

Owl Monkeys (*Aotus* spp.) Perform Self- and Social Anointing in Captivity

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Key Words

Owl monkeys · *Aotus* · Anointing · Millipede · Fur rubbing

Abstract

Several species of primates, including owl monkeys (*Aotus* spp.), anoint by rubbing their fur with odiferous substances. Previous research has shown that capuchin monkeys (*Cebus* and *Sapajus*) anoint socially by rubbing their bodies together in groups of two or more while anointing. Owl monkeys housed at the DuMond Conservancy have been observed to anoint over the last 10 years, and we report detailed new information on the anointing behavior of this population, including descriptions of social anointing which occurs frequently. We first investigated the occurrence of self-anointing in 35 *Aotus* spp. presented with millipedes. Detailed descriptions regarding body regions anointed were obtained for all anointers (n = 28). The median duration for a self-anointing bout was 3.6 min (range from approx. 2 s to 14.15 min). While the latency and length of anointing bouts showed considerable interindividual differences, no statistically significant differences were found between sexes, wild- or captive-born owl monkeys or across age groups. However, we found the lower back and tail were anointed at a rate significantly greater than other body parts, but there were no differences in these patterns across sex or wild- or captive-born owl monkeys. More recently, social anointing was investigated in 26 *Aotus* spp. presented with millipedes, of which half were observed to anoint socially. The average duration for all social anointing bouts was 72.88 s, with a median duration of 30 s (range 5–322 s). A detailed ethogram was also generated that included behaviors that were performed while anointing, including facial expressions and vocalizations. The intraindividual variability for 8 monkeys used in both investigations is discussed. These findings extend our knowledge of anointing and confirm the existence of social anointing in another genus with a unique biology (nocturnal and socially monogamous) distinct from capuchins.

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Introduction

Anointing is a fur-rubbing behavior and occurs in several taxa. Self-anointing (or solitary anointing) is typical and characterized as rubbing a material object or foreign substance over different parts of the body [Baker, 1996]. For example, mammals, such as primates, will rub a substance vigorously into their pelage. This striking anointing behavior was not known to be performed by owl monkeys (*Aotus* spp.) until Zito et al. [2003] documented this finding over a decade ago. Similarly, other mammals such as European hedgehogs (*Erinaceus europaeus*) [D'Havé et al., 2005], Siberian chipmunks (*Tamias sibiricus*) [Kobayashi and Watanabe, 1981] as well as various primates – e.g. white-faced capuchins (*Cebus capucinus*) [Baker 1996], spider monkeys (*Ateles geoffroyi*) [Campbell, 2000; Laska et al., 2007], orangutan (*Pongo pygmaeus wurmbii*) [Morrogh-Bernard, 2008] – have been observed to self-anoint as well.

Self-anointing is suggested largely to serve a medicinal function by repelling insects or removing potential vectors for disease [Baker, 1996] as well as being implicated in social and sexual communication [Laska et al., 2007] and influencing social interactions [Paukner and Suomi, 2008, 2012]. Additionally, the possibility that several species may simply self-anoint as a consequence of the reinforcing pleasure derived from interacting with anointing materials has been noted [Baker, 1996; Leca et al., 2007; Lynch Alfaro et al., 2012]. Also, birds are known to grasp arthropods in their beak and actively rub the insect's potential chemicals (e.g. formic acid from Formicidae ants) into their plumage; birds will also land on ant nests and passively allow ants to crawl over their skin [Simmons, 1966]. This behavior, known as anting in birds, is well documented [Groskin, 1943; Whitaker, 1957; Kelso and Nice, 1963; Potter, 1970] with multiple hypotheses regarding digestive, medicinal, maintenance and/or stimulating functions proposed to further explain this behavior [Revis and Waller, 2004].

A wide variety of anointing materials/substances has been observed to elicit this behavior. In *Cebus* spp., plants such as *Citrus*, *Piper*, *Eugenia*, *Capsicum* and *Allium* (onion) as well as millipedes and miscellaneous products including cologne, liquid soap and mud have been observed to elicit anointing behavior. *Sapajus* spp. are more selective, using primarily insects such as Formicidae and carpenter ants, wasps, millipedes and stinkbugs as well as mud and quartz powder [for a full review of anointing materials in each genus, see Lynch Alfaro et al., 2012]. Like capuchins, owl monkeys have been observed to use onion, garlic, live millipedes, millipede-produced benzoquinones and *Piper* leaf extract during anointing [Zito et al., 2003]. Owl monkeys have also been reported to use cinnamon, chives and moths (S. Evans, pers. observation) which have not been observed to be used by capuchins [Lynch Alfaro et al., 2012]. Owl monkeys, like capuchins, may use the millipede's defensive secretions (benzoquinones) for protection against mosquitos and harmful ectoparasites [Weldon et al., 2003; Weldon, 2004]. Finally, white-nosed coati (*Nasua narica* Linnaeus) have been observed in Panama to anoint using *Trattinnickia aspera* (Swart) (Burseraceae) resin for grooming themselves and other members of their group, indicating that the resin is also used within a social context in this mammal species [Gomper and Holyman, 1993].

Social anointing has been observed in capuchins and is becoming a topic of growing interest. For instance, a recent article reviewed self- and social anointing behavior in the genera *Cebus* and *Sapajus* [Lynch Alfaro et al., 2012]. Anointing in ca-

capuchins is distinguished into two distinct types of anointing: (1) individual/solitary anointing, in which individuals will anoint alone or simultaneously with others in the group without engaging in physical contact, and (2) anointing in a social context in which fur-rubbing bouts include contact made by two or more individuals [Baker, 1996; Quinn, 2004; Leca et al., 2007; Meunier et al., 2008]. Leca et al. [2007] demonstrated that white-faced capuchins socially anoint in subgroups with body contact and possibly recruit other group members, while tufted capuchins (*Sapajus* spp.) preferred to self-anoint during most bouts. Furthermore, Leca et al. [2007] suggested white-faced capuchins may socially anoint to strengthen relationships between group members; they socially anoint less discriminately than tufted capuchins. However, Paukner and Suomi [2008] found that tufted capuchins exhibit increased aggressiveness following bouts of fur-rubbing with an onion, indicating that anointing failed to reinforce affiliation or increase social cohesion between group members. Unlike capuchins, most aspects of owl monkey behavior, including anointing, remain to be explored [Fernandez-Duque, 2012]. Owl monkeys anoint naturally at the DuMond Conservancy for Primates and Tropical Forests, and social anointing has been observed anecdotally in this population for several years [Evans et al., 2003]. However, no study has ever described anointing in detail in owl monkeys or systematically explored social anointing in this genus. The purpose of this paper is to expand on the descriptions of anointing behavior in owl monkeys introduced by Zito et al. [2003] and further extend these descriptions to include anointing in a social context.

Anointing is not only unusual, but also composed of a suite of specific behaviors (e.g. vocalizations and social interactions such as millipede sharing may be observed concurrently with anointing [this study]). The following two studies performed at the DuMond Conservancy provide a detailed and comprehensive account of anointing in owl monkeys. The first study provides previously unpublished qualitative and quantitative data from 2002 on self-anointing, including information on different species, ages and sexes, as well as regarding the parts of the body anointed with millipedes. The largest group observed anointing together socially was one family of 4 owl monkeys during the 2002 study, which until then had been undocumented by observers. Although social anointing was not the focus of the first study, this observation prompted the second study, conducted in 2011, which explored the phenomenon in more detail. The latter of these two studies is the first to focus principally on social anointing in owl monkeys following the presentation of millipedes. Our findings are especially relevant to the growing literature on primate sociality because owl monkeys are unique social anointers. Owl monkeys are characterized as nocturnal with socially monogamous family groups [Wright, 1985] making them distinct from the diurnal activity and multi-male/multi-female social system of other primates known to anoint socially (*Cebus* spp. and *Sapajus* spp.).

Method

Owl monkeys were housed at the DuMond Conservancy for Primates and Tropical Forests, Miami, Fla., USA. All adult pairs and singly housed owl monkeys were housed in 2.4 m diameter × 2.4 m height cylindrical, wire mesh enclosures. Owl monkey family groups (1 adult male and female with 1 or more offspring) in each study were housed in 3 m diameter × 3 m height cylindrical, wire mesh enclosures. The outdoor enclosures are located in a densely wooded habitat at the DuMond Conservancy. The first study included 3 species (*A. nancymaae*, *A. azarae bolivien-*

sis and *A. lemurinus grisiemembra*) and 2 hybrid species (*A. lemurinus grisiemembra* × *A. azarae boliviensis* and *A. nigriceps* × *A. trivirgatus*). The second study included 2 species (*A. nancymaae* and *A. azarae boliviensis*) and 1 hybrid species (*A. nancymaae* × *A. azarae boliviensis*). Demographic information regarding species, sex and age of owl monkeys is provided for both studies in table 1a and b, respectively. Each session took place at dusk (ranging between 19.00 and 20.05 h during study 1 and between 18.15 and 20.15 h during study 2) in order to conduct each session during the period of activity for this largely nocturnal genus of New World primate.

Study 1

Thirty-five owl monkeys (*Aotus* spp.) were presented with millipedes in order to describe the self-anointing behavior for this genus. Four family groups, 9 adult pairs and 4 individuals were housed in 17 separate enclosures. From June to September 2002, there were 17 sessions (1 per enclosure), and the observers presented individuals within each enclosure with millipedes (*Anadenobolus monilicornis*, Spirobolida, Rhinocricidae) using 5–8 millipedes in a small plastic dish. These millipedes are a species previously introduced in Florida [Zito et al., 2003] and were collected from areas of dense foliage and moisture surrounding the enclosures at the DuMond Conservancy.

Bouts of self-anointing were recorded for individual monkeys. A bout began when an individual began to anoint by interacting with the millipede and ended after a 1-min cessation of anointing. Three observers recorded data on the latency to first anoint during a session as well as the number and duration of anointing bouts using behavioral sampling and continuous recording [Martin and Bateson, 1993]. The regions of the owl monkey's body that were anointed were recorded. Sessions ranged between 15 and 35 min, and a session was terminated once anointing ceased for at least 3 min, with 1 session terminated by deteriorated observation conditions because of failing light.

In an interobserver reliability test, a simple index of concordance (percentage agreement) [Martin and Bateson, 1993] was performed with an agreement of 92%. A Shapiro-Wilk test for normality revealed that the distribution of our data was nonnormal (duration: $p < 0.001$; latency: $p < 0.001$). We therefore performed a series of nonparametric statistical analyses to test hypotheses concerning whether differences in our dependent measures exist between owl monkeys with different biological characteristics (sex, origin of birth and age). A Mann-Whitney U test was used to analyze scores of latency to anoint and duration of anointing bouts (cumulative per individual) between sexes as well as between wild-caught and captive-born monkeys. A Kruskal-Wallis test was used to determine any differences in latency or duration scores between monkeys belonging to 4 separate age ranges in years (0–4; >4–10; >10–15; ≥15). Wild-caught animals were assigned into an age range based on their importation records. A χ^2 goodness-of-fit test and a test for independence were used to evaluate individual preferences for regions of the body anointed by owl monkeys. Finally, we evaluated intraindividual consistency in anointing bout duration. There is neither a previously estimated time established as the typical anointing duration time nor is there a prior method in the literature on designating anointing bouts as short or long for owl monkeys. We used the time encompassing the majority proportion of anointing bouts as a cutoff criterion to describe behavioral consistency in owl monkeys that anointed for 2 or more bouts within a session. Nonparametric tests were 2-tailed, and all statistical analyses were performed using the VassarStats statistical computational website (<http://vassarstats.net/>) and R statistical software with an alpha designated at 0.05.

Study 2

The extent of social anointing in this genus was determined by presenting 26 *Aotus* spp. from 3 family groups and 8 adult pairs with millipedes. A total of 8 owl monkeys tested in 2002 were also tested in this study and are identified in table 1b. Subjects were observed between January and June 2011. The same species of millipede was collected and presented to owl monkeys following the method described in study 1 (see above).

A total of 28 sessions were performed during the course of the study, with approximately 2 sessions performed per enclosure. Three observers defined 7 behaviors that had not been previously described for *Aotus* spp. (see ethogram, table 2). Then, the 3 observers recorded data on all

Table 1. A breakdown of the demographic information relating to the species, sex and age of each owl monkey housed individually (I), in a pair (P) or family group (FG)

a List of *Aotus* spp. subjects from 2002

| Housing | Individual | Species | Sex | Age |
|---|------------|--|-----|----------|
| <i>Owl monkeys that socially anointed</i> | | | | |
| FG18 | Lavender | <i>A. nancymaae</i> | F | WC |
| FG18 | Buster | <i>A. nancymaae</i> | M | WC |
| FG18 | Lilac | <i>A. nancymaae</i> | F | 3 years |
| FG18 | Lily | <i>A. nancymaae</i> | F | 1 year |
| <i>Owl monkeys that self-anointed only</i> | | | | |
| P01 | Violet | <i>A. nancymaae</i> | F | 5 years |
| P01 | Needles | <i>A. nancymaae</i> | M | 5 years |
| P03 | Chewbaka | <i>A. lemurinis grisiemembra</i> × <i>A. azarae boliviensis</i> | M | 13 years |
| P03 | Missy | <i>A. nancymaae</i> | F | WC |
| P05 | Georgie | <i>A. azarae boliviensis</i> | F | 11 years |
| P05 | Gallileo | <i>A. azarae boliviensis</i> | M | 16 years |
| P06 | Darwin | <i>A. nancymaae</i> | M | WC |
| P07 | Matilda | <i>A. nancymaae</i> | F | WC |
| P07 | Winky | <i>A. nancymaae</i> | M | WC |
| P08 | Ashley | <i>A. nancymaae</i> | M | 6 years |
| P19 | Mango | <i>A. lemurinis grisiemembra</i> | F | 18 years |
| P19 | Warrior | <i>A. lemurinis grisiemembra</i> | M | WC |
| P20 | Peanut | <i>A. nancymaae</i> | M | WC |
| P20 | Betsy | <i>A. azarae boliviensis</i> | F | WC |
| FG14 | 400 | <i>A. nigriceps</i> × <i>A. trivirgatus</i> | M | 7 years |
| FG14 | Ollie | <i>A. nigriceps</i> | M | WC |
| FG16 | Rhett | <i>A. nancymaae</i> | M | WC |
| FG16 | Cola | <i>A. nancymaae</i> | F | 3 years |
| FG16 | Scarlet | <i>A. nancymaae</i> | F | WC |
| FG17 | Theo | <i>A. nancymaae</i> | M | 2 years |
| I02 | Han Solo | <i>A. nancymaae</i> | M | WC |
| I12 | Rose | <i>A. nancymaae</i> | F | 4 years |
| I13 | Pinegirl | <i>A. nancymaae</i> | F | 3 years |
| I15 | Carradog | <i>A. nancymaae</i> | M | 6 years |
| <i>Owl monkeys that did not anoint (self or social)</i> | | | | |
| P06 | Cat | <i>A. nancymaae</i> | F | 4 years |
| P08 | Nina | <i>A. nancymaae</i> | F | 5 years |
| P09 | Marylyn | <i>A. nancymaae</i> | F | 9 years |
| P09 | Sammy | <i>A. nancymaae</i> | M | WC |
| FG14 | Santa | <i>A. nigriceps</i> × <i>A. trivirgatus</i> | M | 8 years |
| FG16 | MC 85 | <i>A. nancymaae</i> | F | 2 years |
| FG17 | Yanni | <i>A. nancymaae</i> | M | WC |

Table 1 (continued)**b** List of *Aotus* spp. subjects from 2011

| Housing | Individual | Species | Sex | Age |
|---|------------|--|-----|----------|
| <i>Owl monkeys that socially anointed</i> | | | | |
| P10 | Stevie | <i>A. nancymaae</i> | M | 16 years |
| P10 | Georgie* | <i>A. azarae boliviensis</i> | F | 20 years |
| P18 | Mr. Fuzzy | <i>A. azarae boliviensis</i> | M | 10 years |
| P18 | Miss Fuzzy | <i>A. azarae boliviensis</i> | F | 11 years |
| P4 | Missy* | <i>A. nancymaae</i> | F | WC |
| P4 | Dean | <i>A. nancymaae</i> | M | 8 years |
| P8 | Nina* | <i>A. nancymaae</i> | F | 14 years |
| P8 | Vincent | <i>A. nancymaae</i> | M | WC |
| P12 | Mojo | <i>A. nancymaae</i> | M | 15 years |
| P12 | Cleo | <i>A. nancymaae</i> | F | 11 years |
| FG20 | Betsy* | <i>A. azarae boliviensis</i> | F | WC |
| FG20 | Peanut* | <i>A. nancymaae</i> | M | WC |
| FG20 | Crunchy | <i>A. nancymaae</i> × <i>A. azarae boliviensis</i> | F | 4 years |
| <i>Owl monkeys that self-anointed only</i> | | | | |
| P2 | Connie | <i>A. nancymaae</i> | F | WC |
| P2 | Spruce | <i>A. nancymaae</i> | F | 8 years |
| P5 | Dorie | <i>A. nancymaae</i> | F | 5 years |
| P5 | Curie | <i>A. nancymaae</i> | M | 7 years |
| P13 | Yanni* | <i>A. nancymaae</i> | M | WC |
| P13 | Pinegirl* | <i>A. nancymaae</i> | F | 12 years |
| FG9 | Judy | <i>A. nancymaae</i> | F | 2 years |
| FG9 | Lawford | <i>A. nancymaae</i> | M | 7 years |
| FG9 | Juliet | <i>A. nancymaae</i> | F | 6 years |
| <i>Owl monkeys that did not anoint (self or social)</i> | | | | |
| FG15 | Hootie | <i>A. nancymaae</i> | F | 3 years |
| FG15 | Rose* | <i>A. nancymaae</i> | F | 13 years |
| FG15 | Gill | <i>A. nancymaae</i> | M | WC |
| FG15 | Iago | <i>A. nancymaae</i> | M | 4 years |

The abbreviation WC denotes an owl monkey that was born in the wild. Asterisks denote individual subjects used in both studies (n = 8).

occurrences (continuous recording) of the behaviors included in the ethogram as well as the frequency and duration of social anointing bouts during each session. An arithmetic mean of duration was calculated for each enclosure group that socially anointed, with the arithmetic mean of all social anointing bouts reported below. A bout of social anointing was defined as any period during which 2 or more of the subjects established physical contact and rubbed their bodies against each other while anointing. Each social anointing bout ended when all the monkeys involved physically separated and were beyond arm's reach of one another (approx. 20 cm). Once subjects were presented with millipedes, they were observed for 5-min periods to record the frequency and duration of each bout of social anointing. If an individual owl monkey did not anoint within the first 5 min (either individually or socially), then the session was terminated, and the

Table 2. Ethogram of behaviors observed during anointing

| Behavior | Definition | Reference |
|--|--|---------------------------|
| Anointing | In the presence of an eliciting substance, the entire hand including fingers and palm is pressed or rubbed into the fur in one or many regions of the body | this study |
| Social anointing | Two or more monkeys simultaneously rub against each other while anointing, transferring the eliciting object or substance from their fur to others (or vice versa) | this study |
| <i>Behaviors exclusive to social anointing</i> | | |
| Alloanointing | Using the hands to rub the eliciting object or substance into the fur of another | this study |
| <i>Behaviors during anointing (self or social)</i> | | |
| Millipede transfer | Movement of [millipede] from the hand or mouth of one monkey to the hand or mouth of another monkey | Wolovich et al. [2006] |
| Begging for millipede | Potential recipient extending hand or mouth toward [millipede] held by possessor regardless of whether approach was initiated by the recipient or possessor | Wolovich et al. [2006] |
| Drooling | Saliva exuding from the mouth slowly | this study |
| Writhing | Moving with a twisting or contorted motion while rubbing body against the walls of an enclosure or against the body of another monkey | this study |
| Teeth barring | Mouth is open, with the jaws clenched or apart; may be accompanied by a squint | this study |
| Reach back | Reach onto the back with one hand, either with or without eliciting substance in hand, typically initiates anointing | this study |
| <i>Behaviors not exclusive to anointing</i> | | |
| Lip smack | Quick, repeated opening and closing of mouth without food in mouth | Wolovich and Evans [2007] |
| Squint | Both eyes slightly close for ≥ 1 s | Wolovich and Evans [2007] |
| Mount | Male approaches female from behind and grasps the female's lower back with both hands while placing his pubic area against her anogenital region | Moynihan [1964] |
| Tail twine | Two monkey tails overlap in a region other than the base of the tail | Wolovich and Evans [2007] |
| Sneeze | A rapid audible exhalation of air | Moynihan [1964] |
| Social sniff (nose) | Moves nose towards another monkey's nose (≤ 1 cm) when neither monkey possesses food | Moynihan [1964] |
| <i>Vocalizations heard during anointing</i> | | |
| Trills/purrs ^{a, b, c} | A 'bubbling' series of low-pitched notes, uttered very rapidly one right after the next | Moynihan [1964] |
| Hoots ^{a, c} | Low-pitched, moderately prolonged and moderately loud sounds | Moynihan [1964] |
| Chirps/peeps ^{a, b, c} | Both given as high-frequency alarm calls | Herrera, unpubl. |

Superscript letters denote whether vocalizations occurred during self-anointing (^a), social anointing (^b) or outside the context of anointing (^c).

subject(s) was identified for the purpose of this study as a nonanointer. If an individual owl monkey anointed (either individually or socially), the observation would continue for an additional 5 or 10 min, and for a maximum of 15 min, if anointing continued during the session. The observers from study 2 reached a percentage agreement of 96% for behaviors observed using the reliability test described in study 1.

Results

Study 1

Self-anointing was observed in our population of owl monkeys from 2002. Owl monkeys used their hands to manipulate the millipede, holding it in place while biting onto it and subsequently using their hands to rapidly rub the millipede into their fur and various areas of the body. There were a total of 47 bouts of self-anointing from 17 sessions. Twenty-eight out of a total 35 monkeys (80%) self-anointed, with 7 monkeys (20%) not performing the behavior at all. The median latency to self-anoint was 3.6 min with a range from 0 (i.e. immediately) to 28.2 min. The median duration for a self-anointing bout was 3.73 min (range from approx. 2 s to 14.15 min), with an interquartile range of 5.7 min. A Mann-Whitney U test failed to detect a difference in the latency to first anoint [$U(1) = 119$, $p = 0.33$, $r = 0.18$] between male (median = 3.15 min; $n = 15$) and female (median = 4.45 min; $n = 13$) anointers. Additionally, no difference was detected for cumulative duration of anointing bouts [$U(1) = 106$, $p = 0.71$, $r = 0.07$] between male (median = 3.1 min) and female (median = 4.2 min) anointers. Figure 1a compares the distribution of cumulative duration and latency scores between sexes, whereas figure 1b compares these score distributions according to birth categories (wild-caught or captive-born). Similarly, no difference was detected for latency [$U(1) = 106.5$, $p = 0.70$, $r = 0.07$] between wild-caught (median = 4.05 min; $n = 13$) and captive-born (median = 3.15 min; $n = 15$) owl monkeys. Our test also failed to detect a difference for cumulative duration [$U(1) = 75.5$, $p = 0.32$, $r = 0.19$] between wild-caught (median = 186 s) and captive-born (median = 324 s) owl monkeys. Similar to our latency measures in figure 1b, our data on the cumulative duration of anointing bouts for wild-caught monkeys contained 1 outlier that anointed for 15 min (in fact over 2 times greater than the next-largest duration: 6.35 min). We performed a secondary analysis excluding this data point. However, our Mann-Whitney U test did not reveal a difference in cumulative duration with this exclusion [$U(1) = 61.5$, $p = 0.16$, $r = 0.26$]. A Kruskal-Wallis test failed to detect a difference between our age groups in their cumulative duration score [$H(3) = 2.64$, $p = 0.45$], with a median of 3.4 min for monkeys aged 0–4 years ($n = 5$), 1.15 min for those aged 4–10 years ($n = 6$), 3.13 min for those aged 10–15 years ($n = 6$) and 4.2 min for monkeys aged ≥ 15 years ($n = 11$). Furthermore, no difference was found between age groups for their latencies [$H(3) = 5.48$, $p = 0.14$] with a median of 4.07 min for the youngest age group, 3.1 min for the second age group, 4.05 min for the third and 3.15 min for the oldest age group. Individuals of every species investigated were observed to anoint (note: no *A. trivirgatus* were represented in either study, but an *A. nigriceps* \times *A. trivirgatus* hybrid was observed to anoint; table 1a).

Analysis of body parts anointed revealed that the lower back (28%), base/length of tail (23%) and outer thigh (11.5%) were the 3 most frequently anointed regions out of the 19 body parts observed to be anointed by owl monkeys (listed in descending

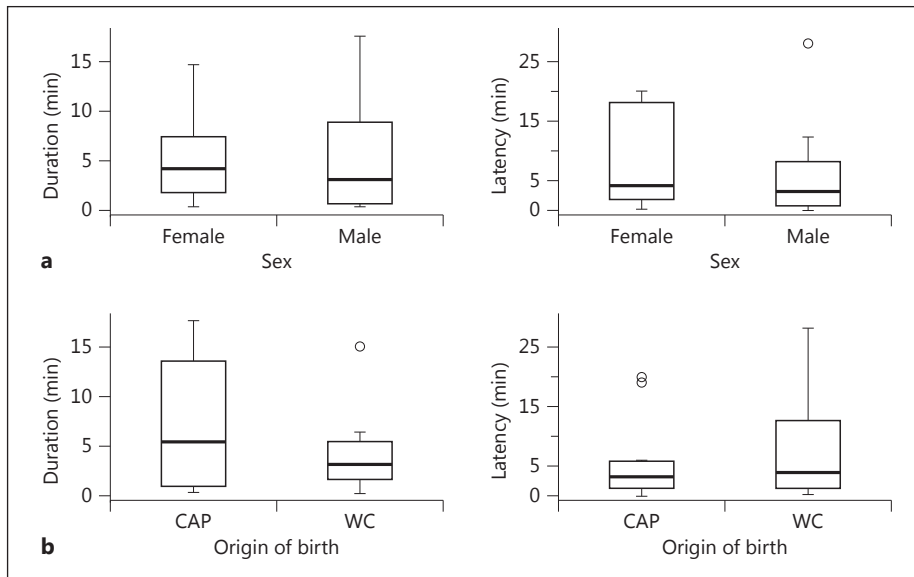


Fig. 1. Distribution of duration and latency scores for all self-anointing bouts recorded in study 1 and grouped by sex (**a**) and birth (**b**) category; CAP = captive-born; WC = wild-caught. The bold horizontal bar represents the median; the box plotted contains the central 50% of data (box limits reflect lower and upper quartiles, respectively). Whiskers represent the range of data excluding the outliers which are plotted as open circles and are 3/2 times greater than the upper quartile.

order from most frequently anointed: (1st) lower back; (2nd) base/length of tail; (3rd) outer thigh; (4th) inner thigh; (tied 5th) end of tail and abdomen; (tied 7th) upper back, perineum, feet, arms, hands, and chest; (tied 13th) head, middle back, dorsal cervical area, sides, shins, neck and underarms. A χ^2 goodness-of-fit test revealed that individual preference for regions of the body anointed following the presentation of a millipede was statistically significant [$\chi^2(18) = 154.16, p < 0.01$]. Further analysis of the first body part anointed at the start of a session indicated a similar preference. Of the same 19 regions, the lower back was anointed first 57% of the time and second 35%. Furthermore, the base/length of tail (first: 32%; second: 19%) and outer thigh (first: 7%; second: 12%) were preferred at the onset of anointing as well. Our χ^2 analysis indicated that these differences in which regions were anointed first [$\chi^2(18) = 70.01, p < 0.01$] and second [$\chi^2(18) = 59.03, p < 0.01$] were statistically significant. Our χ^2 test for independence failed to detect differences between sex [$\chi^2(2) = 3.14, p = 0.21$] or between captive-born and wild-caught monkeys [$\chi^2(2) = 1.77, p = 0.41$] with regard to these 3 regions preferred most when first anointing. That is, the frequency with which owl monkeys anoint any of these 3 regions first did not differ between the sexes or between wild-caught and captive-born owl monkeys.

We observed intraindividual consistency in anointing bout duration as well as interindividual variability between individuals that anointed for more than 1 bout ($n = 12$). Approximately 52% of all self-anointing bouts were less than 2 min, and 48%

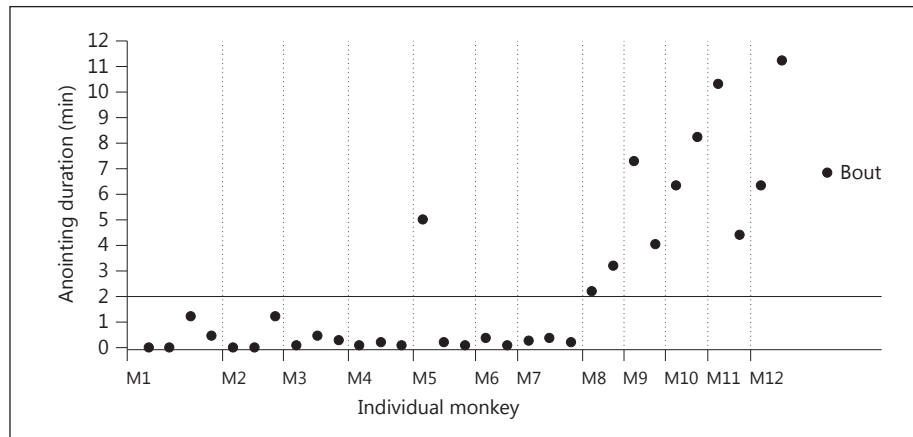


Fig. 2. Twelve *Aotus* spp. show individual differences in anointing behavior. When subjects anoint more than once, their bout durations tend to either be routinely short (less than 2 min) or long (2 min or more).

were between 2 and 14.15 min. We simply described individual anointing bouts as either characteristically short (less than 2 min; $n = 6$) or longer than what was typical of the 52% majority (2 or more min; $n = 5$) when an individual anointed more than once during a session. We made these designations because of the degree of variation in duration spread across the latter 48% of monkeys that anointed for more than 2 min and more than once. One monkey was observed to anoint for variable durations. Figure 2 distinguishes between short bout ($n = 20$) and long bout ($n = 11$) durations for 12 owl monkeys observed to anoint twice or more and summarizes the observed consistency in anointing duration per individual and in differences across individuals. Finally, although social anointing was not the primary focus of the first study, one case of social anointing was observed in one family group (FG18; table 1a) in which members of this group not only self-anointed, but also socially anointed by rubbing up against one another simultaneously as one group.

Study 2

We observed a total of 23 separate bouts of social anointing out of the 28 sessions performed in 2011. Thirteen owl monkeys (50% of the study population) from 5 adult pairs and 1 family group were observed to socially anoint simultaneously by rubbing their bodies against another individual(s) that was also anointing. Information regarding the arithmetic mean for social anointing duration per enclosure is summarized in table 3. The total arithmetic mean for the duration of all social anointing bouts was calculated as 72.88 s (median = 30 s; range from 5 to 322 s). Descriptive statistics and the distribution of duration scores are illustrated in the boxplot in figure 3. Nine owl monkeys from 3 pairs and 1 family group were observed to only self-anoint (35%), while 1 family group comprised of 4 monkeys did not anoint at all (15%). A total of 40 bouts of self-anointing were recorded using the initiation and termination criterion for bouts in study 1.

Fig. 3. Distribution of duration scores for all social anointing bouts recorded in study 2. The bold horizontal bar represents the median (30 s); the box plotted contains the central 50% of data (box limits reflect lower and upper quartiles, respectively). Whiskers represent the range of data excluding the outliers which are plotted as open circles and are 3/2 times greater than the upper quartile.

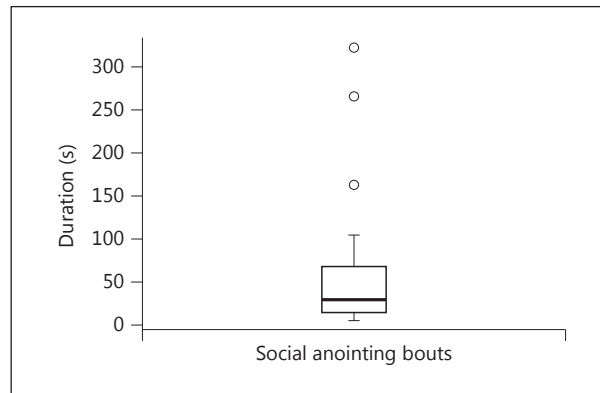


Table 3. Summary of data collected from social anointers

| Owl monkeys that socially anointed | Monkeys in enclosure, n | Sessions, n | Social anointing bouts, n | Arithmetic mean of duration, s |
|------------------------------------|-------------------------|---------------|---------------------------|--------------------------------|
| <i>Enclosure</i> | | | | |
| Pair 10 | 2 | 4 | 7 (2 sessions) | 41.71 |
| Pair 18 | 2 | 2 | 2 (2 sessions) | 138 |
| Pair 4 | 2 | 4 | 2 (1 session) | 5.5 |
| Pair 8 | 2 | 2 | 1 (1 session) | 24 |
| Pair 12 | 2 | 2 | 5 (2 sessions) | 88 |
| Family group 20 | 3 | 2 | 6 (2 sessions) | 67.17 |
| <i>Total</i> | 13 (26 total) | 16 (28 total) | 23 (10 sessions) | 72.88 |

Five adult pairs and 1 family group socially anointed.

Writhing was seen frequently among individual and social anointers, but other behaviors were seen less frequently: reaching back ($n = 16$), millipede transfers ($n = 9$), eye squinting ($n = 7$), lip smacks ($n = 6$), drooling ($n = 3$), teeth barring ($n = 2$), mount ($n = 2$) and begging for the millipede ($n = 2$). Our monkeys emitted vocalizations such as chirps and trills during self- and social anointing. Two cases of allo-anointing were observed in this study and exclusively during social anointing. The regions of the body that an individual owl monkey anointed during social anointing included the dorsolateral trunk, head, base and terminal section of the tail, hands and hind feet, extremities and proximal areas of the shoulder and hips. Figure 4 illustrates some of the different anointing behaviors observed in this study.

Eight owl monkeys from study 1 were included in this study with intraindividual variability demonstrated between these two studies. Four monkeys who originally were self-anointers in 2002 now socially anointed with their respective mates/family members (Betsy, Georgie, Missy and Peanut). One female (Pinegirl) remained a self-

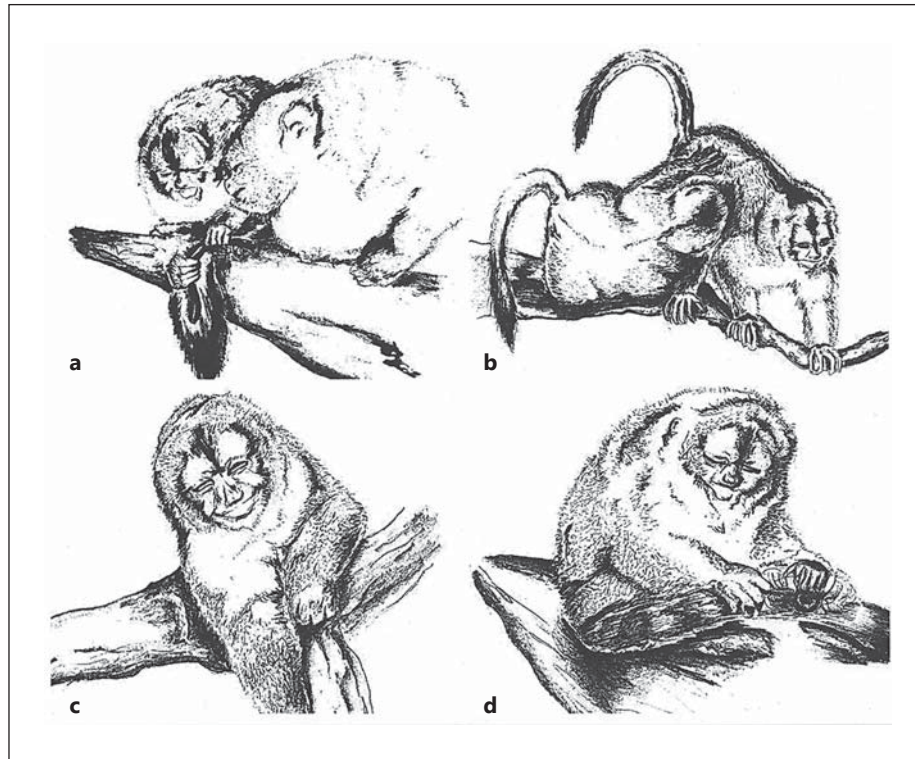


Fig. 4. Different owl monkey behaviors observed during anointing. **a** Millipede sharing. **b** Twisting of the body against a family member. **c** Squinting of the eyes. **d** Vigorous self-anointing of the tail with a millipede. Illustrations by Michael J. Hernandez-Salazar.

anointer in 2002 and this study. One male (Yanni) and one female (Nina) that did not anoint in the first study were observed to self-anoint and socially anoint, respectively, in this study and with different social companions. In contrast, a self-anointing female (Rose) that did self-anoint while housed alone in the first study was not observed to anoint at all in this study and neither did any of her social companions (FG15; table 1b). Of these 8 monkeys, Pinegirl and Rose were the only 2 to go from an individually housed to socially housed arrangement. Finally, *A. nancymaae* comprised approximately 82% of our monkeys investigated in study 2 (excluding hybrids). Of these *A. nancymaae*, 38% socially anointed and 43% only self-anointed (81% self-anointed when including social anointers – all of which self-anointed).

General Discussion

We described individual and social anointing behavior in *Aotus* spp. with live millipedes. Owl monkeys vigorously rubbed the foreign object or substance against themselves as well as engaged in physical contact with their pair partner and/or oth-

er family group members. We have demonstrated that anointing is a very robust behavior observed in the 5 species investigated from both studies. The observation that all but 1 nonanointer were *A. nancymaae* (excluding 1 *A. nigriceps* × *A. trivirgatus* hybrid) is likely due to their overwhelming overrepresentation in this colony. No differences were observed between the two sexes, wild caught versus captive born, or across age groups. The distribution of data in figure 1b demonstrates slight differences in which wild-caught owl monkeys self-anoint for shorter durations and take longer to start anointing. Although not significant, this information may indicate subtle influences that an animal's life history may have on their behavioral repertoire, which is also borne out by the observation that hand-raised owl monkeys very readily anoint (S. Evans, pers. observation).

There is currently no information on anointing in wild owl monkeys. Therefore, until more information is obtained, it will be difficult to know if the potential diversity of anointing materials (including millipedes) or relative abundance of these materials in the wild may contribute to behavioral differences and offer a possible avenue of future research. The millipede species used in these studies is believed to have been introduced to South Florida in, at the latest, 2001 [Carreno et al., 2013], shortly before our first study in the owl monkey habitat. This may in part explain the slight differences we observed between wild-caught and captive-born monkeys given their probable limited familiarity with this particular anointing object.

Our findings extend our knowledge of social anointing to a new genus of neotropical primate and emphasize similarities in anointing style between capuchins and owl monkeys, as indicated by the areas of the body that were anointed as well as their similar use of millipedes [Lynch Alfaro et al., 2012]. The significant preference to anoint the lower back recorded in our first study coincides with the frequency of performing the 'reach back' behavior noted in our second study (table 2), which has also been observed in capuchins [Weldon et al., 2003] and provides a more complete picture of the behavioral processes which occur during anointing. Owl monkeys have been observed to reach back frequently in anticipation of a familiar anointing substance (e.g. millipedes) suggesting that this behavior is characteristic of anointing (S. Evans, pers. observation). Like capuchins, owl monkeys initially use their hands to manipulate or bite the millipede, then they use their hands to rub the substance throughout their own fur and body as well as any other's by rubbing themselves or the millipede against conspecifics [Baker, 1996]. Also, owl monkeys were observed to share the millipede just like the wedged-capped capuchins (*Cebus olivaceus*) observed by Valderrama et al. [2000]. Millipedes elicit a strong anointing response in *Aotus* spp. [Evans et al., 2003], and we observed energetic and vigorous self- and social anointing that featured the same characteristic drooling and writhing described in *Cebus* spp. [Baker, 1996; Weldon et al., 2003] as well as the additional behaviors described in this study.

It is suggested that anointing serves several different functions, largely related to medicinal strategies against potential vectors of disease [Weldon, 2004] as well as in social communication. The medicinal application of foreign substances as a potential explanation for self-directed anointing in primates is well documented within the literature, ranging from the black lemur's (*Eulemur macaco*) use of millipedes [Birkinshaw, 1999] to the use of *Commelina* by orangutans as a possible antibacterial [Morrow-Bernard, 2008]. Topical treatment using plants and insect-produced chemicals can reduce potential health complications by treating wounds and skin problems.

Similarly, anointing can work 'defensively' against ectoparasites, microbial pathogens and/or other vectors for disease given the repelling and insecticidal properties of the various anointing materials used [Valderrama et al., 2000; Weldon, 2004; Lynch Alfaro et al., 2012]. The generally hot and humid climate and habitat of Miami, Fla., yield ideal conditions for abundant populations of mosquito species to thrive [Rey et al., 2006]. While it is possible that anointing with millipedes can protect owl monkeys from mosquitoes in this environment, further studies are needed to confirm this.

A social function has also been proposed for anointing behavior [Baker, 1996; Leca et al., 2007; Meunier et al., 2008; Paukner and Suomi, 2008]. For example, black-handed spider monkeys in Panama have been reported to self-anoint using 3 separate Rutaceae species; it is suggested that this behavior may have a social function in scent marking that relies primarily on olfactory communication [Campbell, 2000]. Observations on free-ranging spider monkeys in Mexico revealed that anointing had no correlation with seasonality, temperature, humidity or time of day, when protection against noxious stimuli or skin infection would be most relevant [Laska et al., 2007]. The aromatic odors produced by these selected plant materials may serve to communicate social status or possibly increase sexual attractiveness [Laska et al., 2007] in ways that likely involve glands located on the sternal region of the trunk [Campbell, 2000].

The function of social anointing is less clear, but it may assist in the transferring of an odiferous substance from the fur of one social companion to another. Social anointing between white-faced capuchins is suggested, like grooming, to provide an affiliative function that strengthens the relationship(s) between members and social cohesion within this species [Baker, 1996]. In one study, individual tufted capuchins that were separated from their group and then reintroduced after self-anointing received more aggression and less affiliation from group members (although the anointed individual's overt behavior was not reported to have changed), also indicating that self-anointing can significantly influence patterns of social behavior between group members [Paukner and Suomi, 2012].

Future research should investigate the patterns of aggression and affiliation within owl monkey family groups in the periods before, during and following social anointing in order to systematically record data on the possible bonding function of this unusual phenomenon. Also, the role of social experience with pair partners may have influenced anointing behavior and be responsible for the intraindividual differences observed in the 8 monkeys used in both studies who could have changed their anointing behavior to match that of their social companions. These differences could be further explored by investigating differences between pairs in their anointing behavior (including categorical measures of anointing intensity, duration latency; fig. 2) and differences between individuals in regard to their rates of self- and social anointing. A more comprehensive account of the function of anointing behavior could be made clearer by focusing on the social interactions that occur concurrently with self- and social anointing in pairs and family groups. These studies are the first to provide a detailed description of self-anointing in *Aotus* spp. as well as confirm the existence of social anointing behavior in this genus.

Acknowledgments

The authors thank John Giovannetti, Cher Moody, Eric Vicaria and Bruce Ramil for assisting in data collection and Michael J. Hernandez-Salazar for his illustrations. We also thank 3 anonymous referees for their insightful comments during the development of this paper. All procedures were approved and performed in compliance with the DuMond Conservancy Institutional Animal Care and Use Committee protocols No. 2001-06 and 2007-04.

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