American Journal of Primatology 73:1–16 (2011)

RESEARCH ARTICLE

Anointing Variation Across Wild Capuchin Populations: A Review of Material Preferences, Bout Frequency and Anointing Sociality in *Cebus* and *Sapajus*

JESSICA W. LYNCH ALFARO[1]*, LUKE MATTHEWS[2], ADAM H. BOYETTE[3,4], SHANE J. MACFARLAN[3,4], KIMBERLEY A. PHILLIPS[5], TIAGO FALÓTICO[6], EDUARDO OTTONI[6], MICHELE VERDERANE[6], PATRÍCIA IZAR[6], MEREDITH SCHULTE[3], AMANDA MELIN[7], LINDA FEDIGAN[7], CHARLES JANSON[8], AND MICHAEL E. ALFARO[9]
[1]*Center for Society and Genetics, University of California-Los Angeles, Los Angeles, California*
[2]*Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts*
[3]*Department of Anthropology, Washington State University, Pullman, Washington*
[4]*Department of Anthropology, Washington State University, Vancouver, Washington*
[5]*Department of Psychology, Trinity University, San Antonio, Texas*
[6]*Department of Experimental Psychology, Institute of Psychology, University of São Paulo, São Paulo, Brazil*
[7]*Department of Anthropology, University of Calgary, Calgary, Canada*
[8]*Division of Biological Sciences, University of Montana, Missoula, Montana*
[9]*Department of Ecology and Evolutionary Biology, University of California-Los Angeles, Los Angeles, California*

The frequency of anointing bouts and the materials used for self- and social anointing vary across capuchin species in captivity, but there is little published data on capuchin anointing in the wild. Here we present previously unpublished data on anointing behaviors from capuchin monkey populations at ten different field sites and incorporate these data into a review of the anointing literature for captive and wild capuchins. Using a comparative phylogenetic framework, we test four hypotheses derived primarily from captive literature for variation in anointing between wild untufted capuchins (*Cebus*) and tufted capuchins (*Sapajus*), including that (1) the frequency of anointing is higher in *Cebus*, (2) *Cebus* uses a higher proportion of plant species to insect species for anointing compared with *Sapajus*, (3) anointing material diversity is higher in *Cebus*, and (4) social indices of anointing are higher in *Cebus*. We found that wild *Cebus* anoints more with plant parts, including fruits, whereas wild *Sapajus* anoints more with ants and other arthropods. *Cebus capucinus* in particular uses more plant species per site for anointing compared with other capuchins and may specialize in anointing as an activity independent from foraging, whereas most other capuchin species tend to eat the substances they use for anointing. In agreement with captive studies, we found evidence that wild *Cebus* anoints at a significantly higher frequency than *Sapajus*. However, contrary to the captive literature, we found no difference in the range of sociality for anointing between *Cebus* and *Sapajus* in the wild. We review anointing in the context of other Neotropical primate rubbing behaviors and consider the evidence for anointing as self-medication; as a mechanism for enhanced sociality; and as a behavioral response to chemical stimuli. Am. J. Primatol. 73:1–16, 2011.

Key words: fur rubbing; phylogeny; sociality; self-medication; *Cebus*; *Sapajus*

INTRODUCTION

Anointing behaviors can be solitary or social. Self- or solitary anointing occurs when an individual grasps and wipes a foreign substance, such as leaves, *Citrus* fruits, mud or insects, against its fur, and rubs and scratches its fur with hands or feet [Baker, 1996]. Self-anointing occurs in several taxa within the Platyrrhini [capuchin monkeys: Oppenheimer, 1969; owl monkeys: Zito et al., 2003; lion tamarins: Guidorizzi & Raboy, 2009; titi monkeys and squirrel monkeys: Fragaszy et al., 2004], as well as in other primates [black lemurs: Birkinshaw, 1999; orang-utans: Morrogh-Bernard, 2008]. Social anointing, or the simultaneous topical application of a foreign substance over the body by multiple individuals while in physical contact, has been described in the wild only in capuchin monkeys, including white faced capuchins, *Cebus capucinus* [Baker, 1996, 1997; Buckley, 1983; Oppenheimer, 1969; Panger, 1998; Perry, 1996], weeper capuchins, *C. olivaceus* [Valderrama et al., 2000], and white

Contract grant sponsors: UCLA Center for Society and Genetics; NSF; Contract grant number: 0833375.

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

Received 21 November 2010; revised 12 May 2011; revision accepted 16 May 2011

DOI 10.1002/ajp.20971
Published online in Wiley Online Library (wileyonlinelibrary.com).

fronted capuchins, *C. albifrons* [Field, 2007]. Typically a self-anointing animal is approached by others, who rub against the material held by the bout initiator, retrieve dropped pieces to rub on their bodies, or rub their bodies over and in between those with the material [Baker, 1996]. These behaviors are also called fur rubbing, and they can be extremely energetic or even frenzied, and highly social, with a cluster of several monkeys drooling, writhing and rubbing against one another [Baker, 1999].

Anting is anointing that uses ants as the material rubbed into the fur. Anting is termed passive if an animal sits on an anthill and lets ants crawl all over the body, then crushes and rubs them into the fur [Verderane et al., 2007]. In contrast, an animal exhibiting active anting will pick up and apply ants to certain parts of its fur, rubbing the fur with the ant's secretions of formic acid [Verderane et al., 2007]. Anting has been described in wild *C. capucinus* [Longino, 1984] and semi-free tufted capuchins, *Sapajus* sp. [Falótico et al., 2007; Verderane et al., 2007] (For clarity, throughout the paper, *Sapajus* will refer to tufted or robust capuchins: *Sapajus nigritus, S. libidinosus*, *S. apella. S. paraguayanus, S. xanthosternos*, and *Cebus* will refer to untufted or gracile capuchins: *C. olivaceus, C. albifrons, C. capucinus*, a distinction supported by both morphological [de Sousa e Silva Júnior, 2001] and molecular data [Lynch Alfaro et al., submitted]). Anting has not been described in other primate species, although solitary anting does occur commonly in birds [Revis & Waller, 2004] and some other mammals [Clucas et al., 2008; Xu et al., 1995]. Little is known about anting, or anointing in general, in wild tufted capuchins (*Sapajus*) or in *Cebus* species other than *C. capucinus*.

Captive experimental studies suggest significant differences between the two types of capuchin monkey, *Cebus* and *Sapajus*, in terms of preference for certain anointing materials, frequency of anointing, and the social nature of anointing. Although captive research has shown that both *Cebus* and *Sapajus* respond to millipede secretions with anointing [Weldon et al., 2003], *Cebus* responds more strongly than *Sapajus* to *Citrus* and onions for anointing, with a higher frequency of anointing bouts [Leca et al., 2007]. Furthermore, in Leca et al.'s [2007] captive study comparing sociality of anointing, *Sapajus* individuals were almost always observed to self-anoint without social contact (4% social with onions; 0% social with *Citrus*), but captive *C. capucinus* displayed a significantly higher ratio of social to solitary fur rubbing bouts with both *Citrus* (49% social) and onions (15% social) [Leca et al., 2007]. In other captive studies, *Sapajus* individuals remained solitary or only occasionally formed small social groups for anointing. *Sapajus apella apella* in captivity almost always anointed alone, and the rare social anointing bouts (3 of 260 bouts) involved only two participants each [Quinn, 2004]. A study at four zoos in Argentina also reported that all bouts of anointing observed for *S. paraguayanus* were solitary [Giudice & Pavé, 2007].

Captive studies suggest that *Cebus* is more social and affiliative during anointing, has a broader template for anointing materials, and has a higher frequency of anointing behavior in comparison to *Sapajus* [Leca et al., 2007]. Although anointing seemed to enhance social bonds and increase affiliative social interactions in captive *C. capucinus*, captive tufted capuchins (*Sapajus* sp.) spent more time alone and had more agonistic interactions with one another after anointing compared with a control period [Leca et al., 2007]. Another colony of captive *Sapajus* was also found to spend more time apart, have more aggression, and shorter affiliative acts following anointing with onions in comparison to a control period [Paukner & Suomi, 2008].

In this article, we incorporate previously unpublished data on anointing behaviors from capuchin monkey populations at multiple field sites into a review of the anointing literature for captive and wild capuchins. Using a comparative phylogenetic framework, we test four hypotheses derived primarily from captive literature for variation in anointing between untufted capuchins (*Cebus*) and tufted capuchins (*Sapajus*) in the wild, including that: (1) the frequency of anointing is higher in *Cebus*, (2) *Cebus* uses a higher proportion of plant species to insect species for anointing compared with *Sapajus*, (3) anointing material diversity is higher in *Cebus*, and (4) social indices of anointing are higher in *Cebus*. Finally, we incorporate our findings more broadly into a review of anointing in comparison to other rubbing behaviors observed in Neotropical primates, and consider anointing as self-medication; as a behavioral response to chemical stimuli; as a mechanism for sociality; and as a by product of foraging or an actively sought resource.

New Reports of Anointing Behaviors in the Wild

Here we present new evidence from four *Sapajus* populations in Brazil, four populations of *Cebus albifrons* in Peru, Ecuador and Trinidad, and two populations of *C. capucinus* in Costa Rica, to extend our knowledge of anointing variation across wild capuchin populations. Data were collected post-hoc from field researchers studying capuchin monkeys, through a standardized questionnaire (available upon request), and missing data are a result of incomplete questionnaire responses due to different field methodologies for data collection at different sites. The questionnaire requested information on the frequency of anointing, the materials used for anointing, the social nature and individuals involved in anointing, the use of anointing materials as food, and the association of urine

washing (urinating on the hands and/or feet and rubbing them together [Hunter, 1981]) or urine rubbing (after urine washing, spreading the urine across the body by rubbing the fur on the back, tail, limbs and throat with urine-soaked hands or feet [Hill, 1960]) with anointing behaviors.

TUFTED CAPUCHINS

S. libidinosus: Boa Vista

At Fazenda Boa Vista, Gilbués, Piauí state, Brazil, Verderane collected data on *S. libidinosus* anointing during the course of a larger study on capuchin behavior [Izar et al., submitted]. Verderane reports that anointing at Boa Vista was relatively rare (Table I). She observed six bouts of anointing in the Zangado group, at a frequency of 0.41 bouts per 100 observation hours; and 8 bouts of anointing in the Chicão group, at the frequency of 1.6 bouts per 100 hr of observation (see Table I for combined frequency/100 hr observation). In the Zangado group, all bouts were with Formicidae ants; in the Chicão group, Formicidae ants were also the preferred anointing material (6 of 8 bouts).

Capuchins at Boa Vista frequently combined ant rubbing with urine washing. All sex and age classes anointed, and monkeys occasionally ate ants or ant larvae before, during or after anointing with ants. Ants were usually found in trees, including branches, buriti palm hollows, and ant's nests under tree bark or in the treetops. The capuchins rubbed ants onto themselves, and rubbed their bodies into other individuals and sometimes into the tree trunks. Verderane notes that anointing bouts at Boa Vista were most often solitary (71.5% solitary, see Table II), in strong contrast to her own observations of capuchins at Tietê Ecological Park [Verderane et al., 2007], where the capuchins were highly social when anting. At Boa Vista, most events were active anting, but passive anting also occurred.

S. libidinosus: Serra da Capivara

During a 23-month study in the Caatinga at Serra da Capivara National Park, State of Piauí, Brazil [see Falótico & Ottoni, 2009], Falótico observed 17 bouts of anointing across two social groups (Pedra Furada and Bocão) of *S. libidinosus* (Table I). These included 12 bouts with ants, three with millipedes, and two others with unidentified insects (most likely a cricket or praying mantis; and a hemipteran southern green stink bug). All anting bouts were active, with capuchins discovering ants

TABLE I. Mean Number of Anointing Bouts per 100 hr of Observation for Capuchins

Species	Location	Number of bouts	Contact hours	Mean bouts/ 100 hr
C. capucinus	Curú, Costa Rica [Baker, 1999]	**151**	**1914.5**	**7.9**
C. capucinus	Palo Verde, Costa Rica [Panger, 1998]	**49**	**629**	**7.8**
C. capucinus	**Quepos, Costa Rica [Schulte, this review]**	**7**	**251.5 (focal hours)**	**2.8**
C. capucinus	**Santa Rosa, Costa Rica [Melin, this review]**	**7**	**533 (focal hours)**	**1.3**
C. albifrons	**Bush Bush, Trinidad [Phillips, this review]**	**23**	**336 (focal hours)**	**6.9**
C. albifrons	**Tiputini, Ecuador [Matthews, this review]**	**38**	**800**	**4.8**
C. olivaceus	Masaguaral, Venezuela [Valderrama et al., 2000]	**27**[a]	**~329 observation hours**	**~8.2**
Sapajus nigritus	**Caratinga, Brazil [Lynch Alfaro, this review]**	**3**	**1,114**	**0.3**
Sapajus sp.	São Paulo, Brazil [Verderane et al., 2007]	**27**	**1,550**	**1.7**
Sapajus libidinosus	**Boa Vista, Gilbués, Brazil Zangado & Chicão groups (combined) [Verderane, this review]**	**14**	**1,970**	**0.7**
Sapajus libidinosus	**Serrra da Capivara, Brazil Pedra Furada & Bocão groups (combined) [Falótico, this review]**	**17**	**1,717**	**1.0**
Sapajus libidinosus	Serrra da Capivara, Brazil Jurubeba & Oitenta groups (combined) [Mannu & Ottoni, 2009]	**8**[b]	**701.5**	**1.1**
Sapajus libidinosus	**Brasilia, D.F., Brazil [Salgado Pinha, pers. comm.]**	**0**	**67 (focal hours)**	**0**
Sapajus paraguayanus (captive)	4 zoos in Argentina [Giudice & Pavé, 2007]	**5**	**1,232**	**0.4**

Bold script indicates observations at this site published first here in this review.
[a]28 months total study with 78 fur rubbing bouts observed; rate calculated from 27 bouts in ~329 observation hours from Jan to July 1995 and Feb to July 1998. For data from Valderrama et al. [2002], observation hours estimated from minimum monthly hours plus maximum monthly hours/2 × number of observation months.
[b]8 bouts may underestimate total anointing bouts, as Mannu and Ottoni [2009] reported anointing only in association with tool use.

TABLE II. Comparison Across Wild and Captive Studies of Percentage of Anointing Bouts that Occurred With More Than One Individual in Social Contact, and the Maximum Number of Individuals that were Observed Together in Social Contact During a Single Anointing Bout

Species	Location	% Social	Maximum individuals
Cebus capucinus	Curú, Costa Rica [Baker, 1996]	**54.7%**	**7**
Cebus capucinus	Trujillo, Honduras [Buckley, 1983]	?	**4**
Cebus capucinus	Quepos, Costa Rica [Schulte, this review]	**42.9%**	**5**
Cebus capucinus	**Santa Rosa, Costa Rica [Fedigan & Melin, this review]**	**57.1%**	**4* (up to 10)**
Cebus albifrons	**Bush Bush, Trinidad [Phillips, this review]**	**0%**	**1**
Cebus albifrons	**Tiputini, Ecuador [Matthews, this review]**	?	**8**
Cebus albifrons	**Misahualli, Ecuador [Boyette & McFarlan, this review]**	?	**3+**
Cebus olivaceus	Masaguaral, Venezuela [Valderrama et al., 2000]	**46%**	**4**
Cebus albifrons	**Manu National Park, Peru [Janson, this review]**	?	**3–4 (several clusters)**
Sapajus nigritus	**Caratinga, Brazil [Lynch Alfaro, this review]**	**100%**	**4**
Sapajus nigritus	**Carlos Botelho, Brazil [Izar, this review]**	?	**2 or 3**
Sapajus sp.	Tietê, São Paulo, Brazil [Verderane et al., 2007]	**~52%**	**14**
Sapajus libidinosus	**Boa Vista, Piaui, Brazil [Verderane, this review]**	**50% (Zang. group)**	**5**
		13% (Chicão group)	**3**
Sapajus libidinosus	**Serra da Capivara, Brazil [Falótico, this review]**	**35.3%**	**5**
Sapajus apella (*apella*)	Raleighvallen, Suriname [Leca et al., 2007]	**Rarely social**	**2**
Cebus capucinus (captive)	Strasbourg, France [Leca et al., 2007]	**49.3% (citrus)**	**9**
		15% (onions)	**4**
Sapajus paraguayanus (captive)	4 zoos in Argentina [Giudice & Pavé, 2007]	**0%**	**1**
Sapajus apella (*apella*) (captive)	California [Quinn 2004]	**1%**	**2**
Sapajus sp. (captive)	Strasbourg, France [Leca et al., 2007]	**0% (citrus)**	**1**
		4% (onions)	**4**

Bold script indicates data at this location reported first in this review.
*During focal follows.

by breaking open branches or foraging in rotten tree trunks. The millipede and hemipteran were not eaten, but the cricket (or praying mantis) and in four cases some of the ants were consumed after anointing. All sex and age classes anointed, and urine washing was incorporated into the anointing behaviors for all the different kinds of insects by at least one or more individuals.

S. nigritus: Carlos Botelho State Park

At Carlos Botelho State Park, Sao Paulo state, Brazil, where on-going studies of *S. nigritus* have been conducted since 2002 [Izar, 2004; Izar et al., submitted], Izar and students reported the only material yet observed for anointing is the spiny green caterpillar (species unknown) in ''a few instances'' over several years of study. The monkeys tended to rub or roll the caterpillar on a branch first, and then rub it on themselves. Izar observed up to two to three individuals anointing in social contact at this site.

S. nigritus: Caratinga Biological Station

A previously habituated group of *S. nigritus* was studied for 1 year at Caratinga Biological Station, Minas Gerais, Brazil [Lynch Alfaro, 2005, 2008]. Lynch Alfaro observed three social anointing bouts, each of which occurred in the fork of the same tall tree. The material used was unidentified social insects, possibly ants or wasps. Two adult males, an adult female and a juvenile male were the largest social group observed anointing. No food was ingested during the anointing bouts.

NONTUFTED CAPUCHINS

C. albifrons: Tiputini Biodiversity Station, Ecuador

In a group of eight wild white-fronted capuchins, *C. albifrons*, studied by Matthews in Tiputini Biological Station in Ecuador [see Matthews, 2009a,b], monkeys were observed anointing with the male flower of the palm *Phytelephas* sp. and with wet or dry mud. The monkeys were observed eating

both the flowers and the mud. The clay-rich mud was widely available on the forest floor at this site, so monkeys did not go to particular mud holes. Mud anointing ranged from solitary to the entire group of eight animals in contact. In some self-anointing episodes, an individual retrieved mud from the same place on the ground as another monkey, or used mud that another monkey left behind on a tree.

C. albifrons: Misahualli, Ecuador

Misahualli, a small Amazonian town in eastern Ecuador, has one important draw for tourists: a group of human commensal white-fronted capuchins, *C. albifrons*, who live within the town center [Field, 2004]. Boyette and MacFarlan videorecorded a bout of anointing with laundry soap by capuchins at this site (Fig. 1). In fact, local informants report that the monkeys take soap ''all the time'' for bathing, and Field [2007] reports observing fur rubbing multiple times during research here, including the use of many human-introduced substances such as onion, DEET repellent, cigarettes, bleach, hot peppers, *Citrus* spp., liquid soap, and cologne.

C. albifrons: Manu National Park, Peru

During his comparative behavioral studies of *S. macrocephalus* and *C. albifrons* at Manu National Park [see Janson, 1986], Janson observed *Cebus*, but not *Sapajus*, collecting large half-rotten *Alibertia curviflora* fruits from the ground, then running back to trees to anoint. At a given time there could be three to five separate nuclei of socially anointing monkeys, with each containing three to four individuals. Janson reports that everyone in the group participated in social anointing except for the very subordinate or very young. *C. albifrons* individuals also anointed with *Genipa americana*, a fruit that they also ate.

C. albifrons trinitatus

On Trinidad, *C. albifrons* monkeys studied by Phillips [see Phillips, 1998] self-anointed with seed pods at relatively high frequency, and in visual contact with one another, but never in social contact. Individuals broke apart the pod of *Pentaclethra macroloba* (Fabaceae/Mimosoideae) and used the inner part of the pod to scratch/rub themselves, so that the inside of the pod was in

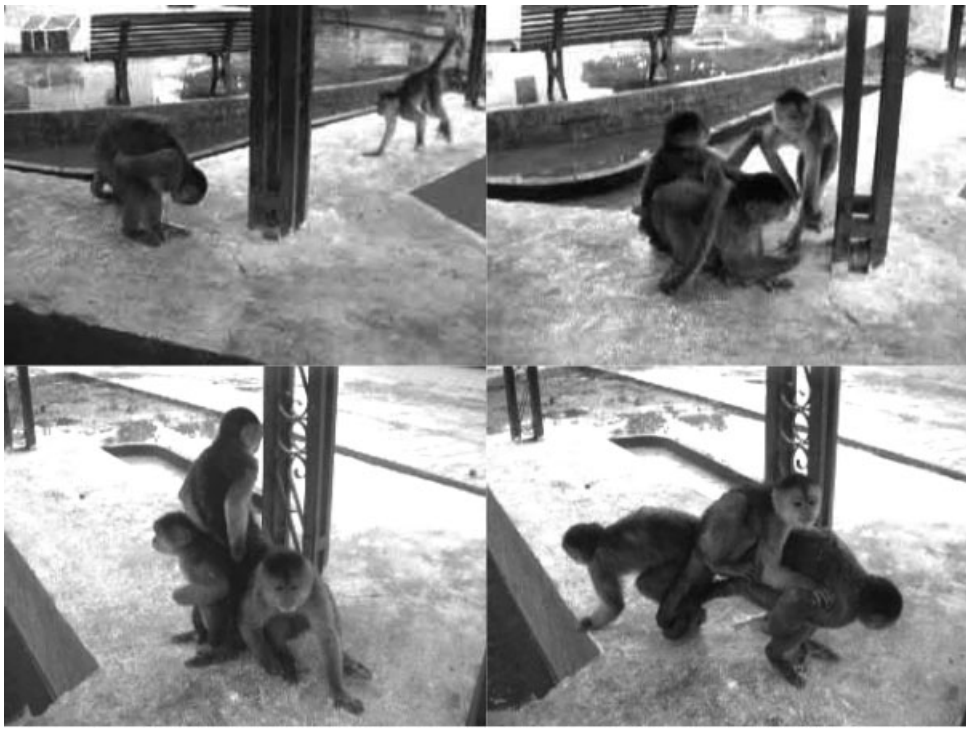

Fig. 1. (**A**)–(**D**) Social anointing sequence in *Cebus albifrons* at Misahualli, Ecuador. Boyette and MacFarlan videorecorded (Fig. 1A–D) a bout of social anointing at Misahualli, in which a capuchin, *A*, already wet from the rain, entered a *tienda* and grabbed a small plastic bag of white powdered laundry or dishwashing detergent. *A* then broke open the bag, spreading the powder on a bench, and immediately commenced rubbing the powder on its wet fur, using all four limbs and tail to spread the powder over its body. *A* was joined by individual *B* who, next to but not in contact with *A*, swept up some of the soap and began to self-anoint. *A* and *B* were then joined by *C*, and from this point on the three monkeys were in contact, rubbing the soap on themselves and pressing into one another. At no time during this bout did any of the three monkeys actively rub soap into each other's fur; all rubbing behavior was self-directed, although the monkeys used one another's bodies for support during anointing.

contact with the animal while rubbing. Trinidad capuchins ate the *Pentaclethra* seeds—in both mature and immature states—after breaking open the pods.

C. capucinus: Quepos

Schulte (in preparation) observed capuchin anointing in her year-long study at Manuel Antonio National Park, Quepos, Costa Rica. Her research focused on *C. capucinus* groups with frequent interactions with tourists; these monkeys anointed with wet wipes stolen from tourists, with packaged orange juice, and with wild limes. All age and sex classes were observed anointing, in groups of up to five individuals.

C. capucinus: Santa Rosa

O'Malley and Fedigan [2003] reported anointing with the prickly fine-haired *Sloanea terniflora* fruit at Santa Rosa National Park in Costa Rica, and MacKinnon provided a picture of three Santa Rosa capuchins anointing with *Piper* leaves in the Complete Capuchin [Fragaszy et al., 2004; p 103]. Here Melin adds observations of capuchins self- and social anointing with *Piper* leaves, social anointing with pooled water from a *Hymenaea courbaril* tree crevice, and self-anointing with stink bugs (accompanied by urine washing). Fedigan observed capuchins anoint with mud from a water hole, and retrieve mint leaves from plants on the ground to anoint in trees. Milar's focal animal data includes social anointing groups of up to four individuals, whereas Fedigan reports social anointing by up to 10 monkeys at a time.

Variation in Substances Used for Anointing

The distribution of field sites where anointing has been reported in wild or feral capuchins, including those observations reported here for the first time, is depicted in Figure 2, with materials used listed in Table III. The longest studied and northernmost capuchins, *C. capucinus*, have been reported to use at least 20 genera of plants for anointing. This includes up to 12 different plant species used at a single site, Lomas Barbudal [Baker, 1999; Perry, 1996], and significant overlap across sites in preferred plant species (for example, *Citrus*, *Piper*, and *Pithecellobium* are all used by *C. capucinus* for anointing at multiple sites). Plant use dominates anointing behavior at all the long-term field sites in Central America, although ants, millipedes, stinkbugs, and caterpillars have also been reported as anointing materials.

The South American nontufted *Cebus* species have been less well studied, but anointing behavior in wild *C. albifrons* includes the use of *A. curviflora* and *G. americana* fruit at Manu National Park, palm flowers and mud at Tiputini, and many

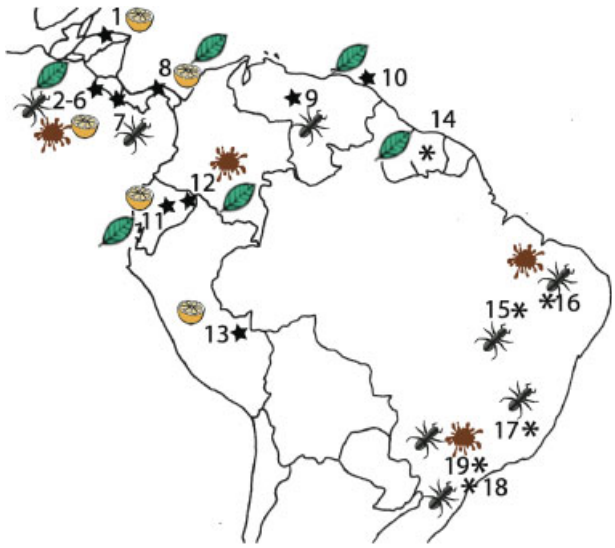

Fig. 2. Known geographic distribution of anointing in wild capuchin monkeys, and materials used by location. Key: Stars indicate *Cebus* localities and asterisks indicate *Sapajus* localities. Cut lime symbol indicates fruit use, leaf symbol indicates plant part use other than fruit, ant symbol indicates insect use, and splat symbol indicates use of mud, clay, or quartz powder. Sites 2–6 are lumped together due to their close proximity. See Table III for corresponding locations and details of materials used. [Color figures can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

human-introduced substances in Misahualli. In Trinidad, *C. albifrons* also preferentially uses plant parts. In contrast, so far wild *C. olivaceus* have been reported to use millipedes only [Valderrama et al., 2000]. Although within-site diversity of anointing materials appears much higher in *C. capucinus* than for other *Cebus* species, it is possible that the greater focus on anointing by *C. capucinus* researchers may bias this result due to a higher number of observation hours in which anointing substances are being recorded in this species.

Sapajus species have been reported to use various plant, insect, and human-produced materials for anointing in captivity (*Sapajus* sp.: onions, tobacco, formic acid, living ants, eau de cologne, ammonia, oil of lavender, orange juice [Nolte, 1958]; *S. xanthosternos*: spiders, grasshoppers, and other insects [Hill, 1960]; *S. paraguayanus*: water with bleach, onion [Giudice & Pavé, 2007]). In the wild, however, they anoint primarily with arthropods and dirt. *Sapajus* species have been observed using quartz powder [Mannu & Ottoni, 2009], ants [Verderane et al., 2007], mud, worms, caterpillars, stink bugs, millipedes, and crickets or praying mantises (Table III). One exception in Suriname is that *S. apella* was reported to anoint with rotten bamboo leaves [Leca et al., 2007]. Capuchins often forage in bamboo for insects, so it is possible the bamboo leaves may have contained ants or other insects as well. Alternatively, the rotten or fermented leaves may have produced alcohol, a known stimulus for self-anointing in captivity.

TABLE III. Anointing Materials Used at Different Locations by Capuchin Species

Map	Location	Species	Material	Citation
1	Trujillo, Honduras	*Cebus capucinus*	*Citrus*	Buckley, 1983
2	Santa Rosa, Costa Rica	*Cebus capucinus*	*Sloanea terniflora* fruit, ***Piper, Hymenaea courbaril* water, mint, stink bugs, mud**	O'Malley and Fedigan, 2005; Melin, Fedigan, and MacKinnon, this review
3	Curú, Costa Rica	*Cebus capucinus*	*Clematis* stems, *Piper* leaves, *Sloanea* seed pods, and *Citrus* fruit juice and rinds	DeJoseph et al., 2002; Baker, 1999
4	Lomas Barbudal, Costa Rica	*Cebus capucinus*	*Citrus; Piper marginatum* leaves and *Piper tuberculatum* immature fruits; *Pithecellobium saman* and *Hymenaea courbaril* sap; unripe *Capsicum*, *Trichilia americana*, *Jacquinia pungens* and *Eugenia salamanensis* fruit; *Caesalpinia eropstacjus* and *Miconia argentea* plants; *Gliricidia sepium;* stinkbugs, millipedes, caterpillars	Baker, 1999; Perry, 1996, 2008
5	Palo Verde, Costa Rica	*Cebus capucinus*	*Citrus*, *Pithecellobium samans* tree water, *Piper* leaves, insects, vine leaves, mud	Panger, 1998
6	Quepos, Costa Rica	*Cebus capucinus*	**packaged orange juice, wet wipes, limes**	Schulte, this review
7	Corcovado National Park, Costa Rica	*Cebus capucinus*	*Camponotus sericeiventris* or carpenter ants	Longino, 1984
8	Barro Colorado Island, Panama	*Cebus capucinus*	*Annona*, *Dieffenbachia*, *Eugenia nesiotica*, *Laetia thamnia, Protium, Tetrathylacium johansenii* and *Virola surinamensis*	Baker, 1996; Oppenheimer, 1969
9	Masaguaral, Venezuela	*Cebus olivaceus*	millipedes (*Orthoporus dorsovittatus*)	Valderrama et al., 2000
10	Bush Bush, Trinidad	*Cebus albifrons*	***Pentaclethra macroloba* seed pods**	Phillips, present review
11	Misahualli, Ecuador	*Cebus albifrons*	onion, DEET repellent, cigarettes, bleach, hot peppers, *Citrus* spp., liquid soap, cologne; **powdered detergent**	Field, 2007; Boyette and MacFarlan, present review
12	Tipituni, Ecuador	*Cebus albifrons*	**wet or dry mud**, ***Phytelephas* palm flowers**	Matthews, present review
13	Manu National Park, Peru	*Cebus albifrons*	*Alibertia curviflora* fruit; ***Genipa americana* fruit**	reported by C. Janson in Baker, 1999; Janson, present review
14	Raleighvallen, Suriname	*Sapajus apella*	rotten bamboo leaves	N. Gunst, pers. obs. in Leca et al., 2007
15	Fazenda Boa Vista, Gilbués, Piauí, Brazil	*Sapajus libidinosus*	**Formicidae ants (genus unidentified), southern green stink bugs (*Nezara viridula*), and caterpillars**	Verderane, this review
16	Serra da Capivara, Brazil	*Sapajus libidinosus*	quartz powder; **ants, millipedes and possibly southern green stink bugs and crickets or praying mantis**	Mannu and Ottoni, 2009; Falótico, this review
17	Caratinga Biological Station, Brazil	*Sapajus nigritus*	**ants or wasps**	Lynch Alfaro, present review
18	Carlos Botelho, São Paulo, Brazil	*Sapajus nigritus*	**spiny green caterpillars**	Izar, present review
19	Tietê Ecological Reserve, São Paulo, Brazil	*Sapajus* sp.	carpenter ants; **worms, mud**	Verderane et al., 2007; Falótico and Ottoni, present review

See Figure 2 for corresponding map. Bold script indicates materials reported here first for that location.

Anointing materials may vary from group to group even in the same *Sapajus* population. This may be due to cultural tradition; in other words, choice of particular materials for anointing may be an enduring behavior pattern shared among group members and dependent in part on social learning [Fragaszy & Perry, 2003]. At Serra da Capivara, the Pedra Furada and Bocão groups (see above) specialized in ants and other insects for anointing. However, animals in two other groups (Jurubeba and Oitenta) were observed to use ''hammer'' stones to pulverize quartz pebbles embedded in conglomerate rock, and then to anoint the face, chest, and hands with the powder produced [Mannu & Ottoni, 2009]. In these groups, anointing frequency was similar that for the Pedra Furada and Bocão groups (Table I), but they used completely different materials. This suggests that even long-term studies that examine one or two groups may underestimate the total diversity in anointing materials for a given population.

Even with this caveat, the evidence suggests *Cebus* has a wider template for plant use in anointing. In contrast, *Sapajus* most commonly performs anointing with ants, and there are no reports of the use of seed pods, flowers, or fruits for anointing in the wild within this clade. Table IV shows materials that are used at more than one site for anointing in wild capuchins.

Variation in Frequency of Anointing Behaviors in Capuchin Monkeys

The frequency of anointing bouts is highly variable across field sites (Table I), with a distinct difference in anointing bout frequency when comparing *Sapajus* to *Cebus* (Table V). Anointing was never observed during 67 hr of focal animal follows on *S. libidinosus* in Brasilia, Brazil [Pinha, personal communication]. Anointing was also extremely rare in *S. nigritus* at Minas Gerais, Brazil, but an order of magnitude more frequent for some *C. capucinus* in Costa Rica and *C. olivaceus* in Venezuela.

In general, all *C. capucinus, C. olivaceus*, and *C. albifrons* populations had a relatively high frequency of anointing bouts. However, anointing occurred rarely at Trujillo, Honduras, the northernmost edge of *C. capucinus* range, where it was observed only in September during a year-long study [Buckley, 1983]. At Trujillo, the only cases were in response to monkeys salvaging discarded oranges and grapefruits from the researcher and local human residents; no *Citrus* trees were available in the monkeys' home range, and no other types of anointing were reported [Buckley, 1983]. This suggests how

TABLE IV. Comparison of Materials Used for Anointing at Multiple Sites, by Capuchin Genus

Material	*Cebus* ($n = 13$ sites)	*Sapajus* ($n = 6$ sites)
Plants		
Citrus	6 (46%)	0
Piper	4 (31%)	0
Pithecellobium	2 (15%)	0
Capsicum	2 (15%)	0
Eugenia	2 (15%)	0
Hymenaea	2 (15%)	0
Sloanea	2 (15%)	0
Insects		
Ants	1 (8%)	4 (67%)
Stinkbugs	2 (15%)	2 (33%)
Millipedes	2 (15%)	1 (17%)
Caterpillars	1 (7%)	2 (33%)
Other		
Mud/clay/powder	3 (23%)	2 (33%)

The six most used plants across field sites are used exclusively by *Cebus*, and in contrast, the four most used arthropods are all used at a higher percentage of *Sapajus* sites than *Cebus* sites. Dirt (mud, clay, or quartz powder) is used at multiple sites and by both *Sapajus* and *Cebus*.

TABLE V. Main Hypotheses Tested and Results Obtained for Variation in Anointing Between *Cebus* and *Sapajus* in the wild

Hypothesis	Results
Cebus anoints at a higher frequency than *Sapajus*	SUPPORTED. *Cebus* anointing bouts per 100 observation hours were significantly more frequent compared to *Sapajus* (P-value < 0.05 in phylogenetic ANOVA)
Cebus anoints with a higher diversity of materials than *Sapajus*	NOT SUPPORTED. There was no overall difference between *Cebus* and *Sapajus* in number of items used per site (phylogenetic ANOVA, NS). However, *Cebus capucinus* did use significantly more plant species per site for anointing compared to all other capuchin species (phylogenetic ANOVA, P-value < 0.05)
Cebus uses plants more for anointing and *Sapajus* uses insects more	SUPPORTED. *Cebus* utilized a significantly higher proportion of plant species to insect species per site compared to *Sapajus* (P-value < 0.05 in phylogenetic ANOVA)
Cebus has a higher proportion of social to self-anointing bouts compared to *Sapajus*	NOT SUPPORTED. In wild groups, *Cebus* anointing bouts showed a range from 0 to 55% social (vs. solitary), with up to 8 individuals anointing together; *Sapajus* ranged from 13 to 100% social (vs. solitary), with up to 14 individuals anointing simultaneously

important the presence of appropriate stimuli is to invoke anointing behaviors, even for *C. capucinus*. On the other hand, *Piper* and *Eugenia* plants were available at Trujillo, and capuchins ate *Eugenia* fruits, but they were never observed to anoint with any of these plants [Buckley, 1983], despite *C. capucinus* preference for these genera for anointing at other Central American sites (see Fig. 2). This may suggest intraspecific variation in cultural practices or material preferences for anointing within *C. capucinus*.

Social vs. Solitary Anointing

Frequency of social to self-anointing and size of anointing groups varied across populations (Table II). All age and sex classes participate in social anointing in both *Cebus* and *Sapajus*. In *Cebus*, anointing behavior ranged from relatively social, with approximately 50% of bouts social in wild *C. capucinus* populations, to completely solitary, as found in *C. albifrons* from Trinidad (Table II).

In the wild, at some sites, *Sapajus* was only observed to anoint in small groups or alone, as seen in captivity (Table II). However, at Caratinga, Serra da Capivara, and Boa Vista, four or five individuals anointed together, the same maximum as found for some *Cebus* populations (see Table II). In fact, for *Sapajus* sp. in São Paulo, Brazil, anting bouts were as frequently collective (involving multiple individuals anointing simultaneously, 52%) as solitary (48%) [Verderane et al., 2007]. These social clusters could involve up to 14 individuals socially anointing on the same anthill, more than that reported for any other capuchin species.

Variation in Anointing Across *Cebus* and *Sapajus*: A Phylogenetic Perspective

As a preliminary investigation into the evolution of anointing behaviors, we performed ancestral states reconstruction for three behaviors using a recently developed phylogeny of capuchin monkeys [Lynch Alfaro et al., submitted]. The phylogeny was constructed by assembling a Cytochrome *b* data matrix of 57 capuchin monkey sequences (30 *Cebus*, 27 *Sapajus*) that encompass the range of capuchin distribution across Central and South America, and then performing a BEAST [Drummond & Rambaut, 2007] timetree analysis on the data [Lynch Alfaro et al., submitted]. For our analyses here, we pruned the tree to the sequences that represented the closest match to the geographic locations for field sites in this study. We performed all ancestral states analyses in R [R Core Development Team, 2011] using the ace function in APE [Paradis et al., 2004]. To test whether *Cebus* and *Sapajus* differed significantly in anointing behaviors, we performed phylogenetic ANOVAs [Garland et al., 1993] using the phy.anova function in GEIGER [Harmon et al., 2009].

We tested the hypothesis that in the wild *Cebus* anoints at a higher frequency than *Sapajus,* as found in captive studies [Leca et al., 2007]. Variation in anointing frequency shows a clear phylogenetic signal (Fig. 3), with the *Sapajus* clade showing infrequent anointing compared with the *Cebus* clade. Phylogenetic ANOVA reveals this difference to be significant ($P < 0.05$; Table V).

Anointing behavior was first reported in the wild in *C. capucinus* [Oppenheimer, 1969], and most subsequent field research on anointing has focused on this species, with reports of a wide breadth of materials used at most sites (Fig. 2). Although reconstruction of ancestral states does not reveal a general trend of higher diversity of anointing materials in *Cebus* than *Sapajus* (Fig. 4; phylogenetic ANOVA, NS; see Table V), *C. capucinus* did use significantly more plant species per site for anointing compared with other capuchin species (phylogenetic ANOVA, *P*-value < 0.05; see Table V). *C. capucinus* appears unique among capuchins in its explosive diversity of plant types used for anointing, but continued research will illuminate whether this difference has in part related to observation bias, with more researchers in Central America focusing on anointing as part of their research protocol. The one site where *Sapajus* appears to have a relatively diverse material preference, Serra da Capivara, is the site where data on anointing has been collected for the most groups of *Sapajus* ($n = 4$) [Mannu & Ottoni, 2009; Falótico, this review].

We mapped the relative proportion of plant species used compared with insect species used for anointing per field site, to determine whether there was a phylogenetic signal for preference for plants vs. arthropods as anointing materials (Fig. 5). Ancestral state reconstruction suggests that ancestral *Cebus* preferentially utilized plants for anointing, and that there has been one transition to predominant use of arthropods: millipedes in *C. olivaceus*. It will be important to observe anointing behaviors at more than one field site to determine whether millipedes are used across the range of *C. olivaceus*, or whether plants are more important in other locations. For *Sapajus*, the reconstruction is different; the ancestral *Sapajus* population used proportionately fewer plants for anointing, and there is only one transition to plants as the dominant anointing material in *Sapajus*, at Raleighvallen (rotten bamboo; see Fig. 2). Ancestral state reconstruction suggests that *Cebus* and *Sapajus* have evolved significant differences in the proportion of plant items vs. insect items used for anointing behaviors (phylogenetic ANOVA, $P < 0.05$; see Table V).

GENERAL DISCUSSION

Anointing Compared with Other Rubbing Behaviors in NEOTROPICAL PRIMATES

The most similar anointing to capuchin monkeys occurs in owl monkeys, *Aotus*. A wild owl monkey has

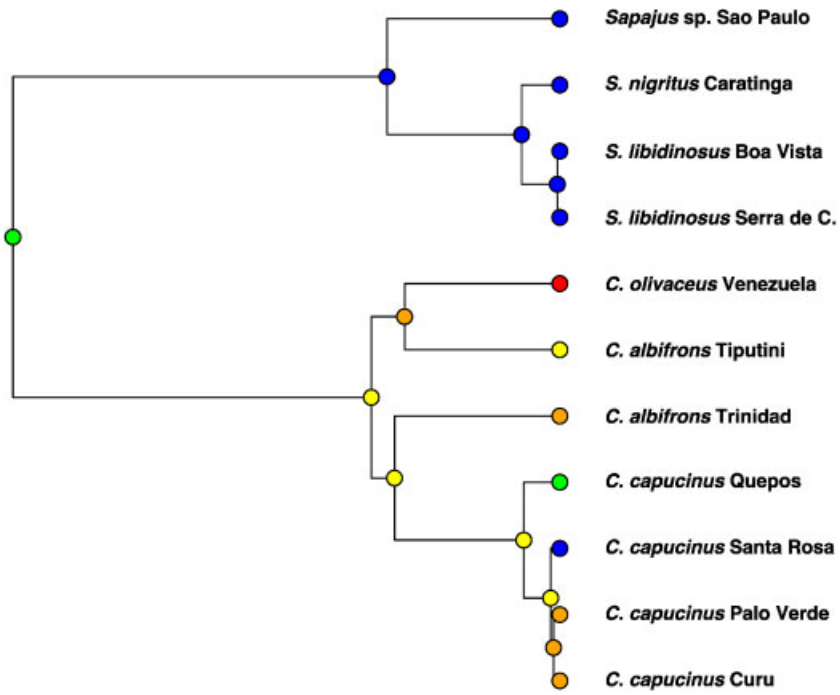

Fig. 3. Maximum likelihood reconstruction of ancestral anointing frequencies in *Cebus* and *Sapajus*. Topology based upon Lynch Alfaro et al. [submitted]. Bout frequency data were assigned to the most closely related tip species in the tree. Blue = fewer than 2 bouts per 100 observation hours; Green ≥ 2–4 bouts/100 hr; Yellow ≥ 4–6 bouts/100 hr; Orange ≥ 6–8 bouts/100 hr; and Red = more than 8 bouts per 100 observation hours. [Color figures can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

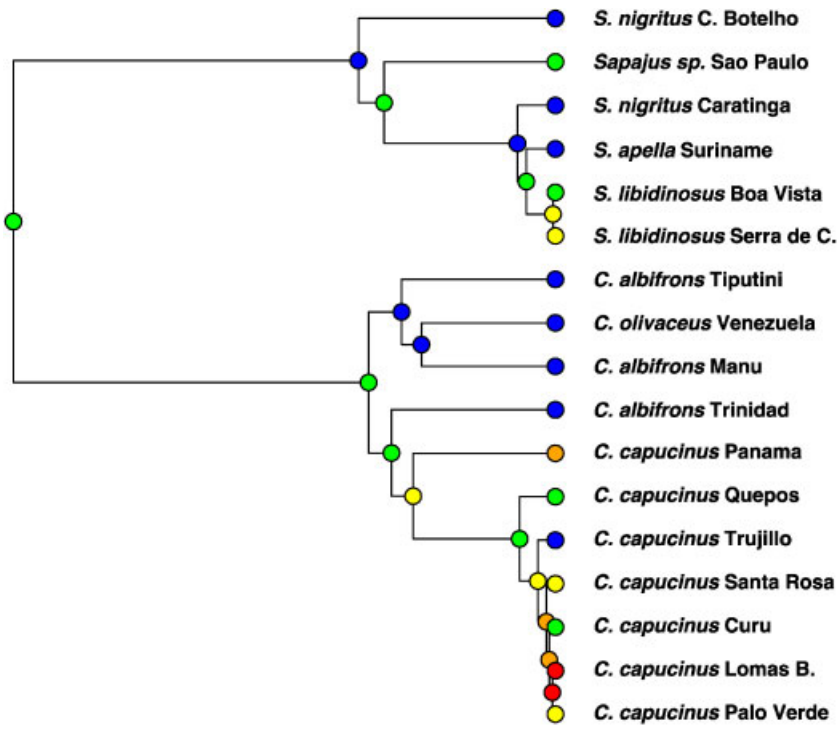

Fig. 4. Maximum likelihood reconstruction of ancestral number of anointing materials. Topology based upon Lynch Alfaro et al. [submitted]. Blue = two or fewer items reported as a material used for anointing at a given site; Green = 3–4 items/site; Yellow = 5–6 items/site; Orange = 7–8 items/site; and Red = 9 or more items used for anointing at a given site. We excluded Misahualli from this analysis because of the high human impact at this site, as most of the anointing items were human-made or human-introduced goods [Field, 2007]. [Color figures can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

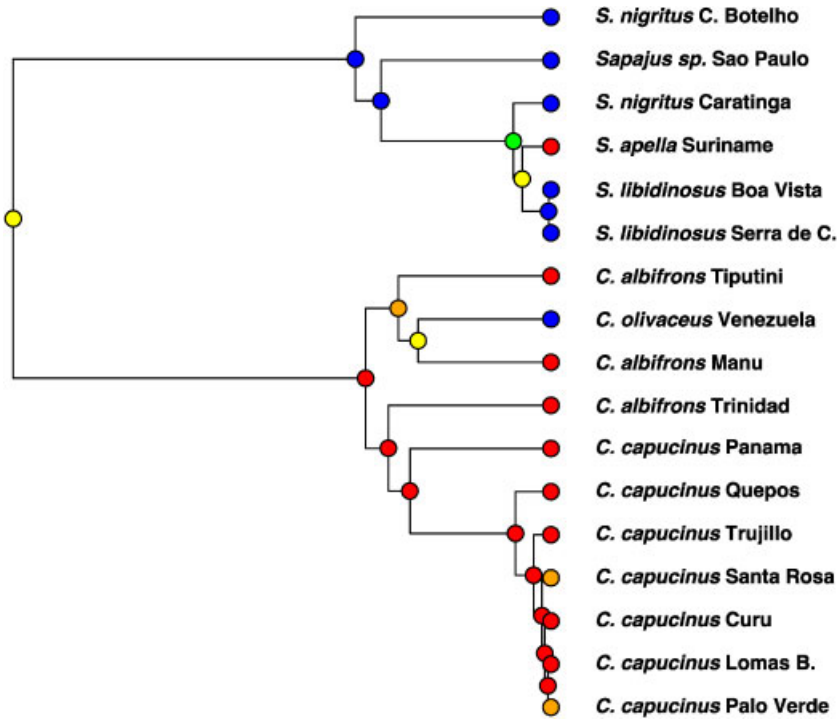

Fig. 5. Maximum likelihood reconstruction of ancestral proportion of plant items used during anointing behavior. Topology based upon Lynch Alfaro et al. [submitted]. Blue = Plant items (counted per species, and including fruits, flowers, stems, leaves, seed pods, etc.) make up 20% or less of total items used for anointing; Green = Plants >20–40% of total items; Yellow = Plants >40–60% of total items; Orange = Plants >60–80% of total items; Red = Plants >80–100% of total times used for anointing at that site. Lomas Barbudal data is based on Perry [1996]. [Color figures can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

been observed self-anointing with a leaf [C. Wolovich, personal communication], and captive owl monkeys self-anoint in response to onion, garlic, chives, live millipedes, millipede-produced benzoquinones and an extract of *Piper* leaves, all used by *Cebus* as well [Zito et al., 2003]. Owl monkeys also are reported to self-anoint with cinnamon, chives, and moths [S. Evans, personal communication], materials that to our knowledge have never been tested on capuchins. *Citrus* never elicits anointing in any owl monkeys [Zito et al., 2003; Evans, personal communication]. Owl monkeys not only self-anoint, they also perform social anointing [Evans et al., 2003; Zito et al., 2003]. In recent captive observations of owl monkey (*Aotus nancymaae* and *A. azarae*) social anointing ($n = 5$ groups), their bouts with millipedes appear identical to social anointing in capuchin monkeys [Evans, personal communication]. Similarities between anointing behavior in owl monkeys and capuchins suggest that this behavior may have been present in their common ancestor.

Solitary rubbing behaviors in other platyrrhines include lion tamarins self-anointing with plant exudates, including *Thyrsodium spruceanum* (Anacardiaceae), as well as *Myroxylon* sp. (Fabaceae), a known medicinal plant with larvicidal properties in its resin [Guidorizzi & Raboy, 2009]. Titi monkeys and squirrel monkeys self-anoint in captivity [Fragaszy et al., 2004]. Chest rubbing has been observed in capuchins [*S. nigritus:* Lynch Alfaro, cited in Fragaszy et al., 2004; *S. libidinosus:* Verderane, this review], howler monkeys [Young, 1982], owl monkeys [Moynihan, 1964], and woolly monkeys [White et al., 2000]. Spider monkeys rub pungent *Citrus* or *Zanthoxylum* leaves mixed with their own saliva onto their chest, and then vigorously rub their chest against tree branches [Campbell, 2000]. In woolly monkeys chest rubbing can include the application of saliva to a material where the chest is then rubbed vigorously, saturating the chest fur with saliva [White et al., 2000]; in contrast, in capuchins, the alpha male may salivate onto his chest in copious amounts, then rub his wet chest on a tree trunk, saturating the trunk with saliva [*S. libidinosus:* Verderane, this review]. Woolly monkeys also perform anogenital rubbing as a type of scent marking behavior [Di Fiore et al., 2006]. Muzzle rubbing in callitrichids [Heymann et al., 1989] may function to spread saliva mixed with ingested substances around the mouth and face. Urine washing is common in several neotropical primates (i.e. squirrel monkeys, capuchin monkeys) and urine rubbing is observed as a component of anointing behavior in both *Sapajus* and *Cebus* when anointing with insects, but not plants [this review].

Anointing, chest rubbing, muzzle rubbing, anogenital rubbing, and urine rubbing all cause the spread of saliva, urine, glandular secretions, and/or

other pungent materials around the external body, and are used at varying frequencies across platyrrhine species. Other than in capuchin and owl monkeys, these behaviors are exclusively performed alone, not in social contact, although the function of several of these behaviors has been hypothesized as territorial, social or reproductive signaling through olfactory cues [Di Fiore et al., 2006; Heymann, 2006]. The targeting of a particular restricted location on the body for some forms of rubbing (i.e. chest rubbing, muzzle rubbing) may indicate that those types of rubbing are less likely to serve repellent, fungicide or curative functions, in comparison to anointing or urine rubbing that spread the substance across most of the body. Next we consider the evidence for anointing as a means for self-medication.

Anointing as Self-Medication

Experimental evidence suggests that anointing is effective in reducing parasite diversity or parasite load in capuchins, consistent with the interpretation of anointing behavior as a defensive function [Hart, 1997]. Plants used by wild *C. capucinus* for anointing in Costa Rica are also chosen for medicinal purposes by humans there, and capuchin anointing increases significantly during the wet season, when the risk of parasitic infection is the highest [Baker, 1996, 1999]. Wild *C. olivaceus* use millipedes for anointing more frequently during the wet season, when mosquitoes are most likely to serve as vectors for botflies [Valderrama et al., 2000]. Weldon et al. [2003] found that female yellow mosquitoes exhibited fewer landings and fed less frequently in the presence of benzoquinones from the very millipedes used by *C. olivaceus*. In semi-free ranging *Sapajus* sp. in Brazil, capuchins rub carpenter ants, *Camponotus rufipes*, onto their bodies at a higher frequency during the height of nymph season for the tick species *Amblyomma cajennense* [Falótico et al., 2007; Verderane et al., 2007]. Experimental work showed that formic acid from the carpenter ants *Sapajus* sp. used for anointing significantly repelled tick nymphs [Falótico et al., 2007; Verderane et al., 2007]. These seasonal differences in capuchin behavior suggest that capuchins anoint to reduce ectoparasite loads when parasite infections are most likely [Baker, 1999; Falótico et al., 2007; Valderrama et al., 2000; Verderane et al., 2007].

Three new candidates for potential monkey self-medication are reported here. The *P. macraloba* seed pods used by *C. albifrons* in Trinidad may be used by the monkeys as a curative. Other monkey species avoid the bark and seeds of *P. macroloba*; they are toxic and contain an alkaloid, paucine [Flores, 2002; Joker & Salazar, 2000; Orwa et al., 2009]. Scientists as well as South and Central American Indian groups ascribe medicinal properties to this plant species, which is used both as anti-venom against snakebites [da Silva et al., 2005, 2007], and as a curative for ulcers and insect bites [Orwa et al., 2009]. As such, *P. macroloba* merits further investigation for potential antiseptic, insect repellant, or antifungal properties.

Another candidate for its use as a repellant or a deterrent to predators is the stink bug, which may be used as an anointing material by capuchins at Boa Vista and Serra de Capivara in Brazil, and at Lomas Barbudal and Santa Rosa, Costa Rica (Table III). This insect is well known for its pungent and offensive odor to humans, and these volatile chemicals are used by the bug as a deterrent to predators [Moraes et al., 2008]. The stink bug is considered a pest because of the toxic saliva it injects into commercial plant crops [Moraes et al., 2008].

Finally, the fruit of *G. americana*, or genipap, used for anointing and eaten by *C. albfrons* in Peru, is used as insect repellant by South American Indians, is eaten in quantity as a vermifuge, and has been shown to have intense antibiotic activity in all parts of the fruit [Morton, 1987].

Anointing as a Behavioral Response to Chemical Stimuli

Weldon et al. [2003] experimentally demonstrated they could elicit anointing in captive *C. capucinus* and *Sapajus* sp. by isolating benzoquinones like those from the millipedes *C. olivaceus* use for anointing in the wild. Control compounds without the same odor did not elicit anointing, indicating an olfactory cue [Weldon et al., 2003]. Wild *C. capucinus* anoint with millipedes at Santa Rosa, Costa Rica [Perry, 2008]; here we report the first evidence for the use of millipedes for *Sapajus* (by *S. libidinosus* at Serra da Capivara).

The specific chemicals that elicit anointing behavior appear to vary across species. *C. capucinus* preferentially anoints with *Citrus* in the wild [Baker, 1999; Buckley, 1983; Panger, 1998]. In contrast, neither limes nor lemons elicited anointing in captive *S. apella*, although the same individuals did anoint when tested with onions [Quinn, 2004]. In another captive study, *Sapajus* sp. responded to lemons for solitary but not social anointing, and at a significantly lower rate compared with *C. capucinus* given the same stimulus [Leca et al., 2007]. In the wild, at Caratinga, *S. nigritus* peeled and ate tangerines (*Citrus*) several times in the course of the year; however, no individual was observed to anoint in response to these *Citrus* fruits or peels [Lynch Alfaro, unpublished data].

Another example of a possible difference in response to chemical stimuli is for hot peppers, *Capsicum*. At Caratinga, *S. nigritus* individuals ingested hot peppers, *Capiscum* sp., on several occasions, but never were observed to anoint with them [Lynch Alfaro, unpublished data]; in contrast,

Capsicum hot peppers were used for anointing in both *C. capucinus* [Perry, 1996] and *C. albifrons* [Field, 2007]. The active component of these peppers is capsaicin, an irritant that causes the sensation of burning on contact, and several related compounds are called capsaicinoids, which may serve as antifungals [Tewksbury et al., 2008]. More comparative research is needed on variation in chemical receptor pathways for citrus and pepper compounds across capuchin species.

Capuchins respond differently to leaf-cutting ants vs. carpenter ants. At Caratinga, even the strong stimulus of hundreds of pinching leaf-cutter *Atta* ants during their nuptial flight did not elicit any true anting bouts in *S. nigritus* (i.e. no active crushing of ants on the fur or rubbing them onto the body), even though monkeys were covered in ants, and scratched themselves in an extremely agitated state [Lynch Alfaro, personal observation]. In contrast, social and solitary anointing occur relatively often in response to carpenter ants in *Sapajus* sp. at Tietê Ecological Park, Sao Paulo.

An important difference between the ants involved at the two sites is that the carpenter ants, *C. rufipes*, at Tietê produce formic acid [Falótico et al., 2007], but the herbivorous leaf cutter ants, genus *Atta*, do not produce formic acid or any other noxious sting, although they do defend themselves well by pinching [Powell, 1991]. Although there is at least one report of birds (i.e. *Agriocharis*) performing both passive and active anting behavior with leaf-cutter ants [Sugihara & Heston, 1981], the great majority of bird species perform anting behavior with Formicine ants (such as the carpenter ants), which do sting and secrete a variety of chemicals, including formic acid [Revis & Waller, 2004]. This suggests that for capuchin monkeys, it is the chemical compounds either injected by the ant or crushed into the skin (and made volatile) by the monkey, and not the physical sensation of being crawled on or pinched, that induces their anointing behaviors with ants.

Even comparing two sites where anting occurs with Formicidae ants, differences in abundance and distribution of ant colonies can affect the nature of capuchin anting. At Tietê Ecological Park, ants make enormous anthills in the ground, and they are easily found and extracted in great quantities. In contrast, at Boa Vista, ants form nests well-protected within tree holes, and ants are found only in small quantities when the monkeys are foraging. These differences may well account for the differences seen in the social nature and in the intensity of anting behaviors at these two sites, with anting more social and high intensity at Tietê and more often less active and solitary at Boa Vista.

Ecological Origins of Social Anointing

Self-anointing is more widespread across platyrrhines, but social anointing is restricted to owl monkeys and capuchin monkeys. What ecological circumstances would drive increased sociality of anointing? In our video of anointing in *C. albifrons* (Fig. 1), all anointing was self-directed—no individual actively directed its rubbing behavior toward another individual. This is consistent with social anointing behavior observed in *C. capucinus* at Curu [Baker, 1999]; however, Perry [2008] reported that in *C. capucinus* at Lomas Barbudal some group members actively anointed the fur of infants who were too young to anoint themselves. In social anointing with millipedes in *C. olivaceus* there were no reported instances of one individual actively sharing or spreading millipede secretions onto another individual's fur [Valderrama et al., 2000]. Millipede anointing was not kin-biased; it occurred among all sex and age classes, and among individuals that did not usually form alliances together [Valderrama et al., 2000].

Social anointing might arise out of tolerated theft of resources, in which an individual that did not help acquire the resource is nevertheless able to gain access to and share in the resource [Blurton Jones, 1987]. Blurton Jones [1987] hypothesizes that theft will be tolerated when the resource follows a diminishing returns curve of benefit gained from the resource against the amount of resource held, and when the resource is found unpredictably, rarely, and in large amounts. Perry [1996] reports that for *C. capucinus*, aggression and sexual behavior were common during anointing, and that when a substance used for anointing was easily monopolized, such as for *Hymenaea* and *Pithecellobium*, there was intense competition for the materials. Buckley [1983] concurred that anointing was a highly prized opportunity (capuchins approached humans at close proximity to obtain *Citrus*), and that monkeys tried to escape from others to maintain their anointing materials. In contrast, with mud or ants there seems to be little competition and the whole group may share the resources without agonism.

Another explanation for increased sociality in anointing is through mutualism. It may benefit capuchins to rub up against each other to spread the substance on hard to reach areas. It may be worth sharing the substance with others in return for being able to spread the substance more thoroughly around the body [Perry, 2008].

We hypothesize that the material properties, distribution, and local abundance of the anointing material determine capuchin social dynamics during anointing bouts. An abundant resource like mud following rain is not easily monopolized. However, sharing it from a neighbor might be a preferable option to risking travel on the ground to acquire a new mud patch, and mud will rapidly and easily spread through mutual rubbing. Millipedes tend to be solitary, and as such would be a highly prized contestable resource—Valderrama et al. [2000]

suggests that a millipede can be shared by a maximum of four individuals for anointing. Single flowers may be too small to provide enough material for multiple individuals, and so solitary anointing may be more common with this item. Leaves or carpenter ants tend to be locally plentiful, so should not incite contest competition; but rubbing against saturated fur may more quickly deliver the effect compared with starting from ''scratch'' with a new leaf or new anthill, and so these materials may allow for large nonagonistic social groupings.

Social Facilitation and Cultural Variation of Anointing Material Preferences

Although capuchins do not actively share food, several species [*S. apella* (*macrocephalus*): Izawa, 1979; *C. capucinus*: Perry & Rose, 1994; *S. libidinosus:* Mannu & Ottoni, 2009] are reported to be highly tolerant when conspecifics take food resources from them, known as passive sharing. Adults are especially tolerant of juveniles taking away food [Fragaszy et al., 1997], including that acquired through tool use [Ottoni & Izar, 2008], and passive sharing has been suggested as an aid in juveniles' acquisition of both food and tool-use preferences. Social anointing could serve a similar function, facilitating the transfer of preferences for particular anointing materials. Such an adaptation toward socially learned preferences could also explain the apparent cultural variation in materials used for anointing. For example, at Boa Vista, Verderane observed two cases in which a juvenile approached an anting alpha male, observed the anting behaviors, and then began anting as well. Social facilitation may be an important developmental component of anointing in wild capuchins, as suggested from captive experiments [Meunier et al., 2008], and it may lead to cultural variation both within and across populations.

Anointing as Incidental By-Product of Foraging or Actively Sought Resource

Capuchins are destructive foragers with a high tolerance for trying novel food sources and sorting through rotting debris, getting stung by insects, or being injured by spiny plants in order to attain hard-to-acquire food items. This diverse palate and permissive attitude toward unpleasant stimuli may have facilitated the experimentation with plant or animal materials that taste terrible—materials that would be avoided by other primates—with subsequent use for anointing [Valderrama et al., 2000]. But does anointing simply occur as a by-product of active foraging? Or once a substance triggers anointing behavior, is it actively sought out as a resource independent from foraging for food?

Perry [1996] reports that of eleven plant species *C. capucinus* used for anointing at Lomas Barbudal, none of them were both ingested and used for anointing on the same day. Baker [1999] concurs that capuchins will anoint opportunistically, but they will also go out of their way to retrieve plants for anointing. In contrast, in both Trinidad and Ecuador, *C. albifrons* ate and anointed with the same materials in direct succession (flowers, mud, and seed pods), and at several sites in Brazil, *Sapajus* consumed ants or other insects as well as anointing with them. It seems, then, that anointing has become more specialized and independent of feeding behavior in *C. capucinus*, but perhaps remains more incidental and food-related in other capuchin species. However, Perry [2008] does report that stinkbugs are a staple food in the Lomas Barbudal *C. capucinus* diet, and that a few of the monkeys crush them and self-anoint with them before eating them. Insect anointing is less frequent [Perry, 2008] and perhaps more incidental for *C. capucinus*, whereas anointing with plants has become a specialized activity independent from feeding.

Future Directions

In this article, our aim was to consider capuchin monkey anointing in a comparative framework across species and localities. However, data on anointing are almost completely lacking for the enormous Amazon Basin (see Fig. 2), the largest part of capuchins' distribution and the major area of sympatry between *Cebus* and *Sapajus*. Manu National Park, Peru (Fig. 2, location 13) is one location for which we have long-term behavioral data on both *Cebus* and *Sapajus* in the Amazon, and at this site *Cebus* anointed with plants but *Sapajus* was never observed anointing [Janson, this review]. Studying sympatric capuchins as they utilize the same habitat can control for plant and insect availability and allow for a direct comparison of material preferences, anointing frequency and the social nature of anointing in the wild. If, in fact, capuchin monkeys are seeking out medicinal properties of plants and insects, the Amazon is an untapped, incredibly rich resource base to explore *Cebus* and *Sapajus* behavioral strategies for self-medication.

ACKNOWLEDGMENTS

Funding was provided by the UCLA Center for Society and Genetics and NSF BCS-0833375 to J.L.A. Some ideas presented in this review were stimulated through discussions under the auspices of the WSU/UW IGERT Program in Evolutionary Modeling (IPEM) funded by NSF under Grant DGE-0549425. A.H.B. and S.J.M. thank Eric Hartman and Celeste Henrickson for their help in data collection. This research adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates.

REFERENCES

Baker M. 1996. Fur rubbing: use of medicinal plants by capuchin monkeys (*Cebus capucinus*). American Journal of Primatology 38:263–270.

Baker M. 1997. Identification and selection of fur rubbing materials by white-faced capuchin monkeys (*Cebus capucinus*). American Journal of Primatology 42:93.

Baker ME. 1999. Fur rubbing as evidence for medicinal plant use by capuchin monkeys (*Cebus capucinus*): ecological, social, and cognitive aspects of the behavior [Dissertation]. Dissertation Abstracts International 3870.

Birkinshaw CR. 1999. Use of millipedes by black lemurs to anoint their bodies. Folia Primatologia 70:170–171.

Blurton Jones NG. 1987. Tolerated theft, suggestions about the ecology of sharing, hoarding and scrounging. Social Science Information 26:31–54.

Buckley JS. 1983. The feeding behavior, social behavior and ecology of the white-faced monkey, *Cebus capucinus*, at Trujillo, Northern Honduras, Central America [Dissertation], Dissertation Abstracts International 1143.

Campbell CJ. 2000. Fur rubbing behavior in free-ranging black-handed spider monkeys (*Ateles geoffroyi*) in Panama. American Journal of Primatology 51:205–208.

Clucas B, Rowe MP, Owings DH, Arrowood PC. 2008. Snake scent application in ground squirrels, *Spermophilus* spp.: a novel form of antipredator behaviour? Animal Behaviour 75:299–307.

da Silva JO, Coppede JS, Fernandes VC, Sant'Ana CD, Ticli FK, Mazzi MV, Giglio JR, Pereira PS, Soares AM, Sampaio SV. 2005. Antihemorrhagic, antinucleolytic and other antiophidian properties of the aqueous extract from *Pentaclethra macroloba*. Journal of Ethnopharmacology 100:145–152.

da Silva JO, Fernandes RS, Ticli FK, Oliveira CZ, Mazzi MV, Franco JJ, Giuliatti S, Pereira PS, Soares AM, Sampaio SV. 2007. Triterpenoid saponins, new metalloprotease snake venom inhibitors isolated from *Pentaclethra macroloba*. Toxicon 50:283–291.

DeJoseph M, Taylor RSL, Baker M, Aregullin M. 2002. Fur-rubbing behavior of capuchin monkeys. Journal of the American Academy of Dermatology 46:924–925.

de Sousa e Silva Júnior J. 2001. Especiação nos macacos-prego e caiaras, gênero *Cebus* Erxleben, 1777 (Primates, Cebidae) [dissertation]. Universidade Federal do Rio de Janeiro.

Di Fiore A, Link A, Stevenson PR. 2006. Scent marking in two western Amazonian populations of woolly monkeys (*Lagothrix lagotricha*). American Journal of Primatology 68: 637–649.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214.

Evans S, Weldon P, Gioannetti J, Moody C, Vicaria E. 2003. Anointing in owl monkeys. American Journal of Primatology 60:135.

Falótico T, Ottoni EB. 2009. Capuchin monkeys of caatinga: many tools for many things. Abstracts of the 46th Annual Meeting of the Animal Behavior Society, Pirenópolis, GO, 72p.

Falótico T, Labruna MB, Verderane MP, Izar P, Ottoni EB. 2007. Repellent efficacy of formic acid and the abdominal secretion of carpenter ants (Hymenoptera: Formicidae) against *Amblyomma* ticks (Acari: Ixodidae). Journal of Medical Entomology 44:718–721.

Field MY. 2004. Effect of human cohabitation on activity budgets in white-fronted capuchin monkeys (*Cebus albifrons*) in Ecuador: a pilot study. American Journal of Physical Anthropology 123:94.

Field MY 2007. If you give a monkey an onion: an introduction to fur rubbing in human-commensal white-fronted capuchin monkeys (*Cebus albifrons*). American Journal of Physical Anthropology 44:108.

Flores EM. 2002. *Pentaclethra macroloba* (Willd.) Kuntze. In: Vozzo JA, editor. Tropical tree seed Manual. Agricultural handbook 721. Washington: Forest Service, United States Department of Agriculture. p 601–604.

Fragaszy DM, Perry S. 2003. Towards a biology of traditions. In: Fragaszy DM, Perry S, editors. The biology of traditions: models and evidence. Cambridge: Cambridge University Press.

Fragaszy DM, Feuerstein JM, Mitra D. 1997. Transfers of food from adult to infants in tufted capuchins (*Cebus apella*). Journal of Comparative Psychology 111:194–200.

Fragaszy DM, Fedigan LM, Visalberghi E. 2004. The complete capuchin: the biology of the genus Cebus. New York: Cambridge University Press.

Garland Jr T, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265–292.

Giudice AM, Pavé R. 2007. Cebus paraguayanus in zoos: the spontaneous expression of species-specific behaviors. Neotropical Primates 14:65–71.

Guidorizzi CE, Raboy BE. 2009. Fur-rubbing with plant exudates in wild golden-headed lion tamarins (*Leontopithecus chrysomelas*). American Journal of Primatology 71:75.

Harmon L, Weir J, Brock C, Glor R, Challenger W, Hunt G. 2009. GEIGER: analysis of evolutionary diversification. R package version 1.3-1. http://CRAN.R-project.org/package = geiger

Hart BL. 1997. Behavioral defense. In: Clayton DH, Moore JC, editors. Host-parasite evolution: general principles and avian models. Oxford: Oxford University Press.

Heymann EW. 2006. Scent Marking Strategies of New World Primates. American Journal of Primatology 68:650–661.

Heymann EW, Zeller U, Schwibbe MH. 1989. Muzzle rubbing in the moustached tamarin, *Saguinus mystax* (Primates: Callitrichidae) —behavioural and histological aspects. Zeitschrift fuer Saeugetierkunde 54:265–275.

Hill WCO. 1960. Primates: comparative anatomy and taxonomy, IV: Cebidae, Part A. Edinburgh: University Press.

Hunter AJ. 1981. Chemical communication, aggression and sexual behaviour in the owl monkey *Aotus trivirgatus griseimembra*) [Dissertation]. University of London.

Izar P. 2004. Female social relationships of *Cebus apella nigritus* in a southeastern Atlantic forest: an analysis through ecological models of primate social evolution. Behavior 141:71–99.

Izawa K. 1979. Foods and feeding behavior of wild black-capped capuchin monkeys (*Cebus apella*). Primates 20: 57–76.

Janson CH. 1986. Capuchin counterpoint. Natural History 95: 44–53.

Joker D, Salazar R. 2000. *Pentaclethra macroloba* (Willd.) Kuntze. Seed Leaflet 35.

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.

Longino JT. 1984. True anting by the capuchin, *Cebus capucinus*. Primates 25:243–245.

Lynch Alfaro JW. 2005. Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 67:313–328.

Lynch Alfaro J. 2008. Scream-embrace displays in wild black-horned capuchin monkeys. American Journal of Primatology 70:551–559.

Mannu M, Ottoni E. 2009. 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 71:242–251.

Matthews LJ. 2009a. Intragroup behavioral variation in white-fronted capuchin monkeys (*Cebus albifrons*): mixed evidence

for social learning inferred from new and established analytical methods. Behaviour 146:295–324.
Matthews LJ. 2009b. Activity patterns, home range size, and intergroup encounters in *Cebus albifrons* support existing models of capuchin socioecology. International Journal of Primatology 30:709–728.
Meunier H, Petit O, Deneunbourg JL. 2008. Social facilitation of fur rubbing behavior in white-faced capuchins. American Journal of Primatology 70:161–168.
Moraes MCB, Pareja M, Laumann RA, Borges M. 2008. The chemical volatiles (semiochemicals) produced by neotropical stink bugs (Hemiptera: Pentatomidae). Neotropical Entomology 37:489–505.
Morrogh-Bernard HC. 2008. Fur-rubbing as a form of self-medication in *Pongo pygmaeus*. International Journal of Primatology 29:1059–1064.
Morton J. 1987. Fruits of warm climates. Miami: Julia F. Morton.
Moynihan M. 1964. Some behavior patterns of platyrrhine monkeys. I. The night monkey (*Aotus trivirgatus*). Smithsonian Miscellaneous Collections 146:1–84.
Nolte A. 1958. Beobachtungen Über Das Instinktverhalten Von Kapuzineraffen (*Cebus apella* L.) in Der Gefangenschaft. Behaviour 12:183–207.
O'Malley RC, Fedigan L. 2003. Variability in food-processing behavior among white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. American Journal of Physical Anthropology 172:63–73.
Oppenheimer JR. 1969. Behavior and ecology of the white-faced monkey, *Cebus capucinus*, on Barro Colorado Island, C. Z [Dissertation]. Dissertaion Abstracts I 442–443.
Orwa C, Mutua A, Kindt R, Jamnadass R, Simons A. 2009. Agroforestry Database: a tree reference and selection guide, version 4.0.
Ottoni E, Izar P. 2008. Capuchin monkey tool use: overview and implications. Evolutionary Anthropology 17:171–178.
Panger MA. 1998. Hand preference and object-use in free-ranging white faced capuchin monkeys (*Cebus capucinus*) in Costa Rica [Dissertation]. Dissertation Abstracts I 3193.
Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.
Paukner A, Suomi SJ. 2008. The effects of fur rubbing on the social behavior of tufted capuchin monkeys. American Journal of Primatology 70:1007–1012.
Perry SE. 1996. Social relationships in wild white-faced capuchin monkeys, *Cebus capucinus* [Dissertation]. Dissertation Abstracts International 3194.
Perry S. 2008. Manipulative monkeys: the capuchins of Lomas Barbudal. Cambridge: Harvard University Press.
Perry SE, Rose L. 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. Primates 35:409–415.
Phillips KA. 1998. Tool use in wild capuchin monkeys (*Cebus albifrons trinitatis*). American Journal of Primatology 46: 259–261.
Powell R. 1991. The educational value of leaf-cutting ant colonies and their maintenance in captivity. International Zoo Yearbook 30:97–107.
Quinn JP. 2004. Fur rubbing behavior in a captive group of *Cebus apella apella* monkeys. Masters Abstracts 71.
Revis HC, Waller DA. 2004. Bactericidal and fungicidal activity of ant chemicals on feather parasites: an evaluation of anting behavior as a method of self-medication in songbirds. Auk 121:1262–1268.
Sugihara G, Heston K 1981. Field notes on winter flocks of the ocellated turkey (*Agriocharis ocellata*). Auk 98: 396–398.
Tewksbury JJ, Reagan KM, Machnicki NJ, Carlo TA, Haak DC, Calderón Peñaloza AL, Levey DJ. 2008. Evolutionary ecology of pungency in wild chilies. Proceedings of the National Academy of Sciences USA 105:11808–11811.
Valderrama X, Robinson JG, Attygalle AB, Eisner T. 2000. Seasonal anointment with millipedes in a wild primate: a chemical defense against insects? Journal of Chemical Ecology 26:2781–2790.
Verderane MP, Falótico T, Resende BD, Labruna MB, Izar P, Ottoni EB. 2007. Anting in a semifree-ranging group of *Cebus apella*. International Journal of Primatology 28: 47–53.
Weldon PJ, Aldrich JR, Klun JA, Oliver JE, Debboun M. 2003. Benzoquinones from millipedes deter mosquitoes and elicit self-anointing in capuchin monkeys (*Cebus* spp.). Naturwissenschaften 90:301–304.
White BC, Dew SE, Prather JR, Stearns MJ, Schneider E, Taylor S 2000. Chest-rubbing in captive woolly monkeys (*Lagothrix lagotricha*). Primates 41:185–188.
Xu Z, Stoddart DM, Ding H, Zhang J. 1995. Self-anointing behavior in the rice-field rat, *Rattus rattoides*. Journal of Mammalogy 76:1238–1241.
Young OP. 1982. Tree-rubbing behavior of a solitary male howler monkey. Primates 23:303–306.
Zito M, Evans S, Weldon PJ. 2003. Owl monkeys (*Aotus* spp.) self-anoint with plants and millipedes. Folia Primatologica 74:159–161.