across capuchin populations and species and suggest these studies would benefit by a more coherent standardization of some methods across sites and research groups to make data more directly comparable. Some areas of urgent need of comparative study include:

Life history: We need basic life history data (e.g., longevity and dispersal patterns) across species, to be used as a starting point to look at the diversity across capuchins, especially for species that have not been studied or are little studied.

Functional morphology: Morphological field studies are poised to take advantage of the variation across both *Cebus* and *Sapajus*, to try to understand the environmental factors affecting the evolution of physical and physiological traits involved in feeding behaviors and locomotion. Data need to be collected across capuchin species and populations on positional behavior, locomotor and postural behavior, and how these intersect with feeding and foraging, and the use of habitat (climbing and clinging behaviors). We want to understand how the diets of capuchins affect what they do, and vice versa. We want to understand the energetic burden, and genetic causes and consequences of morphology: how capuchins eat what they eat, especially in terms of their use of hands, mouths, and tools.

Vocalizations. Vocal variation seems great between *Sapajus* and *Cebus*, but we do not yet know how conservative the vocal repertoire may be within each genus, which kinds of calls evolve more rapidly, and which are highly conserved. Comparative studies may allow us to determine which calls, if any, vary more by habitat type than by species, or vice versa, and which are more conserved across both species and habitats.

Behavioral ecology. There is ample opportunity to study how habitat type and resource abundance and dispersion in time and space affect behavior and social organization. Figure 2 shows the locations of field sites (as in Fig. 1) superimposed on the habitat types across the range of capuchin monkeys. Note the relative paucity of studies in the Amazon and around the northern and western Andes.

Biogeography and paleoecology. This research is needed to identify the precipitating events that led to the divergence between *Cebus* and *Sapajus*, and the subsequent modern diversification and radiation of each genus. These data will enhance our understanding of capuchin evolution and selection pressures.

Genetics. We point to some key areas where more genetic research is needed for capuchin populations:

1. As far as we know, there is no reproductive isolation among *Sapajus* species (or subspecies), and hybridization occurs both in captivity and at points of contact in the wild. There is evidence for hybridization of *S. robustus* $\times$ *S. nigritus*, *S. libidinosus* $\times$ *S. nigritus*, *S. libidinosus* $\times$ *S. flavius* in the wild. In her review of *Sapajus* morphology, Torres [1988; see Rylands et al., 2005] described "core areas" with distinct morphologies and a gradient of variable morphology in the intermediate zones in between the cores. Silva [2001], in general, agreed with this distribution of phenotypes. As of yet, there has been almost no genetic investigation of the degree of introgression/hybridization/reticulation among *Sapajus* species in the wild. Understanding population genetics in these core and intermediate zones would provide a much better picture of gene flow and genetic barriers in wild *Sapajus*.
2. We suggest that field studies include a collection of genetic samples in their protocol (non-invasive collection of fecal samples and minimally invasive collection of hair samples are two options, with protocols available). Establishing laboratories in each habitat country where samples could be sent and sequenced would be a great way to improve understanding of capuchin genetic diversity on a finer scale. To facilitate international collaboration, it would be helpful to establish a clear protocol in each habitat country for how to obtain collection permits to collect biological samples and export permits to take samples out of the country for genetic sequencing.
3. As mentioned in the section on captive studies, a priority is to determine the species or hybrid mix in captive populations.
4. Understanding the distribution of genetic diversity within and across capuchin species will allow for the phylogenetic and population-based analyses for variation in behaviors and morphology. Genetic diversity or difference of neutral markers (i.e., mtDNA, microsatellites) can be used as a proxy for divergence time across populations and allow for inferences about ancestral states. The sequencing of functional genes across individuals within populations has already been useful for looking at color vision variation in white-faced capuchins [Hiwatashi et al., 2010; Melin et al., 2009, 2010], and is an open area for future study.
5. Population genetics will offer new evidence to understand capuchin kinship and sex-biased dispersal. Microsatellites have already been used to test behaviorally based hypotheses about capuchin social organization, such as kinship and paternity, for some species at long-term field

sites [Escobar-Paramo, 2000; Jack & Fedigan, 2006; Muniz et al., 2006, 2010; Perry et al., 2008; Tokuda et al., 2011; Valderrama et al., 2000].

Conservation Challenges and Community Outreach Projects

Nine capuchin taxa have been listed on the IUCN Red List of Threatened Species as Critically Endangered (*Cebus aequatorialis*, *C. albifrons trinitatis*, *C. kaapori*, *S. apella margaritae*, *S. flavius*, *S. xanthosternos*) or Endangered (*Cebus malitiosus*, *C. versicolor*, *Sapajus robustus*). All known capuchin populations are hunted and face habitat loss due to deforestation (Andes, Amazonian, and Atlantic Forest) or desertification (Cerrado and Caatinga areas).

The Amazon is rapidly being fragmented and destroyed on numerous fronts. In Brazil, the arc of deforestation, moving north from the south–east has already destroyed immense areas of forests in Maranhão, eastern Pará, and northern Mato Grosso, and colonization and clear-cutting for agriculture, subsistence and industrial plantations, with massive human expansion is decimating Acre, Rondônia and Mato Grosso. In Peru, the Department of Amazonas is being encroached heavily by humans for agriculture and pastureland. This destruction and fragmentation may, ironically, facilitate primate research in the Amazon, by opening up the forest to human access, but the larger primates along the main tributaries are fast becoming scarce. At the same time, we are losing species and populations without even knowing what was there. As stated above, for some *Cebus* populations, competition with *Sapajus* may interact with anthropogenic changes to increase extinction risk [Lynch Alfaro et al., 2012c].

Fragmentation, encroachment by human settlements and partial destruction of habitat due to logging by local human populations are increasing threats to local populations of *Sapajus* in the Cerrado, Caatinga, and Atlantic Forest. These processes have led to declines in population size, shifting habitat use, and increased overlap in distribution areas between previously allopatric species, such as *S. apella* and *S. libidinosus* at the Amazonian and Caatinga ecotone area in Maranhão, Brazil [Santos, 2010]; *S. libidinosus* and *S. xanthosternos* in the southern Caatinga, Bahia, Brazil [Canale et al., 2009]; and possible hybridization, such as for *S. libidinosus* and *S. flavius* in the northeastern Caatinga, Brazil [Ferreira et al., 2009].

Habitat loss forces capuchin monkeys to occupy marginal environments such as mangrove areas [Santos, 2010] and to raid agricultural crops [Freitas et al., 2008]. Monkey–human conflicts are increasing, with resultant behavioral and dietary changes in the monkeys in proximity to human settlements that can ultimately lead to the extirpation of many local monkey populations [Freitas et al., 2008]. Assessments of the current state of such populations are crucial for defining priorities for conservation. Currently, many of the animals captured from areas with monkey–human conflict are placed in government animal care agencies or released in areas outside their natural distribution [Levacov et al., 2011].

Most short- and long-term field studies are on capuchin monkeys that occupy habitat fragments. Habitat fragmentation leads to genetic isolation between populations of the same species. In northeastern Brazil, for example, forest patches of Atlantic Forest unoccupied by monkeys can be as close as 200 m to areas occupied by capuchin groups, and the reasons why animals do not cross over industrial plantations of sugarcane are unknown [R. Ferreira, personal observation; Oliveira & de Langguth, 2006]. To compound the problem, many of these fragments are privately owned, so these groups are subject to the owners' decisions about which human activities are allowed within each fragment. The genetic diversity of fragment-dwelling capuchins is probably reduced. Health status and pathogen load of groups living in fragments must also be better assessed. Primates living in fragments may present decreased health conditions due to restricted dietary variability and possible increases in endo- and ecto-parasite loads due to increased contact with domestic animals. Besides the possible influence of these factors on socio-behavioral patterns of animals, the population dynamics in fragments may facilitate the spread of diseases between animals. Moreover, capuchins may host parasites transmitted to humans such as *Leishmania* spp., *Trypanosoma cruzi*, and *Toxoplasma gondii* [Montenegro, 2011]. Evaluation of the status of capuchin populations living in fragments is thus an important public health issue.

With the current state of habitat loss and modification in mind, our discussion group agreed that community outreach work is vital for the conservation of *Sapajus* and *Cebus*.

Some of the suggestions were as follows.

Community outreach projects

We need to document and exchange examples of successes and failures in community outreach attempts. What do people think about capuchins in a local area? What are the costs actually caused by capuchins in those conflict areas? Are there attitudes that need to be changed or encouraged? What conservation methods work? How can we best access and pass information to locals and maintain good relationships with local people? Even in habitat countries in localities surrounded by capuchin populations, it can be surprising the number of people that have never seen a monkey or know nothing about their behavior [Varela, 2013]. Educational programs on possible disease transmission between humans and capuchin monkeys are needed in both rural and urban areas. In particular, we hope to diminish the traditional habit of keeping capuchins as pets.

Scientific and educational vehicles

These are necessary to broadcast results of small scale/short-term projects—a high priority for conservation work, for these are rich resources to encourage conservation-minded attitudes in local human communities near capuchin monkeys. The development of an open-access website for capuchin monkey data (photos, location of field sites, information about research at sites/captive research, publications, standardized protocols for data collection) was another suggestion from the group.

Training local students and local guides

We need to engage more students in fieldwork with capuchins. Some suggestions are to include local undergraduates in rapid assessments, to advertise for international volunteers for field research, and to resist the urge to put all students at long-term field sites: the distribution of capuchin monkey research is highly skewed to a few locations, mostly in the more temperate forests at the edge of capuchin's distribution, although this is beginning to change (see Figs. 1 and 2). Researchers with large teams of students might mobilize some of these students into new sites and new studies. Establishing new field sites can be a very difficult enterprise, and the employment of local people as field assistants is often essential, especially for habituating new monkey groups.

Involvement of landowners

Much of the land in habitat countries where capuchins are found is privately owned. We must develop strategies to work with private owners to come up with local solutions for how to best preserve habitat and instill respect for capuchins. This can mean we need to learn public relations skills, including how to sell the idea to individuals or companies. One opportunity is to convey to landowners the capuchins' unique and diverse cognitive abilities that make them a natural flagship group for promoting conservation of wild animals in general.

Political actions

Researchers can face risky situations in areas where illegal activities such as hunting, drug trafficking, and/or tree felling and logging occur. Another challenge to the development of our goals is the government bureaucracy that may impose difficulties and delays, for example, the laws against export of biological/genetic material. Capuchin monkeys are frequently considered low priority in conservation programs because they are seen as abundant, even perceived as pests [Rocha, 2004]. We need to put a concentrated effort towards making governments and granting agencies understand the unique qualities of capuchin monkeys and why they need to be saved and studied on a broad scale. Their unique behaviors can be leveraged to make them into flagship species, charismatic representatives of whole ecosystems in conservation efforts. With encouragement and education, governments in habitat countries might come to recognize and promote capuchins as a national treasure.

Capuchin Action Network

In the previous sections, we tried to show that future research on capuchin monkeys is urgently needed for conservation planning, it requires expertise from diverse areas of knowledge, and it is embedded in political questions regarding the sustained development of human-dominated landscapes throughout Latin America. We also hope we have shown that although each researcher may collect data on any of these questions, a broad understanding of capuchin evolutionary biology can only be achieved by producing comparable data collected by many research groups throughout their range.

At the roundtable we planned the formation of an international CAN. Our position is that the production of knowledge can be enhanced by collaborative enterprise and our political voice is strengthened by uniting. CAN will be composed of researchers and students of all levels interested in understanding capuchin monkeys and promoting their conservation. In particular, we hope that the organization of a capuchin research community with open-access to protocols and published data can encourage and support students in habitat countries in the advancement of their research and conservation efforts. During the joint XV Brazilian and II Latin American Primatology Meetings in Recife, Brazil, in August 2013, we held a workshop session led by Patrícia Izar, Jessica Lynch Alfaro, Renata Ferreira, José de Sousa e Silva Junior, and Anthony B. Rylands to discuss the formation of CAN. A total of 75 participants attended the session, including researchers from Brazil, Argentina, Colombia, Peru, Venezuela, England, Italy, and the United States. We agreed that the overarching goal of CAN is the protection of capuchin monkeys in their natural environments. Initial steps for the formation of the group are to set up a website for CAN and to establish common protocols for the collection of various data types. We hope that CAN will serve not only to improve collaborative efforts at capuchin monkey research and conservation but also as a model for coordinated research on other taxa in Latin America and beyond.

ACKNOWLEDGMENTS

Thanks to all the participants of the Roundtable at the XXIV Congress of the International Primatological

Society, Cancún, Mexico and the Workshop in the 2013 joint XV Brazilian and II Latin American Primatology Meetings, Recife, Brazil. Dorothy M. Fragaszy, Antônio Moura, Luke J. Matthews, Paul Garber, Linda Fedigan, and Anthony B. Rylands contributed useful comments that improved the manuscript. Thanks to the UCLA Institute for Society and Genetics fellows and faculty members for reading and commenting on a draft of this article. Inez Lynch Alfaro helped with map data entry. The authors thank their funding agencies, including National Science Foundation BCS 0833375 (J.W.L.A.); FAPESP and CNPq (P.I.); and CNPq and FAPERN (R.G.F.). Research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. A special thanks to the late Liza M. Veiga for inspiration from her Pitheciine Action Group and her unflagging dedication to capuchin monkeys and other neotropical primates.

REFERENCES

Addessi E, Paglieri F, Beran MJ, et al. 2013. Delay choice versus delay maintenance: different measures of delayed gratification in capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology 127:392–398.

Amaral PJS, Finotelo LFM, de Oliveira EHC, et al. 2008. Phylogenetic studies of the genus *Cebus* (Cebidae-Primates) using chromosome painting and G-banding. BMC Evolutionary Biology 8:169–178.

Back JP, Suzin A, Aguiar LM. 2013. Comportamento social de macacos-prego (*Sapajus* sp.) em um fragmento urbano em Foz do Iguaçu, Alto Rio Paraná. Poster presentation, II Congresso Latino. Americano XV Congresso Brasileiro de Primatologia, Recife, Brazil.

Baldwin JD, Baldwin JI. 1997. Observations on *Cebus capucinus* in southwestern Panama. Primates 18:937–941.

Boinski S. 1988. Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). American Journal of Primatology 14:177–179.

Boinski S, Quatron RP, Swartz H. 2000. Substrate and tool use by brown capuchins in Suriname: ecological contexts and cognitive bases. American Anthropologist 102:741–761.

Boubli JP, Rylands AB, Farias I, Alfaro ME, Lynch Alfaro JW. 2012. *Cebus* phylogenetic relationships: a preliminary reassessment of the diversity of the untufted capuchin monkeys. American Journal of Primatology 74:381–393.

Brito AB, Santos RR, van den Hurk R, et al. 2013. Short-term culture of ovarian cortical strips from capuchin monkeys (*Sapajus apella*): a morphological, viability and molecular study of preantral follicular development in vitro. Reproductive Sciences 20:990–997.

Campos FA, Jack KM. 2013. A potential distribution model and conservation plan for the critically endangered Ecuadorian capuchin, *Cebus albifrons aequatorialis*. International Journal of Primatology. doi: 10.1007/s10764-013-9704-x

Canale GR, Guidorizzi CE, Kierulff MCM, Gatto CAFR. 2009. First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). American Journal of Primatology 71:366–372. doi: 10.1002/ajp.20648

Canavez FC, Ladasky JJ, Muniz JAPC, Seuánez HN, Parham P. 1998. ß2-Microglobulin in neotropical primates (Platyrrhini). Immunogenetics 48:133–140.

Caro T, Sherman PW. 2011. Endangered species and threatened discipline: behavioural ecology. Trends in Ecology and Evolution 26:111–118.

Cazzadore KC. 2007. Estudo do Comportamento Alimentar e de Forrageio de um Grupo de Macacos-prego (*Cebus apella*) no Parque Estadual Matas do Segredo, Campo Grande, MS [Master's thesis]. Universidade Católica Dom Bosco, Campo Grande, Brazil.

Clutton-Brock TH, Sheldon BC. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology and Evolution 25:562–573.

Defler TR. 1979a. On the ecology and behavior of *Cebus albifrons* in eastern Colombia: I. Ecology. Primates 20:475–490.

Defler TR. 1979b. On the ecology and behavior of *Cebus albifrons* in eastern Colombia: II. Behavior. Primates 20:491–502.

Defler TR. 1982. A comparison of intergroup behavior in *Cebus albifrons* and *Cebus apella*. Primates 23:383–392.

Defler TR. 1985. Contiguous distribution of two species of *Cebus* monkeys in El Tuparro National Park, Colombia. American Journal of Primatology 8:101–112.

Defler TR. 2012. Studying primates in eastern Colombia: thirty-five years of a primatological life. Revista de la Academia Colombiana de Ciencias 36:421–434.

Emidio RA, Ferreira RG. 2012. Tool use by capuchin monkeys in the Brazilian Caatinga: variation in energy gain by season and by habitat type. American Journal of Primatology 74:332–343.

Escobar-Paramo P. 2000. Inbreeding avoidance and the evolution of male mating strategies [dissertation]. State University of New York, Stony Brook, NY.

Falotico T, Ottoni E. 2014. Stone throwing as a sexual display in wild female bearded capuchin monkeys, *Sapajus libidinosus*. PLoS ONE 8:e79535.

Fedigan LM, Jack KM. 2004. The demographic and reproductive context of male replacements in *Cebus capucinus*. Behaviour 141:755–775.

Fedigan LM, Jack KM. 2012. Tracking monkeys in Santa Rosa: Lessons from a regenerating Costa Rican dry forest. In: Kappeler P, Watts D, editors. Long-term field studies of primates. Springer Press. p 165–184.

Fedigan LM, Rosenberger AL, Boinski S, Norconk MA, Garber PA. 1996. Critical issues in cebine evolution and behavior. In: Norconk MA, Rosenberger AL, Garber PA, editors. Adaptive radiations of neotropical primates. New York: Plenum Press. p 219–228.

Ferreira RG, Jerusalinsky L, Silva TCF, et al. 2009. On the occurrence of *Cebus flavius* (Schreber, 1774) in the Caatinga, and the use of semi-arid environments by *Cebus* species in the Brazilian state of Rio Grande do Norte. Primates 50:357–362.

Fragaszy DM, Visalberghi E, Fedigan L. 2004a. The complete capuchin: the biology of the genus *Cebus*. Cambridge: Cambridge University Press.

Fragaszy D, Izar P, Visalberghi E, Ottoni EB, de Oliveira MG. 2004b. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. American Journal of Primatology 64:359–366.

Fragaszy DM, Liu Q, Wright B, et al. 2013. Wild bearded capuchin monkeys (*Sapajus libidinosus*) strategically place nuts in a stable position during nut-cracking. PLoS ONE 8: e56182.

Freitas CH, Setz EZF, Gobbi N, Araujo ARB. 2008. Agricultural crops in the diet of bearded capuchin monkeys, *Cebus libidinosus* Spix (Primates: Cebidae), in forest fragments in southeast Brazil. Revista Brasileira de Zoologia 25:32–39.

Garber PA, Brown E. 2006. Use of landmark cues to locate feeding sites in wild capuchin monkeys (*Cebus capucinus*): an experimental field study. In: Estrada A, Garber PA, Pavelka MSM, Luecke L, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. New York: Springer. p 311–332.

Goulart K, Roney P, Bonci O, et al. 2013. Color discrimination in the tufted capuchin monkey, *Sapajus* spp. PLoS ONE 8: e62255.
Groves CP. 2001. Primate taxonomy. Washington, DC: Smithsonian Institution Press.
Gunst N, Boinski S, Fragaszy DM. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artifacts as an indirect social influence. Behaviour 145:195–229.
Gunst N, Boinski S, Fragaszy DM. 2010. Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (*Cebus apella apella*). Journal of Comparative Psychology 124:194–204.
Haugaasen T, Peres CA. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. American Journal of Primatology 67:243–258.
Hershkovitz P. 1949. Mammals of northern Colombia. Preliminary report no. 4: monkeys (primates), with taxonomic revisions of some forms. Proceedings of the U.S. National Museum 98:323–427.
Hershkovitz P. 1955. Notes on the American monkeys of the genus *Cebus*. Journal of Mammalogy 36:449–452.
Hiwatashi T, Okabe Y, Tsutsui T, et al. 2010. An explicit signature of balancing selection for color vision variation in New World monkeys. Molecular Biology and Evolution 27:453–464.
Izar P, Nakai ES. 2006. Fission-fusion in tufted capuchin monkeys (*Cebus apella nigritus*) in Brazilian Atlantic Forest. International Journal of Primatology 27:226.
Izar P, Stone A, Carnegie SD, Nakai ES. 2009. Sexual selection, female choice and mating systems. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB, editors. South American primates: testing new theories in the study of primate behavior, ecology, and conservation. New York: Springer. p 157–189.
Izar P, Verderane MP, Peternelli-dos-Santos L, et al. 2012. Flexible and conservative features of social systems in tufted capuchin monkeys: comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. American Journal of Primatology 74:315–331.
Izawa K. 1979. Foods and feeding behavior of wild black-capped capuchin (*Cebus apella*). Primates 20:57–76.
Izawa K. 1980. Social behavior of the wild black-capped capuchin (*Cebus apella*). Primates 21:443–467.
Izawa K. 1999. Social changes within a group of wild black-capped capuchins, VI. Field Studies of Fauna and Flora, La Macarena, Colombia 13:1–6.
Jack KM, Campos FA. 2012. Distribution, abundance, and spatial ecology of the critically endangered Ecuadorian capuchin (*Cebus albifrons aequatorialis*). Tropical Conservation Science 5:173–191.
Jack KM, Fedigan LM. 2006. Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In: Estrada A, Garber PA, Pavelka MSM, Luecke L, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. New York: Springer. p 367–386.
Jack K, Fedigan LM. 2009. Explaining female dispersal in a female philopatric species, *Cebus capucinus*. Behaviour 146:471–497.
Janson CH. 1984. Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift fuer Tierpsychologie 65:177–200.
Janson CH. 1985. Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18:125–138.
Janson CH. 1986a. Capuchin counterpoint. Natural History 95:44–53.
Janson CH. 1986b. The mating system as a determinant of social evolution in capuchin monkeys (Cebus). In: Else JG, Lee PC, editors. Primate ecology and conservation. New York: Cambridge University Press. p 169–179.
Janson CH. 1990a. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:922–934.
Janson CH. 1990b. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:910–921.
Janson CH. 2000. Primate socio-ecology: the end of the golden age. Evolutionary Anthropology 9:73–86.
Janson C, Baldovino MC, Di Bitetti M. 2011. The group life cycle and demography of brown capuchin monkeys (*Cebus apella nigritus*) in Iguazú National Park, Argentina. In: Kappeler P, Watts D, editors. Long-term field studies of primates. Berlin: Springer-Verlag. p 185–212.
Kappeler PM, van Schaik CP, Watts DP. 2012. The values and challenges of long-term field studies. In: Kappeler PM, Watts DP, editors. Long-term field studies of primates. Berlin: Springer-Verlag. p 3–8.
Kierulff MCM, Canale GR, Suscke P. 2005. Monitoring the yellow-breasted capuchin monkey (*Cebus xanthosternos*) with radiotelemetry: choosing the best radio-collar. Neotropical Primates 13:32–33.
Leca JB, Gunst N, Petit O. 2007. Social aspects of fur-rubbing in *Cebus capucinus* and *C. apella*. International Journal of Primatology 28:801–817.
Lernould JM, Kierulff MCM, Canale G. 2012. Yellow-breasted capuchin *Cebus xanthosternos*: support by zoos for its conservation—a success story. International Zoo Yearbook 46:71–79.
Levacov D, Jerusalinsky L, Fialho M de S. 2011. Levantamento dos primatas recebidos em Centros de Triagem e sua relação com o tráfico de animais silvestres no Brasil. In: Melo FR, de Mourthé Í, editors. A Primatologia no Brasil – 11. Belo Horizonte, Brazil: Sociedade Brasileira de Primatologia. p 281–305.
Littlefield K. 2009. Husbandry guidelines for white fronted capuchin Monkey. *Cebus albifrons* Mammalia: Primates: Cebidae. Richmond, Western Sydney: Institute of TAFE. Available online at: http://nswfmpa.org/Husbandry%20Manuals/Published%20Manuals/Mammalia/White%20Fronted%20Capuchin.pdf [accessed 7 March 2014]
Lynch Alfaro JW. 2007. Subgrouping patterns in a group of wild *Cebus apella nigritus*. International Journal of Primatology 28:271–289.
Lynch Alfaro JW, Boubli JP, Olson LE, et al. 2012a. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. Journal of Biogeography 39:272–288.
Lynch Alfaro JW, Matthews L, Boyette AH, et al. 2012b. Anointing variation across wild capuchin populations: a review of material preferences, bout frequency and anointing sociality in *Cebus* and *Sapajus*. American Journal of Primatology 74:299–314.
Lynch Alfaro JW, Silva JS Jr, Rylands AB. 2012c. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. American Journal of Primatology 74:273–286.
Mannu M, Ottoni EB. 2008. The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools. American Journal of Primatology 70:1–10.
Manson JH, Perry S, Parish AR. 1997. Nonconceptive sexual behavior in bonobos and capuchins. International Journal of Primatology 18:767–786.
Manson JH, Rose LM, Perry S, Gros-Louis J. 1999. Dynamics of female–female relationships in wild *Cebus capucinus*: data from two Costa Rican sites. International Journal of Primatology 20:679–706.
Martins WP. 2010. Densidade Populacional e Ecologia de um Grupo Macaco-Prego-de-Crista (*Cebus robustus*; Kuhl, 1820)

na Reserva Natural Vale [dissertation]. Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.
Matthews LJ. 2009. Activity patterns, home range size, and intergroup encounters in *Cebus albifrons* support existing models of capuchin socioecology. International Journal of Primatology 30:709–728.
Matthews LJ. 2012. Variations in sexual behavior among capuchin monkeys function for conspecific mate recognition: a phylogenetic analysis and a new hypothesis for female proceptivity in tufted capuchins. American Journal of Primatology 74:287–298.
Melin AD, Fedigan LM, Hiramatsu C, et al. 2009. Fig foraging by dichromatic and trichromatic *Cebus capucinus* in a tropical dry forest. International Journal of Primatology 30:753–775.
Melin AD, Fedigan LM, Young HC, Kawamura S. 2010. Can color vision variation explain sex differences in invertebrate foraging by capuchin monkeys? Current Zoology 56:300–312.
Miller LE. 1998. Dietary choices in *Cebus olivaceus*: a comparison of data from Hato Piñero and Hato Masaguaral, Venezuela. Primate Conservation 18:42–50.
Montenegro MMV. 2011. Ecologia de *Cebus flavius* (Schreber, 1774) em remanescentes de Mata Atlântica no estado da Paraíba [dissertation]. Universidade de São Paulo, São Paulo, Brazil.
Morton FB, Lee PC, Buchanan-Smith HM. 2013. Taking personality selection bias seriously in animal cognition research: a case study in capuchin monkeys (*Sapajus apella*). Animal Cognition 16:677–684.
Moura AC. 2007. Stone banging by wild capuchin monkeys: an unusual auditory display. Folia Primatologica 78:36–45.
Moura ACA, Lee PC. 2004. Capuchin stone tool use in Caatinga dry forest. Science 306:1909.
Muniz L, Perry S, Manson J, et al. 2006. Father-daughter inbreeding avoidance in a wild primate population. Current Biology 16:156–157.
Muniz L, Perry S, Manson JH, et al. 2010. Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. American Journal of Primatology 72:1118–1130.
Nakai ES. 2007. Fissão-fusão em *Cebus apella nigritus*: flexibilidade social como estratégia de ocupação de ambientes limitantes [Masters thesis]. Universidade de São Paulo, São Paulo, Brazil.
Nieves M, de Oliveira EHC, Amaral PJS, et al. 2011. Analysis of the heterochromatin of *Cebus* (Primates, Platyrrhini) by micro-FISH and banding pattern comparisons. Journal of Genetics 90:111–117.
Oliveira MM, de Langguth A. 2006. Rediscovery of Marcgrave's capuchin monkey and designation of a neotype for *Símia Flavia* Schreber, 1774 (Primates, Cebidae). Boletim do Museu Nacional, nova série, Rio de Janeiro 523:1–16.
Oliveira SG, Lynch Alfaro JW, Veiga LM. 2014. Activity budget, diet and habitat use in the critically endangered Ka'apor capuchin monkey (*Cebus kaapori*) in Pará State, Brazil: a preliminary comparison to other capuchin monkeys. American Journal of Primatology (this issue).
Opazo JC, Wildman DE, Prychitko T, Johnson RM, Goodman M. 2006. Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). Molecular Phylogenetics and Evolution 40:274–280.
Oppenheimer JR. 1969. Behavior and Ecology of the White-faced Monkey, *Cebus capucinus*, on Barro Colorado Island, C.Z. [dissertation]. Dissertation Abstracts I 442–443.
Ottoni EB, Izar P. 2008. Capuchin monkey tool use: overview and implication. Evolutionary Anthropology 17:171–178.
Ottoni EB, Mannu M. 2001. Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. International Journal of Primatology 22:347–358.
Perelman P, Johnson WE, Roos C, et al. 2011. A molecular phylogeny of living primates. PLoS Genetics 7:1–17.
Perry S. 2011. Social traditions and social learning in capuchin monkeys (*Cebus*). Philosophical Transactions of the Royal Society of London B Biological Sciences 366:988–996.
Perry S, Baker M, Fedigan L, et al. 2003. Social conventions in wild white-faced capuchin monkeys—evidence for traditions in a neotropical primate. Current Anthropology 44:241–268.
Perry S, Manson JH, Muniz L, Gros-Louis J, Vigilant L. 2008. Kin-biased social behaviour in wild adult female white-faced capuchins (*Cebus capucinus*). Animal Behaviour 76:187–199.
Perry S, Godoy I, Lammers W. 2012. The Lomas Barbudal Monkey Project: two decades of research on *Cebus capucinus*. Kappeler PM, Watts DP, editors. Long-term field studies of primates. Berlin: Springer-Verlag. p 141–163.
Phillips KA. 1998. Tool use in wild capuchin monkeys (*Cebus albifrons trinitatis*). American Journal of Primatology 46:259–261.
Phillips KA, Thompson CR. 2013. Hand preference for tool-use in capuchin monkeys (*Cebus apella*) is associated with asymmetry of the primary motor cortex. American Journal of Primatology 75:435–440.
Pinto MCM. 2006. Padrão Comportamental de um Grupo de Macacos-prego (*Cebus apella cay* Illiger, 1815) no Parque Estadual Matas do Segredo, Campo Grande, MS [master's thesis]. Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil.
Queiroz HL. 1992. A new species of capuchin monkey, genus *Cebus* Erxleben, 1777 (Cebidae: Primates) from eastern Brazilian Amazonia. Goeldiana Zoologia 15:1–13.
Resende BDD, Mannu M, Izar P, Ottoni EB. 2004. Interaction between capuchins and coatis: nonagonistic behaviors and lack of predation. International Journal of Primatology 25:1213–1224.
Rímoli J, Geacopello L, Corsino O, Rímoli AO. 2002. Padrão geral de atividades de um grupo de macacos-pregos-paraguaios (*Cebus libidinosus paraguayanus*, Fischer, 1829) em um fragmento florestal em Mato Grosso do Sul: uma análise preliminar. Livro de Resumos do X Congresso Brasileiro de Primatologia. Belém, Pará: Sociedade Brasileira de Primatologia, CNPq. p 75.
Rímoli J, Vieira TBDC, Corrêa Neto UJ, Rímoli AO. 2005. Macacos-pregos-amarelos (*Cebus apella cay*, Illiger, 1815, Primates, Cebinae): uma análise sazonal e longitudinal do comportamento em um fragmento de floresta de Galeria em Terenos, Mato Grosso do Sul. Livro de Resumos do XI Congresso Brasileiro de Primatologia. Porto Alegre: Sociedade Brasileira de Primatologia. p. 159.
Rímoli J, Fernandes O Jr, Odalia-Rímoli A. 2009. Comportamento de macacos-pregos-amarelos (*Cebus cay*, Illiger, 1815, Primates, Cebidae) em um fragmento de Floresta de Galeria em Campo Grande, Mato Grosso do Sul. Livro de Resumos do XXVII Encontro Anual de Etologia & 1° Simpósio Latino-Americano de Etologia. São Paulo, Brazil: Editora da Sociedade Brasileira de Etologia, v. I.
Rimpley K, Buchanan-Smith HM. 2013. Reliably signaling a startling husbandry event improves welfare of zoo-housed capuchins (*Sapajus apella*). Applied Animal Behaviour Science 147:990–997.
Robinson JG. 1986. Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory. Smithsonian Contributions to Zoology 431:1–60.
Robinson JG. 1988. Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus*. Behaviour 104:202–232.
Rocha VJ. 2004. Macaco-Prego, como controlar esta nova praga florestal? Florest 30:95–99.
Rose L, Perry S, Panger M, et al. 2003. Interspecific interactions between *Cebus capucinus* and other species: data from three Costa Rican sites. International Journal of Primatology 24:759–796.

Rosenberger AL. 2012. New World monkey nightmares: science, art, use, and abuse (?) in platyrrhine taxonomic nomenclature. American Journal of Primatology 74:692–695.
Ruiz-García M, Castillo MI, Vásquez C, et al. 2010. Molecular phylogenetics and phylogeography of the white-fronted capuchin (*Cebus albifrons*; Cebidae, Primates) by means of mtCOII gene sequences. Molecular Phylogenetics and Evolution 57:1049–1061.
Ruiz-García M, Castillo MI, Ledezma A, et al. 2012a. Molecular systematics and phylogeography of *Cebus capucinus* (Cebidae, Primates) in Colombia and Costa Rica by means of the mitochondrial COII gene. American Journal of Primatology 74:366–380.
Ruiz-García M, Castillo MI, Lichilín-Ortiz N, Pinedo-Castro M. 2012b. Molecular relationships and classification of several tufted capuchin lineages (*Cebus apella*, *Cebus xanthosternos* and *Cebus nigritus*, Cebidae), by means of mitochondrial cytochrome oxidase II gene sequences. Folia Primatologica 83:100–125.
Rylands AB, Mittermeier RA. 2013. Family Cebidae (capuchins and squirrel monkeys). In: Mittermeier RA, Rylands AB, Wilson DE, editors. Handbook of the mammals of the world. Volume 3. Primates, Barcelona: Lynx Edicions. p 348–389.
Rylands AB, Kierulff MCM, Mittermeier RA. 2005. Some notes on the taxonomy and distributions of the tufted capuchin monkeys (*Cebus*, Cebidae) of South America. Lundiana 6:97–110.
Rylands AB, Mittermeier RA, Bezerra BM, Paim FP, Queiroz HL. 2013. Species accounts of Cebidae. In: Mittermeier RA, Rylands AB, Wilson DE, editors. Handbook of the mammals of the world. Volume 3. Primates. Barcelona: Lynx Edicions. p 390–413.
Sampaio DT, Ferrari SF. 2005. Predation of an infant titi monkey (*Callicebus moloch*) by a tufted capuchin (*Cebus apella*). Folia Primatologica 76:113–115.
Santos RR. 2010. Uso de Ferramentas por Macacos-Prego em Manguezais [dissertation]. Universidade Federal do Rio Grande do Norte, Natal, Brazil.
Scarry C. 2013. Between-group contest competition among tufted capuchin monkeys, *Sapajus nigritus*, and the role of male resource defence. Animal Behaviour 85: 931–939.
Schneider H, Sampaio MIC, Harada ML, et al. 1996. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP intron 1 and e-globin sequences. American Journal of Physical Anthropology 100:153–179.
Schneider H, Canavez FC, Sampaio I, et al. 2001. Can molecular data place each neotropical monkey in its own branch? Chromosoma 109:515–523.
Schneider H, Sampaio I. 2013. The systematics and evolution of New World primates – A review. Mol. Phylogenet. Evol. Available online at: http://dx.doi.org/10.1016/j.ympev.2013.10.017
Silva JS Jr. 2001. Especiação nos Macacos-prego e Caiararas, Gênero *Cebus* Erxleben, 1777 (Primates, Cebidae) [dissertation]. Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
Spironello WR. 1991. Importância dos frutos de palmeiras (Palmae) na dieta de um grupo de *Cebus apella* (Cebidae, Primates) na Amazonia Central. In: Rylands A, Bernardes AT, editors. A Primatologia no Brasil 3. Belo Horizonte, Brazil: Sociedade Brasileira de Primatologia. p 285–296.
Spironello WR. 2001. The brown capuchin monkey (*Cebus apella*): ecology and home range requirements in Central Amazônia. Bierregaard RO Jr, Gascon C, Lovejoy TE, Mesquita R, editors. Lessons from Amazônia: the ecology and conservation of a fragmented forest. New Haven: Yale University Press. p 271–283.
Terborgh J. 1983. Five new world primates: a study in comparative ecology. Princeton, NJ: Princeton University Press.
Tokuda M, Izar P, Martins MM, Galetti PM Jr. 2011. Dispersão de Machos e Fêmeas de *Sapajus nigritus*, Evidenciada por Análises Genéticas. Livro resumos do XIV Congresso Brasileiro de Primatologia, p 139.
Torres C. 1988. Resultados preliminares de reavaliação das raças do macaco-prego *Cebus apella* (Primates: Cebidae). Revista Nordestina de Biologia 6:15–28.
Valderrama X, Robinson JG, Melnick DJ. 2000. Females control male reproductive success in wedge-capped capuchins, based on genetic and behavioral data. American Journal of Physical Anthropology 30:308.
Varela L. 2013. Percepção de Conflitos e Conhecimento Local sobre o Macaco-prego (*Sapajus* spp.) em Áreas de Pecuária e Agricultura na Caatinga do Rio Grande do Norte [thesis]. Universidade Federal do Rio Grande do Norte, Natal, Brazil.
Wheeler B, Tiddi B, Kalbitzer U, et al. 2013. Methodological considerations in the analysis of fecal glucocorticoid metabolites in tufted capuchins (*Cebus apella*). International Journal of Primatology 34:879–898.
Wilson V, Lefevre CE, Morton FB, et al. 2014. Personality and facial morphology: links to assertiveness and neuroticism in capuchins (*Sapajus [Cebus] apella*). Personality and Individual Differences 58:89–94.
Wright BW, Wright KA, Chalk J, et al. 2009. Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among capuchins and implications for interpreting morphological variation. American Journal of Physical Anthropology 140:687–699.
Wright KA, Wright BW, Ford S, et al. 2012. Morphological diversity among tufted capuchins. American Journal of Physical Anthropology 147:307.
Zhang S-Y. 1995. Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French Guiana. International Journal of Primatology 16:489–507.