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Sociosexual Behavior and Chemical Communication of *Aotus nancymaae*

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Abstract Owl monkeys (*Aotus* spp.) are unique because they are the only nocturnal anthropoids. Though medical researchers have used them extensively, thorough descriptions of their social behavior are sparse. We examined in detail the social behavior of 12 male-female captive pairs of *Aotus nancymaae* over an entire year. We compared data from males and females to determine if there are sexual differences in scent-marking, allogrooming, and other sociosexual behavior. We compared observation periods with and without mounting to determine if any behavior is associated with mounting. We present previously unreported behaviors for *Aotus* including urine-drinking and a suite of behaviors that we consider to function in olfactory communication. Males and females differed in their rates of several sociosexual behaviors; males anogenitally sniffed, drank urine, touched, and marked their mates more frequently than females did. We confirm earlier suggestions that allogrooming is rare in *Aotus* and is associated with mounting. Pairs of owl monkeys did not regularly exhibit behaviors that are typical for most monogamous primates but instead displayed a unique suite of behaviors adapted for their nocturnal lifestyle.

Keywords olfaction · pair-bond · scent marking · subcaudal gland · urine drink

Introduction

Owl monkeys (*Aotus* spp.) are nocturnal, and their social behavior is poorly known despite frequent utilization in medical research (Collins 1994; King 1994; Ogden

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1994). They are socially monogamous and live in small groups comprising a single male-female adult pair and ≤3 offspring (Aquino and Encarnación 1994; Fernandez-Duque 2007; Wright 1978, 1985). Monogamous primates typically exhibit pair-specific behaviors such as allogrooming (Carroll 1985; Kleiman 1977; Palombit 1996), embracing (Palombit 1996), joint vocal displays (Muller and Anzenberger 2002), tail-twining (Welker *et al.* 1998), and remaining within close proximity of one another (Fernandez-Duque *et al.* 2000). Kleiman (1977) suggested that the behaviors strengthen the pair bond between the male and female. Because owl monkeys are nocturnal, they may not use the same visual, tactile, and acoustic cues that diurnal species use for their sociosexual interactions. For instance, owl monkeys allogroom rarely and do so immediately before or after copulations (Moynihan 1964). Also, contrary to most other monogamous primates, owl monkeys do not perform vocal duets (Moynihan 1964; Wright 1985).

Owl monkeys may rely on chemical cues for communication between mates and with other conspecifics. Bolen and Green (1997) and Hunter and Dixson (1983) suggested that they use olfaction more than some diurnal primates do. For example, an experimental study revealed that *Aotus nancymaae* successfully use olfactory cues for foraging more than *Cebus apella* do (Bolen and Green 1997). It is likely that owl monkeys also use olfaction for social communication. When researchers experimentally limited olfaction, levels of intrasexual aggression declined, suggesting that chemical signals are important in intraspecific communication (Hunter and Dixson 1983).

Owl monkeys can produce an array of cutaneous chemical cues. They are the only primates with a subcaudal gland (Hanson and Montagna 1962). Scent-marking with it consists of rubbing the perineal region from side to side as the hair over the gland brushes against a substrate (Moynihan 1964). Owl monkeys also have glands on their muzzles and sternal areas (Hanson and Montagna 1962), and captive owl monkeys sniff the muzzles and anogenital areas of conspecifics (Moynihan 1964). Researchers have not described owl monkeys using their sternal glands (Hanson and Montagna 1962; Moynihan 1964; Wright 1985) or the glands on their muzzles to mark surfaces. Because scent-marking is likely to be important in owl monkey communication, a greater understanding of their social behavior would be gained by examining their patterns of scent-marking.

Wild owl monkeys are difficult to observe, and monkeys in laboratories are not likely to exhibit species-typical behaviors; therefore, a seminatural environment is best to study the details of owl monkey sociosexual behavior. The DuMond Conservancy for Primates and Tropical Forests, Inc. (Miami, FL) houses owl monkeys outdoors in a subtropical climate where individuals are exposed to seminatural conditions including fluctuations in moonlight and temperature, which affect behavior in the wild (Fernandez-Duque 2003; Fernandez-Duque and Erkert 2006). The owl monkeys exhibit patterns of birth seasonality similar to that in wild *Aotus azarai* in Argentina (Fernandez-Duque *et al.* 2002; Holbrook *et al.* 2004).

We aimed to describe qualitatively the social interactions between mates as well as to quantify sexual differences in the behavior of captive owl monkeys (*Aotus nancymaae*). We focused particularly on behaviors associated with mating. We especially aimed to describe patterns of scent-marking and predicted that owl monkeys would rely heavily on chemical cues for male-female communication.

Methods

Subjects and Housing

Pairs of captive owl monkeys (*Aotus nancymaae*) at the DuMond Conservancy for Primates and Tropical Forests, Inc. (Miami, FL, USA) consisting of 1 adult male and 1 adult female were in 2.4 m diameter × 2.4 m height cylindrical wire mesh outdoor enclosures. Families of owl monkeys (pairs of adults with offspring) lived in 3 m×3 m cylindrical wire mesh enclosures. Both sizes of enclosures contain a nest box and a variety of perches and platforms. The enclosures are visually separated from one another by dense foliage, but vocalizations from conspecifics in nearby enclosures are audible and olfactory cues may be detectable. We fed the owl monkeys 3 types of monkey chow (LabDiet®) and a fruit and vegetable mix in the early evenings just after sunset. Because the monkeys lived outdoors, they could forage for leaves inside or adjacent to their enclosures as well as for small arthropods and lizards that entered them.

Wolovich observed 12 male-female pairs of captive owl monkeys twice a month from October 2003 to November 2004. Six pairs were newly formed (<1 yr together) and had no offspring at the start of the study. Six pairs were established and had offspring at the start of the study. Wolovich observed 2 or 3 groups each night according to a schedule that was created by pseudorandomizing the order of observations to control for potential cyclical effects of moonlight and female reproductive hormones.

Behavioral Observations

Observations began at dusk or within the following 2 h, after the monkeys had finished eating all of the fruit from their evening feeding. The time corresponds to the time of the night when owl monkeys are most active (Wright 1985). Because owl monkeys are least sensitive to light in the red spectrum (Jacobs 1977), Wolovich used a flashlight with the lens covered by red cellophane to aid in observing behaviors and to identify individuals.

Wolovich monitored both the adult male and female via focal dyad sampling with continuous recording of all social interactions and scent-marking (Table I) during 20-min observation periods. We observed each pair *ca.* twice a month (median=23.5 total observation periods). An older male in 1 pair died 6 mo into the study, which lowered the number of observation periods for that pair (n=14 observation periods). Wolovich recorded the data by hand via a check-sheet. She recorded all approaches to within an arm's reach and withdrawals from within an arm's reach of the subjects' mates to determine if either sex was more responsible for the maintenance of close proximity via Hinde's index of association (Hinde and Spencer-Booth 1967). Wolovich noted any behavior that researchers had not previously described for *Aotus*, operationally defined them, and included them in Table I. She observed the 12 owl monkey pairs for a total of 92 h.

Statistical Analyses

We used Systat version 11.0 for all statistical analyses. We calculated the overall rate (per hour) of each sociosexual behavior for each individual. We used Mann-Whitney

Table I Ethogram of sociosexual behavior for captive owl monkeys

Behavior	Definition	Reference
Allogroom	Touch another individual with added movement of the mouth or fingers	Moynihan 1964
Arch	Back is raised and strongly curved	Moynihan 1964
Squint	Both eyes slightly close for ≥1 s	This study
Food transfer	Movement of food from the hand or mouth of one monkey to the hand or mouth of another monkey	Wolovich *et al.* 2006
Gruff grunt	2–5 notes of low-pitched moderately loud vocalizations uttered with mouth closed but with inflation of the gular sac	Moynihan 1964
Hoot	2 –6 moderately loud pulses (230–380 Hz), each lasting *ca*. 165 ms with no harmonic structure	Moynihan 1964; Wright 1985
Lip-smack	Quick, repeated opening and closing of mouth without food in mouth	This study
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
Partner-marking	Rubs subcaudal gland over the back or head of their mate	This study
Pilo-erection	Hair on tail and body stands out	Wright 1978
Resonant whoop	10–17 notes that increase in volume and intensity; produced by expanding the gular sac	Moynihan 1964; Wright 1978
Scent-mark	Subcaudal: rubs subcaudal gland (at base of tail) against a substrate	Moynihan 1964
	Face: rubs cheek region against a substrate (muzzle rubbing)	Moynihan 1964
	Sternal: rubs sternal region against substrate	
Sneeze	An audible rapid exhalation of air	Moynihan 1964
Social sniff	Nose: moves nose toward another monkey's nose (≤ 1 cm) when neither monkey possesses food	Moynihan 1964
	Anogenital: moves nose toward another monkey's anogenital region (base of tail)	Moynihan 1964
Soft hoot	Low -pitched, moderately prolonged quiet vocalizations, much like the hoot (Moynihan 1964), but barely audible to a human ear in close range (< 2 m)	This study
Tail-twine	2 monkey tails overlap in a region other than the base of the tail	This study
Thrust	Male moves his pelvis rhythmically after mounting a female	Moynihan 1964
Tongue-protrusion	Tongue is rhythmically moved in and out of mouth or tongue is protruded between the lips and extended for a brief amount of time, sometimes associated with a yawn	This study
Touch	Place hand or mouth in another individual's hair	This study
Urine-drink	Licks urine from a substrate or directly midstream	This study
Urine-wash	Urinates on hand and then rubs hand on soles of the back feet	Wright 1985, 1989; Dixson 1994
Yawn	Extended opening of mouth for >1 s, sometimes associated with tongue protrusion	This study

U-tests to determine if there were statistically significant sexual differences in any of the sociosexual behaviors. We compared the rates of mounting and other behaviors between newly formed pairs and established pairs via Mann-Whitney *U*-tests. We considered mounting to occur whether or not thrusting occurred. To determine if the frequency of mounting was uniform throughout the year, we used a Kolmogorov-

Smirnov 1-sample test. To determine which behaviors were related to mounting, we combined data from all observation periods with mounting and separately combined data from all observation periods without mounting for each group in which we observed mounting. We then compared the rates of each behavior between observation periods with and without mounting via Wilcoxon's matched pairs signed ranks tests, weighting each pair equally.

Results

Ethogram of Newly Observed Behaviors

We discovered that owl monkeys engage in urine-drinking, lip-smacking, tongue-protrusion, squinting, and partner-marking. Before urine-drinking, a male approaches a female that is urinating and moves his head toward her anogenital region. He then moves his mouth to the stream of her urine. Sometimes he laps the urine. Males also occasionally lick the urine off a substrate on which a female had urinated, such as the top of the nestbox, perch, or platform. We never observed females drinking the urine of males. Partner-marking consisted of 1 monkey walking over its mate's back or head while pressing its subcaudal gland against it. Only male *Aotus nancymaae* partner-marked. After a partner-marking event, we observed a secretion on the female's fur.

Lip-smacking consists of a rapid oral opening and closing, sometimes accompanied by a faint sound. Tongue-protrusion consists of sticking out the tongue and rapidly pulling it back into the mouth. While tongue-protruding, sometimes a monkey sticks its tongue out once but more often there are several successive iterations. When owl monkeys yawn, a behavior that consists of an extreme opening of the mouth, they sometimes protrude their tongues for an extended period. Males and females lip-smack and tongue-protrude, and the behaviors are brief: usually <5 s). Eye-squinting is a rare behavior that tends to accompany mounting and consists of a monkey holding its eyelids only half open. Sometimes this behavior is accompanied with blinking.

Sternal scent-marking occurred during 6 separate observation periods, all by different individuals (3 males and 3 females). When marking with their sternal glands, the owl monkeys crouched down by flexing all 4 limbs and briefly rubbed the gland against a perch or the top of the nest box. In 1 observation period with sternal-marking, mounting occurred and during another observation period, the male had an erection. One female that sternally scent-marked also lip-smacked. Brief grooming of the hair and skin of an owl monkey's own sternal region or the sternal region of its mate with its hands or mouth also occurred on several occasions.

Three different males briefly suckled their mates' nipples (<5 s), though we could not confirm that they obtained milk. On 1 occasion, no offspring was present but the female appeared to be pregnant. She approached the male, which then groomed her and extended his tongue to her nipple. He then lip-smacked. Another male suckled his mate's nipple on an evening when she was suspected to have aborted because we observed blood on her anogenital region. The male groomed her and, a few minutes later, licked her nipple as she raised her arm above her head,

which is typical when nursing. Afterward, the male tongue-protruded. Hormonal analyses later confirmed that she had aborted (Wolovich 2006). A third male suckled his mate which had a dependent 6-wk-old infant. He approached her, lip-smacked, and self-groomed his sternal area. He then licked her nipple and then lip-smacked.

Sociosexual Behavior

Eight of the 12 male owl monkeys mounted their mates at least once during the study. Males in newly formed pairs mounted females more often (median=0.71/h) than males in established pairs did (median=0.00/h, range=0–0.14) (U=31.5, n_1=7, n_2=5, p=0.021). Mounting occurred uniformly throughout the year (Kolmogorov-Smirnov 1-sample test, n=12, p=0.194) and we detected no physical difference in the appearance of female genitalia during observation periods with mounting and those without mounting. Mountings were brief (5–30 s), and neither males nor females emitted vocalizations just before, during, or after mounts or thrusting. During some mountings, males, females, or both partners squinted. Females occasionally reached 1 arm back and touched males as they thrusted.

In pairs with males that mounted the mate at least once, males and females behaved differently during observation periods with mounting than during those without mounting (Table II). Males were more responsible for maintaining close maintenance of proximity to females during observation periods with mounting. Allogrooming was more frequent during observation periods with mounting than during those without it (Table II). No other behavior was related to mounting (Table II).

Females in newly formed pairs scent-marked with their subcaudal glands, urinated, sneezed, and sniffed the anogenital regions of their mates more frequently than did females in established pairs (Table III). Males in newly formed pairs and established pairs did not differ in the frequency of any recorded behavior (Table IV). For all pairs, males urine-washed, partner-marked, anogenital-sniffed, touched their mates, and drank the mate's urine more frequently than females did (Table V). However, females urinated more frequently than males did (Table V). There is no sexual difference in the rate of subcaudal scent-marking or of muzzle-rubbing. Males occasionally used their subcaudal gland to scent mark on a substrate that had been previously marked by their mates, but Wolovich did not systematically score the behavior.

During a few periods throughout the year (for several weeks at a time), the ventral surface of some of the males' tails were drenched with urine and possibly subcaudal secretions, frequently with a distinct accompanying odor. We never observed the ventral surfaces of the females' tails to be drenched.

Males arched (Moynihan 1964) more often than females did (Table V). Arching was not limited to contexts of agitation but individuals sometimes arched while approaching their mates and nose-sniffing.

The rates of lip-smacking, tongue flicking, and allogrooming do not differ between males and females (Table V). Allogrooming differed from that generally reported for most primates. The grooming bouts were brief (usually <30 s) and were performed coarsely in that the groomer tugged and pulled the pelage with its entire hand or mouth rather than gently parting the hair at precise places on the body.

Table II Behaviors associated with mating

Behavior	Observation periods with mounting	Observation periods without mounting	*N*	T_s	*p*-value
Female					
Arch	0 (0–1.0)	0.12	7	6	0.237
Squint	0 (0–0.40)	0 (0–0.80)	4	n/a	n/a
Gruff grunt	0.08	0.36	6	7	0.753
Lip-smack	0 (0–0.20)	0.12	7	0	0.018
Scent-mark					
Subcaudal	0.62	0.46	7	9	0.398
Muzzle-rub	0 (0–0.50)	0.07	8	7	0.237
Sneeze	0 (0– 0.50)	0.07	5	n/a	n/a
Anogenital sniff	0.45	0.18	7	3	0.063
Soft hoot	0 (0–1.0)	0.03	5	n/a	n/a
Tongue-protrusion	0 (none)	0 (0–0.06)	2	n/a	n/a
Touch	0.24	0.20	8	13	0.889
Urinate	0.65	0.90	7	8	0.310
Urine-wash	0 (0–0.17)	0 (0–0.17)	2	n/a	n/a
Yawn	0 (none)	0 (0–0.17)	2	n/a	n/a
Male					
Arch	0.37	0.19	6	5	0.249
Squint	0 (0–0.80)	0 (0–0.16)	3	n/a	n/a
Gruff grunt	0.10	0.49	8	15	0.647
Lip-smack	0 (none)	0.05	6	0	0.028
Partner-mark	0 (0–1.4)	0.02	4	n/a	n/a
Scent-mark					
Subcaudal	0.50	0.33	8	17	0.889
Muzzle rub	0 (0–0.20)	0.06	4	n/a	n/a
Sneeze	0 (0–3.0)	0.06	4	n/a	n/a
Anogenital sniff	2.0	1.5	8	8	0.161
Soft hoot	0 (0–1.0)	0 (0–0.46)	4	n/a	n/a
Tongue-protrusion	0 (none)	0.02	4	n/a	n/a
Touch	0.75	0.65	8	13	0.484
Urinate	0 (0–1.6)	0.60	8	8	0.161
Urine-drink	0.20	0.19	7	6	0.499
Urine-wash	0 (0–1.2)	0.09	6	6	0.345
Yawn	0 (none)	0 (0–0.15)	2	n/a	n/a
Mutual					
Allogroom	0.34	0.06	6	0	0.028
Food transfer	0 (0–2.0)	0.15	6	10	0.917
Hinde's index of association	–0.021	+0.100	8	6	0.093

Values are hourly rates and represent medians for the 8 males and females observed mounting. When medians=0, ranges are listed in parentheses. We compared data from observation periods with mounting and observation periods without mounting via Wilcoxon's matched pairs signed ranks Test. *N* = number of individuals used for statistical comparisons. When there were ≥2 individuals with no difference their rates of the behavior between the 2 types of observation periods ($N<6$), the statistical test was not applicable (n/a). Significant *p*-values (≤ 0.05) are in bold.

Wolovich observed tail-twining only twice. Tail-twining in owl monkeys is not pronounced, and the tails do not complete a full turn around each other. Instead, the tails simply overlap in a region other than at the base and are held together. Once, we observed tail-twining in a newly paired male and female and their tails remained twined for <1 min. On the other occasion, a male and female twined tails briefly

Table III Differences in the social behavior of female owl monkeys (*Aotus nancymaae*) in newly formed (n=6) and established pairs (n=6)

Behavior	Newly formed pairs	Established pairs	U	p-value
Allogroom mate	0.19	0 (0–0.33)	16.0	0.732
Arch	0.39	0.14	8.5	0.125
Squint	0.06	0 (0–0.22)	12.5	0.295
Food transfer to mate	0.26	0 (0–0.13)	8.0	0.087
Gruff grunt	1.15	1.56	16.5	0.810
Lip-smack	0.32	0.32	19.5	0.807
Partner-mark	None	None		
Scent-mark				
Subcaudal	3.21	0.26	5.0	0.037
Muzzle-rub	0.19	0.13	12.5	0.374
Sneeze	0.25	0 (0–0.22)	6.0	0.046
Anogenital sniff	0.78	0.16	4.5	0.030
Soft hoot	0.25	0 (0–0.86)	11.5	0.266
Tongue-protrusion	0.06	0 (0–0.39)	13.5	0.391
Touch	0.76	0.39	9.0	0.150
Urinate	2.73	1.80	5.0	0.037
Urine-drink	None	None		
Urine-wash	0 (0–0.52)	0 (0–0.12)	17.5	0.902
Yawn	0 (0–0.12)	0 (0–0.11)	17.5	0.902

Values are hourly rates and represent medians. When medians=0, ranges are listed in parentheses. We compared all data using Mann-Whitney U-tests. Resulting p-values below the significant α level of 0.05 are in bold.

(<1 min) while the male was carrying an infant. During both observations periods, the females lip-smacked.

Eight males and 6 females transferred food to their mates, and there is no significant sexual difference in the rate of food transfer (Table V). The subjects transferred all types of food items including provisioned lettuce, monkey chow, and fruit as well as leaves, flowers, and insects that they obtained themselves. Females are slightly more responsible for the close maintenance of proximity between mates (median Hinde's index of association= +0.081, n=12).

Discussion

Researchers had not previously described the sociosexual behavior of owl monkeys. Our findings indicate that they possess a unique composite of communicative behaviors. Most social interactions between mates consist of anogenital- and nose-sniffing, urine-drinking, and partner-marking with the subcaudal gland. Captive owl monkeys frequently use a variety of potential chemical signals including scent-marking with their muzzles, sternal glands, and subcaudal glands as well as urinating and urine-washing. They nasally investigated one another's anogenital regions and muzzles, and males drank their mates' urine and suckled their nipples. The extensive use of chemical communication and relatively low reliance on visual and tactile communication in owl monkeys is unlike behavioral repertoires of diurnal monogamous primates. Such differences may also exist for several species of

Table IV Differences in the social behavior of male owl monkeys (*Aotus nancymaae*) in newly formed (n=6) and established pairs (n=6)

Behavior	Newly formed pairs	Established pairs	U	p-value
Allogroom mate	0.13	0.13	19.0	0.807
Arch	1.42	0.54	7.5	0.092
Squint	0.07	None	9.0	0.059
Food transfer to mate	0.12	.07	16.5	0.806
Gruff grunt	1.59	1.07	14.0	0.522
Lip-smack	0.06	0.18	25.0	0.253
Partner-mark	0 (0–4.3)	0.12	20.0	0.732
Scent-mark				
Subcaudal	1.21	1.80	16.0	0.749
Muzzle-rub	0.12	0.06	16.5	0.798
Sneeze	0.06	0.27	24.5	0.280
Anogenital				
Sniff	4.79	2.58	13.0	0.423
Soft hoot	0.13	0 (0–1.4)	11.0	0.211
Tongue-protrusion	0.06	0.06	18.5	0.932
Touch	2.43	0.99	6.0	0.055
Urinate	1.40	1.90	26.0	0.200
Urine-drink	0.73	0.29	13.0	0.423
Urine-wash	0.21	0.06	14.0	0.507
Yawn	0 (0–0.14)	0 (0–0.12)	17.5	0.902

Values are hourly rates and represent medians. When medians=0, ranges are listed in parentheses. We compared all data using Mann-Whitney U-tests.

Table V Sex differences in the social behavior of captive owl monkeys (*Aotus nancymaae*)

Behavior	Female (n=12)	Male (n=12)	U	p-value
Allogroom mate	0.07	0.13	63.5	0.610
Arch	0.32	0.69	36.0	0.037
Squint	0 (0–0.25)	0 (0–0.88)	74.0	0.886
Food transfer to mate	0.06	0.12	63.0	0.589
Gruff grunt	1.6	1.4	70.5	0.931
Lip-smack	0.32	0.13	97.0	0.143
Partner-mark	None	0 (0–4.29)	36.0	0.006
Scent-mark				
Subcaudal	0.99	1.29	67.5	0.396
Muzzle-rub	0.14	0.06	80.5	0.614
Sneeze	0.13	0.13	68.5	0.834
Anogenital sniff	0.47	2.93	55.5	<0.001
Soft hoot	0.12	0 (0–1.44)	82.0	0.529
Tongue-protrusion	0 (0–0.39)	0.06	60.5	0.458
Touch	0.47	1.67	37.5	0.046
Urinate	1.99	1.57	106.5	0.046
Urine-drink	None	0.40	6.0	<0.001
Urine-wash	0 (0–0.52)	0.14	39.0	0.028
Yawn	0 (0–0.46)	0 (0–0.14)	70.5	0.894

Values are hourly rates and represent medians for 12 females and 12 males. When medians=0, ranges are listed in parentheses. We compared all data using Mann-Whitney U-tests. Resulting p-values below the significant α level of .05 are in bold.

nocturnal monogamous prosimians that groom rarely (*Avahi occidentalis*: Warren and Crompton 1997) or to participate in mutual scent-marking (*Eulemur mongoz*: Curtis and Zaramody 1999).

Chemical Communication

Urine Communication via chemical signals may be important in owl monkeys to monitor female reproductive status. Female owl monkeys urinate frequently and their mates drink their urine. Urine-drinking may allow the males to detect female reproductive state including the time of ovulation, as in other mammals: antelope (Hart and Hart 1987), elephants (*Elephas maximus*, Rasumussen *et al.* 1996), and pandas (*Ailuropoda melanoleuca*, Swaisgood *et al.* 2002). Further support for the hypothesis comes from the fact that males investigated the anogenital region of their mates more often than females did and there was an increased amount of anogenital inspection during observation periods with mounting. Such chemical communication may be especially important in the sociosexual behavior of *Aotus* because they lack visual signals of ovulation (Dixson 1994).

Previous researchers noted urine-washing in *Aotus* (Chambers *et al.* 2004; Dixson 1994; Moynihan 1964; Wright 1989) but we are the first to report a sexual difference. Urine-washing may have a communicative function, e.g., for territorial or reproductive advertisement (Evans 2003). Brown mouse lemurs (*Microcebus ravelobensis*) urine-wash near sleeping sites (Braune *et al.* 2005), and urine-washing in tufted capuchins (*Cebus apella*) and howlers (*Alouatta palliata*) is related to sexual encounters (Jones 2003; Laszlo *et al.* 2004, 2005). Because male owl monkeys urine-washed more frequently than females did, it is likely that it also functions in their communication. However, our findings suggest that urine-washing is not likely to signal sexual interest or receptivity, because the owl monkeys urine-washed both during observation periods with and without mounting. Owl monkeys may urine-wash to mark traveling paths or to advertise territories, and wild *Aotus azarai* in Argentina frequently urine-wash as they move within their territories (Wolovich *et al.* in pres).

Scent-marking The subcaudal gland of owl monkeys is unique in its location and in the structure of the hairs in the surrounding area (Hill *et al.* 1959). Though structurally the gland field is more extensive in males (Hill *et al.* 1959), subcaudal scent-marking by males and females is similar in form and frequency. The subcaudal scent glands of owl monkeys contain chemical information unique to age, sex, and family (MacDonald *et al.* in press); thus it seems likely that subcaudal scent marks are important in intraspecific communication. Other New World primates have anogenital and suprapubic glands (Epple *et al.* 1996) that they use for nonsexual communication such as marking food resources (*Callithrix jacchus*, Coimbra-Filho and Mittermeier 1976; *Callithrix penicillata*, Lacher *et al.* 1981; *Leontopithecus rosalia*, Miller *et al.* 2003) and to advertise estrus (*Saguinus oedipus oedipus*, French *et al.* 1984).

When male owl monkeys partner-mark, they deposit their own scents onto their mates. Though we did not observe it in this study, we also observed female owl monkeys (*Aotus azarai, A. lemurinus*) to partner-mark. Partner-marking in diurnal

New World primates may not be as common as in owl monkeys. Common marmosets (*Callithrix jacchus jacchus*) only rarely used their genital areas to mark their mates (Sutcliffe and Poole 1978). Wild saddleback tamarins (*Saguinus fuscicollis*) partner-mark, but wild moustached tamarins (*S. mystax*) do not (Heymann 2001). With less reliance on visual cues at night, partner-marking may be an important mate-guarding strategy. Scent-marking as a form of mate-guarding in monogamous species may also occur in the form of males marking over the scents of females: klipspringer (*Orotragus oreotragus*, Roberts and Dunbar 2000) and aardwolf (*Proteles cristatus*, Sliwa and Richardson 1998). Because male owl monkeys sometimes marked the place that their mates had marked, they might also use overmarking as a mate-guarding strategy.

Though researchers have reported sternal scent-marking for a variety of primates (Geissmann 1987), we provide the first evidence of its use in *Aotus*. In addition to rubbing their sternal areas against substrates, male and female owl monkeys groomed their own and their mates' sternal regions. These brief occurrences of grooming appeared similar to that of *Callicebus* (Moynihan 1966) and may act to stimulate the gland's secretions or to transfer the secretions to another body part.

Both male and female owl monkeys muzzle-rubbed. Muzzle-rubbing was unrelated to mounting but was often accompanied by sneezing as in callitrichids (Epple *et al.* 1996). Sneezing may promote a rapid inhalation of air and may serve to facilitate the reception of chemical cues from the environment (Estes 1972). Sneezing was independent of sex and mounting behavior.

Flehmen in Aotus? The flehmen response is a distinctive feature of chemo-investigation behavior in terrestrial mammals that is accompanied by a facial grin or grimace (Evans 2003). It is associated with the presence of a vomeronasal organ and a distinct accessory olfactory bulb (Evans 2003). Owl monkeys have a functional vomeronasal organ but the extent that they use it is unknown (Hunter *et al.* 1984). In owl monkeys, lip-smacking, tongue-protrusion, yawning, sneezing, and squinting may be related to olfaction and the use of the vomeronasal organ. Together, the behaviors may represent a type of flehmen response. Researchers have not described flehmen for any New World primate, but ring-tailed lemurs (*Lemur catta*) exhibit flehmen after being presented with conspecific scents (Bailey 1978). Ring-tailed lemurs respond to scents by first sniffing, then licking and lapping, followed by retracting the lip and inspiring rapidly. The response ends with an expiration of air during a gape and by licking one's rhinarium (Bailey 1978).

Mounting Behavior

Mounting occurred more frequently than previously reported for *Aotus* (Dixson 1994; Fernandez-Duque *et al.* 2002). Males mounted both cycling and pregnant females but never lactating females. Mounting was aseasonal, but during our study the births occurred seasonally, between May and October, which were the warmest and wettest months of 2004 (Florida Climate Center), indicating that seasonal reproduction in captive *Aotus* at the DuMond Conservancy for Primates and Tropical

Forests, Inc. coincides with environmental variables that are also linked with birth seasonality in wild *Aotus azarai* in Argentina (Fernandez-Duque *et al.* 2002) and captive *Aotus nancymaae* in Perú (Gozalo and Montoya 1990), though there is a 6-mo hemispheric shift. In Argentina, births occurred just at the beginning of 1 of the 2 rainy seasons, which is accompanied by warmer temperatures and greater fruit availability (Fernandez-Duque *et al.* 2002).

Other Sociosexual Behavior

Males and females display by arching when they are disturbed by conspecifics, loud noises, potential predators, and humans (Moynihan 1964; Wright 1978; Evans, Wolovich, *pers. obs.*). In our study, males and females also arched when approaching mates and it seemed to serve an affiliative purpose. Males arched more frequently than females did, suggesting either that they responded to external threats by displaying more readily than females did or that they arched more frequently in intersexual sniffing, or both.

Males and females rarely groomed mates but there was a greater frequency of allogrooming during observation periods with mounting. Therefore, allogrooming in *Aotus* is unusual in that it occurred rarely, briefly, in association with mounting behavior and the behavior itself appeared coarser than that of other primates.

It is puzzling that a male owl monkey would suckle a female's nipple. Males may gain nutritional benefits but the advantages to females of allowing or even encouraging males (by holding an extended arm overhead) to suckle remain unclear.

The owl monkeys rarely tail-twined and when they did, it appeared less pronounced than in titi monkeys (*Callicebus*; Moynihan 1966; Welker *et al.* 1998). Whereas tail-twining in titi monkeys consists of 1 monkey winding its own tail several times around the monkey's tail (Moynihan 1966; Welker *et al.* 1998), owl monkeys simply overlap tails and hold them together (Moynihan 1966). Tail-twining may have occurred more frequently when owl monkeys were resting, but we gathered our data at a time when the owl monkeys were active. Our observations of food transfers between mates support previous suggestions that food-sharing in owl monkeys may function in social bonding because the food transfers were not unidirectional and included all types of food items (Feged *et al.* 2002; Wolovich *et al.* 2006; Wolovich *et al.* in press).

A complete understanding of owl monkey sociosexual behavior will require an investigation into their extensive vocal repertoire, and we are currently analyzing the acoustic properties of owl monkey vocalizations that, to date, scientists have only briefly described (Moynihan 1964).

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