

Goal-Directed Tail Use in Colombian Spider Monkeys (*Ateles fusciceps rufiventris*) Is Highly Lateralized

Eliza L. Nelson and Giulianna A. Kendall
Florida International University

Behavioral laterality refers to a bias in the use of one side of the body over the other and is commonly studied in paired organs (e.g., hands, feet, eyes, antennae). Less common are reports of laterality in unpaired organs (e.g., trunk, tongue, tail). The goal of the current study was to examine tail use biases across different tasks in the Colombian spider monkey (*Ateles fusciceps rufiventris*) for the first time ($N = 14$). We hypothesized that task context and task complexity influence tail laterality in spider monkeys, and we predicted that monkeys would exhibit strong preferences for using the tail for manipulation to solve out-of-reach feeding problems, but not for using the tail at rest. Our results show that a subset of spider monkeys solved each of the experimental problems through goal-directed tail use ($N = 7$). However, some tasks were more difficult than others, given the number of monkeys who solved the tasks. Our results supported our predictions regarding laterality in tail use and only partially replicated prior work on tail use preferences in Geoffroy's spider monkeys (*Ateles geoffroyi*). Overall, skilled tail use, but not resting tail use, was highly lateralized in Colombian spider monkeys.

Keywords: laterality, hemispheric specialization, spider monkey, tail use

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Behavioral laterality refers to a bias in the use of one side of the body over the other and is commonly studied in paired organs (e.g., hands, feet, eyes, antennae). Less common are reports of laterality in unpaired organs, such as the tongue (Gisel, Schwaab, Lange-Stemmler, Niman, & Schwartz, 1986) or the trunk, which can be moved to the left or the right relative to the body midline (Haakonsson & Semple, 2009; Keerthipriya, Tewari, & Vidya, 2015; Martin & Niemitz, 2003). Among unpaired organs, the tail is a particularly interesting candidate for examining laterality, as tails can vary in function, as well as dexterity, from not prehensile (e.g., dog; Quaranta, Siniscalchi, & Vallortigara, 2007; Siniscalchi, d'Ingeo, & Quaranta, 2017) to partially prehensile (e.g., rat; Rosen, Finklestein, Stoll, Yutzey, & Denenberg, 1984; Ross, Glick, & Meibach, 1981) to fully prehensile and capable of grasping objects like a hand (e.g., spider monkey; Laska, 1998; Laska & Tutsch, 2000). Behavioral biases reflect underlying hemispheric specialization or asymmetric brain function. Laterality is an important principle in brain organization because specialized hemi-

spheres may streamline neural processing and, therefore, have downstream advantages on behavior (Rogers & Vallortigara, 2015; Rogers, Vallortigara, & Andrew, 2013; Vallortigara & Rogers, 2005). The goal of the current study was to examine tail use biases across different tasks in the Colombian spider monkey (*Ateles fusciceps rufiventris*) for the first time.

The majority of studies of primate laterality measured hand use (for reviews, see MacNeilage, 2007; McGrew & Marchant, 1997; Meguerditchian, Vauclair, & Hopkins, 2013; Papademetriou, Sheu, & Michel, 2005). Both context and skill level have been implicated in primate handedness. The postural origins theory proposed by MacNeilage, Studdert-Kennedy, and Lindblom (1987) suggests that hand use biases were driven by ecological context in primates. In the earliest arboreal primates, the left hand was used for smash-and-grab reaching, whereas the right hand was used for postural support. In later species that shifted to terrestrial living, the right hand was freed from postural support and became specialized for skilled manipulation. Fagot and Vauclair (1991) later expanded on the idea of skilled manipulation in measuring laterality with their task complexity hypothesis, which proposed classifying manual actions as either low level (i.e., familiar actions not requiring dexterity such as reaching or foraging) or high level (i.e., novel or challenging actions). According to the task complexity hypothesis, the type of task used for measurement is related to the expression of laterality, with high-level actions being a better indicator of asymmetry as compared with low-level actions. We hypothesized that context and skill level matter for tail use biases in *Ateles*, as they do for the hands.

Similar arguments for context and complexity have been made for lateralized trunk use in elephants. Shoshani (1998) described the following five functions of the trunk: breathing, olfaction, sound production, touch, and manipulation. Touch and manipulation have been examined for behavioral asymmetries. Martin and

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Eliza L. Nelson and Giulianna A. Kendall, Department of Psychology, Florida International University.

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Correspondence concerning this article should be addressed to Eliza L. Nelson, Department of Psychology, Florida International University, 256 Deuxieme Maison Building, 11200 Southwest 8th Street, Miami, FL 33199. E-mail: elnelson@fiu.edu

Niemitz (2003) reported that 100% of wild Asian elephants (*Elephas maximus*) were lateralized for object contact (defined as the direction the trunk curled around an object). No population-level bias was found, as the group was split 51/49 for the right side versus the left side. For retrieval (movements toward the mouth) and reaching (movements away from the mouth), biases were not as robust, with only 59–66% of the subjects exhibiting significant individual preferences. Greater precision is required for the trunk to grasp an object as opposed to for the trunk to move toward/away from the mouth, and these findings suggest that task complexity, or difficulty level, is related to the expression of laterality in elephants. Haakonsson and Semple (2009) expanded on trunk use biases by examining trunk use in feeding versus nonfeeding contexts in captive Asian elephants. Preferences varied within individuals and across the four behaviors examined (feeding: trunk curled around an object; swinging: trunk relaxed moving side to side; self-touching: trunk touching body; sand bathing: trunk used to spray sand on body). Notably, preferences were stronger for feeding than for two of the three nonfeeding behaviors examined (swinging and self-touching). Finally, Keerthipriya et al. (2015) reported stronger preferences for trunk use compared with forefoot use for removing grass during feeding in wild Asian elephants. Trunk preferences were exclusively left or right and consistent over time, whereas forefoot preferences were highly variable with a substantial proportion of individuals showing no bias. These findings prompted Keerthipriya et al. (2015) to propose a modified task complexity hypothesis, which argues for comparing the performance of different organs on tasks with the same goal and within the same context. Thus, there is a call to action to explore other organs besides the hands in evaluating behavioral laterality.

Like the elephant trunk, the spider monkey tail has multiple functions. The tail is used in goal-directed movements to support the body in suspension (e.g., feeding, monitoring) and brachiation and can be used to extend reach (Martin & Niemitz, 2004; Schmitt, Rose, Turnquist, & Lemelin, 2005). The tail can also be wrapped around the body during rest and may serve a thermoregulatory function in this capacity in monkeys, similar to what has been described for other mammals (Hickman, 1979; Wright, 1977). *Ateles* has the longest tail relative to body size among New World monkeys with prehensile tails (Rosenberger, 1983), and the tail is composed of approximately 32 caudal vertebrae with evenly distributed muscles and a hairless tactile pad dense in mechanoreceptors on the distal one third (Ankel, 1972; Lemelin, 1995; Organ, Muchlinski, & Deane, 2011; Organ, Teaford, & Taylor, 2009; Schmitt et al., 2005). The *Ateles* tail is characterized at the sensory level by contralateral somatotopic organization (Pubols & Pubols, 1971). Unlike the dog tail that is under contralateral motor control (Buxton & Goodman, 1967), the spider monkey tail is innervated bilaterally (Fulton & Dusser de Barenne, 1933).

Taxonomy in *Ateles* is contentious, and there is no clear consensus on whether *A. f. rufiventris* is a distinct species or a subspecies of *Ateles geoffroyi* (for discussion, see Rylands, Groves, Mittermeier, Cortés-Ortiz, & Hines, 2006). Although there are no tail laterality data on *A. f. rufiventris*, two prior studies examined tail use asymmetries in *A. geoffroyi*. In a study by Laska (1998), monkeys were tasked with reaching caudally for a raisin placed in one of the following three contexts: alone on a table, suspended on a rope, or placed on top of a vertical stick with a narrow diameter. Observations were also taken twice a day on tail

wrapping while monkeys were at rest. Two thirds of the sample performed the tail manipulation tasks. Notably, all monkeys who used the tail to extend reach were 100% lateralized and consistent in direction across tasks. Tail use on the manipulation tasks was correlated with tail wrapping during rest but not with hand use from a prior study (Laska, 1996). Individually, seven monkeys exhibited a left tail bias and nine monkeys exhibited a right tail bias. Laska and Tutsch (2000) further compared resting tail preferences across three New World monkey species, namely, Geoffroy's spider monkeys (*A. geoffroyi*), squirrel monkeys (*Saimiri sciureus*), and howler monkeys (*Alouatta palliata*). Individual preferences were found in 16 of 20 spider monkeys, 18 of 20 squirrel monkeys, and only 2 of 20 howler monkeys. No individual in any species was exclusively lateralized for resting tail posture, unlike the prior study that examined lateralization for tail manipulation in *A. geoffroyi*.

Before the current study in *A. f. rufiventris*, we informally observed that some monkeys in our captive study group used the tail spontaneously to manipulate objects (e.g., food, enrichment toys) inside and outside their enclosure. We hypothesized that experience in manipulating objects with the tail would be linked to being able to solve novel problems with the tail, and we predicted that only monkeys with tail manipulation experience would solve a series of experimental tail tasks where a desirable object was out of reach of the hands and feet (i.e., accessible only by the tail). As a test of laterality, we made two opposing predictions. If context and complexity influence the expression of laterality in tail use as suggested by prior work in primate hand use and elephant trunk use, we predicted that monkeys would exhibit strong biases for using the tail for manipulation but not for using the tail at rest. Alternatively, if tail use laterality is independent of context and complexity in *Ateles*, as suggested by prior work in *A. geoffroyi*, we predicted no difference in tail use laterality patterns between manipulation and rest.

Method

Subjects

Data were collected from 14 Colombian spider monkeys (*A. f. rufiventris*) housed at the wildlife park Monkey Jungle in Miami, FL. The sample consisted of six male and eight female monkeys who ranged in age from 3 to 50 years at the end of data collection. One monkey in the study group was wild-caught and the remaining monkeys were all captive-born. The social group also included five monkeys of age <2 years who did not participate in the study. Observational resting tail data (wrap task; see Resting tail subsection) were collected from all subjects. Before the current study, a subset of the monkeys ($N = 7$) had been observed to use the tail spontaneously for manipulation. These monkeys were the focus of additional tail use observations across a battery of experimental tasks (aerial, elevated, ground, container, and water tasks; see Experimental tail tasks subsection). Although all the monkeys were exposed to the experimental tail tasks during data collection, only the monkeys who were known to the experimenters to use the tail for manipulation attempted/performed these tasks.

Testing occurred in the monkeys' main elevated outdoor pen ($8.84 \times 3.96 \times 4.47 \text{ m}^3$). Monkeys also had access to an adjoining outdoor pen ($3.30 \times 1.92 \times 1.77 \text{ m}^3$) and an indoor night house

($3.30 \times 1.09 \times 2.72 \text{ m}^3$) during data collection. One monkey (Mason) was moved toward the end of data collection for reasons unrelated to the study and completed the water task in a separate night house area ($2.44 \times 1.83 \times 1.98 \text{ m}^3$). All housing areas were equipped with vertical and horizontal structures. Food and water were freely available during all phases of data collection. Monkeys were fed high-protein commercial chow (Purina LabDiet 5045, United States) and a mixture of fruits and vegetables daily at 8:30 a.m. and 2:30 p.m. Monkeys also received dried fruit and seeds daily from tourists visiting the wildlife park. The Institutional Animal Care and Use Committees of the DuMond Conservancy (Protocol #2012-03) and Florida International University (Protocol #16-047) approved the research, and the study was conducted in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the laws of the United States. The research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. The welfare of the monkeys was monitored at all times during data collection by the Monkey Jungle staff.

Procedure

Resting tail. Resting posture in the spider monkey has been previously described as the tail wrapped sideways around the body while seated (Laska, 1998; Laska & Tutsch, 2000). Monkeys were observed at rest to determine individual preferences for tail wrapping (wrap task; Figure 1A). The tail-wrapping response was scored as left or right in relation to the monkey's midline. Data were collected ad libitum between 9:30 a.m. and 5:30 p.m. One data point was taken per day until 30 data points were obtained for each monkey.

Experimental tail tasks. Experimental data were collected across a series of problem-solving tasks presented to monkeys outside of the enclosure on nonconsecutive test days. A single high-value food item was placed out of reach of the hands and accessible only by the tail in one of the following five conditions:

Aerial task: A grape was placed inside a bowl (5.72 cm in diameter \times 15.24 cm in depth) suspended on a chain [Figure 1(B); Supplemental Video 1 in the online supplemental materials]. **Elevated task** (adapted from Zander & Judge, 2015): A bar (1.5 cm in diameter \times 20.3 cm in length) baited with a marshmallow or a peanut butter and jelly mix on one end was placed on top of elevated bookends [$8.9 \times 26.7 \text{ cm}^2$ base; Figure 1(C); Supplemental Video 2 in the online supplemental materials; bar was elevated to 17.1 cm]. **Ground task:** A peanut was placed on a hard surface at ground level [Figure 1(D)]. **Container task:** A grape was placed inside a transparent container ($13.97 \times 13.97 \times 16.51 \text{ cm}^3$) angled at 21° [Figure 1(E); Supplemental Video 3 in the online supplemental materials]. **Water task:** A marshmallow was floated in a small pool of water [$35.56 \times 22.30 \times 10.16 \text{ cm}^3$; Figure 1(F); Supplemental Video 4 in the online supplemental materials]. In all conditions, a trial consisted of placing the food or baited bar in the apparatus and allowing the focal monkey to solve the task. Monkeys were required to locomote between trials to prevent rote responding. Food in aerial trials was retrieved by first pulling the chain with the tail and then using the hands when the bowl was within reach. Food in ground trials was placed at the monkey's midline. If the food or the bar fell during retrieval or was stolen by another monkey, the trial was considered unsuccessful and excluded from analyses. Up to 10 trials where the monkey solved the task successfully with the tail and obtained the food were recorded on nonconsecutive days until 30 data points were collected on each task. In all tasks, monkeys remained facing the experimenter and brought the tail to one side of the body, keeping the tail under visual control. No monkey ever turned his or her backside toward the cage mesh during a tail attempt. Tail side (left or right) was recorded for each successful trial with respect to the monkey's midline. A monkey was given the designation "did not solve" if he or she did not successfully solve the task or stopped attempting to solve the task after three sessions of exposure.

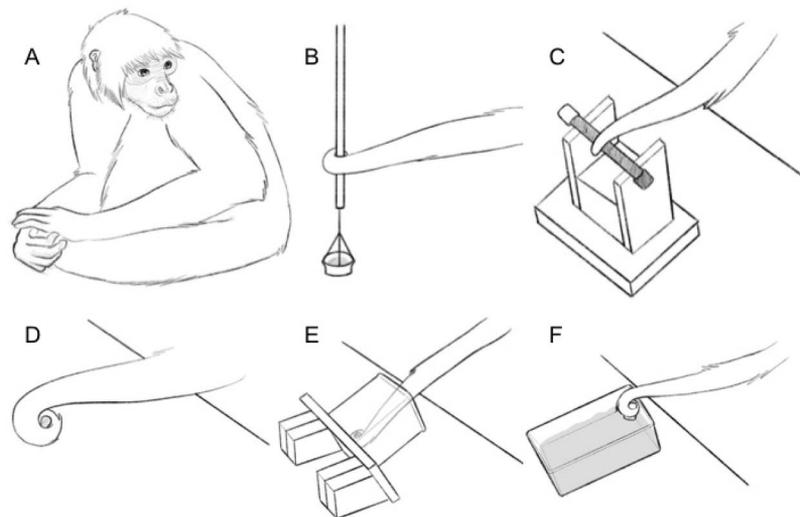


Figure 1. Tail use behaviors: (A) wrap task, (B) aerial task, (C) elevated task, (D) ground task, (E) container task, and (F) water task. See text for task descriptions.

Data Analysis

Tail preferences on each task were characterized at the individual level in the following two ways: direction (left, right, or no bias) and degree (strength of bias). To determine the direction of bias, a laterality index (LI) was calculated by subtracting the number of left tail responses from the number of right tail responses and then dividing by the total number of responses, $LI = (R - L)/(R + L)$. LI scores range from -1.00 (*exclusive left tail use*) to 1.00 (*exclusive right tail use*). LI scores were calculated separately for each measure (LI_{wrap} , LI_{aerial} , $LI_{elevated}$, LI_{ground} , $LI_{container}$, LI_{water}) for monkeys with sufficient data (i.e., 30 data points per task). To determine the strength of bias, the absolute value of each LI (ABSLI) score was computed ($ABSLI_{wrap}$, $ABSLI_{aerial}$, $ABSLI_{elevated}$, $ABSLI_{ground}$, $ABSLI_{container}$, and $ABSLI_{water}$). ABSLI scores range from 0 (*not lateralized*) to 1.00 (*completely lateralized*). Individual preferences were determined by binomial z scores, where $z < -1.96$ = left preference, $z > +1.96$ = right preference, and all other z scores = no preference. These cutoffs correspond to $p < .05$ for two-tailed tests.

The following analyses were conducted on observational tail use data only owing to lack of variability on the experimental tail tasks. Population-level bias was assessed using a one-sample Wilcoxon signed-rank test on LI_{wrap} scores. Mann-Whitney U tests were used to examine the effect of sex on LI_{wrap} and $ABSLI_{wrap}$ scores. Spearman correlations were used to examine relations between age, LI_{wrap} scores, and $ABSLI_{wrap}$ scores. Finally, we previously reported hand preference data on 10 of the 14 monkeys analyzed for tail use preferences in this study (Nelson, Figueroa, Albright, & Gonzalez, 2015). In the prior hand use study, monkeys performed a unimanual reaching task (HI_{reach}) and the coordinated bimanual tube task (HI_{tube}). The Handedness Index (HI) was calculated with the formula $HI = (R - L)/(R + L)$, where R was the number of right hand responses and L was the number of left hand responses. Spearman correlations were also used to examine relations between tail use wrap preferences (LI_{wrap} scores) and hand use preferences (HI scores) for monkeys with both wrap and hand use data available. Statistical analyses were conducted in SPSS Version 20 using an alpha level of .05.

Results

Resting Tail

Individual tail use data and LI scores for the observational wrap task are given in Table 1. LI_{wrap} scores ranged from -0.20 to 0.13 ($M \pm SD = 0.05 \pm 0.10$). All 14 monkeys exhibited no tail-wrapping bias according to binomial z scores using ± 1.96 cutoffs. No monkey was classified as having a left or a right tail-wrapping bias. A one-sample Wilcoxon's signed-rank test on LI_{wrap} scores using a test value of 0 found no group-level tail-wrapping bias ($N = 14$, $z = -1.517$, $p = .129$). There was no effect of sex on LI_{wrap} scores ($U = 26.5$, $p = .740$). $ABSLI_{wrap}$ scores ranged from 0.00 to 0.20, and there was no difference in tail-wrapping preference strength between male and female monkeys ($U = 19.5$, $p = .573$). Age did not correlate with either LI_{wrap} scores ($R_s = .120$, $p = .683$) or $ABSLI_{wrap}$ scores ($R_s = .154$, $p = .599$). LI_{wrap} scores did not correlate with HI_{tube} scores ($R_s = -.110$, $p = .763$,

Table 1

Individual Tail Use Data and Laterality Index (LI) Scores for the Wrap Task

ID	Sex	Age	Rearing	L/R	LI_{wrap}	Binomial z
Jasper	M	3	Captive-bred	16/14	-0.07	-0.18
Uva	M	6	Captive-bred	16/14	-0.07	-0.18
Mason	M	7	Captive-bred	17/13	-0.13	-0.55
Sunday	M	10	Captive-bred	15/15	0.00	0.00
Bon Jovi	M	32	Captive-bred	18/12	-0.20	-0.91
Butch	M	50	Wild-caught	13/17	0.13	+0.55
Jenny	F	3	Captive-bred	15/15	0.00	0.00
Cary	F	6	Captive-bred	17/13	-0.13	-0.55
Molly	F	9	Captive-bred	13/17	0.13	+0.55
Cleo	F	11	Captive-bred	17/13	-0.13	-0.55
Dusky	F	16	Captive-bred	17/13	-0.13	-0.55
Mints	F	27	Captive-bred	15/15	0.00	0.00
CJ	F	28	Captive-bred	16/14	-0.07	-0.18
Carmelita	F	33	Captive-bred	15/15	0.00	0.00

Note. L = left response; R = right response. Preferences were calculated with the formula $LI = (R - L)/(R + L)$. Significance was determined by binomial z scores, where $z < -1.96$ = left preference, $z > +1.96$ = right preference, and all other z scores = no preference.

$N = 10$) or HI_{reach} scores ($R_s = -.423$, $p = .223$, $N = 10$). Finally, $ABSLI_{wrap}$ scores did not correlate with HI_{tube} scores ($R_s = -.023$, $p = .949$, $N = 10$) or HI_{reach} scores ($R_s = .238$, $p = .509$, $N = 10$).

Experimental Tail Tasks

Individual tail use data and LI scores for the experimental tasks are given in Table 2. All LI scores across tasks were either -1.00 (*exclusive left tail use*) or 1.00 (*exclusive right tail use*), with the exception of Cary's performance on the aerial task. Five monkeys exhibited a left tail use preference overall (Sunday, Mason, Mints, Cleo, and Jasper) and two monkeys exhibited a right tail use preference (Cary and Uva), according to binomial z scores using ± 1.96 cutoffs. Only two of the experimental conditions (aerial task and elevated task) were solved by all of the monkeys. Six out of seven monkeys solved the ground task condition. Three out of six monkeys solved the remaining two conditions (container task and water task). We computed ABSLI scores to compare strength of tail use preferences across tasks (Figure 2). ABSLI scores ranged from 0.80 to 1.00, indicating exclusive or near exclusive use of the tail to one side of the body in solving the experimental tasks. Hand preference data (Nelson et al., 2015) were available for five of the seven monkeys who completed the experimental tail tasks and are discussed here descriptively for comparison. Three of the monkeys were consistent in direction (left or right preference) across tail and hand use on all tasks. Uva exhibited a right-hand bias for the unimanual and bimanual tasks during prior testing that matched a right bias for tail manipulation, whereas Mints and Cleo exhibited left biases on all assessments of manual and caudal manipulation. Two monkeys exhibited a left bias for tail manipulation and bimanual manipulation but a right bias for unimanual reaching (Sunday and Mason). There are no hand data on the remaining two monkeys (Jasper and Cary), as they were infants when the previous study took place.

Table 2
Individual Tail Use Data and Laterality Index (LI) Scores for Experimental Tasks

ID	Aerial		Elevated		Ground		Container		Water	
	L/R	LI _{aerial}	L/R	LI _{elevated}	L/R	LI _{ground}	L/R	LI _{container}	L/R	LI _{water}
Sunday	30/0	-1.00	30/0	-1.00	30/0	-1.00	30/0	-1.00	30/0	-1.00
Mason	30/0	-1.00	30/0	-1.00	30/0	-1.00	30/0	-1.00	30/0	-1.00
Mints	30/0	-1.00	30/0	-1.00	30/0	-1.00	30/0	-1.00	30/0	-1.00
Cleo	30/0	-1.00	30/0	-1.00	30/0	-1.00	Did not solve		Did not solve	
Jasper	30/0	-1.00	30/0	-1.00	30/0	-1.00	Did not solve		Did not solve	
Cary	3/27	0.80	0/30	1.00	Did not solve		Did not solve		Did not solve	
Uva	0/30	1.00	0/30	1.00	0/30	1.00	Deceased		Deceased	

Note. Preferences were calculated with the formula $LI = (R - L)/(R + L)$, where LI = Laterality Index, R = Right response, L = Left response. Significance was determined by binomial z scores, where $z < -1.96$ = left preference, $z > +1.96$ = right preference, and all other z scores = no preference. All z scores on the experimental tasks were -5.29 or $\geq +4.20$. Boldface denotes subjects with a significant tail preference.

Discussion

The goal of the current study was to examine tail use for behavioral laterality for the first time in the Colombian spider monkey (*A. f. rufiventris*). We hypothesized that task context (i.e., resting vs. feeding) and task complexity (i.e., whether skill is required to complete the target action) would influence tail laterality in spider monkeys, and we predicted that monkeys would exhibit strong preferences for using the tail for manipulation to solve out-of-reach feeding problems but not for wrapping the tail around the body while at rest. Our results supported our predictions regarding laterality in tail use and only partially replicated prior work on tail use preferences in Geoffroy's spider monkeys (*A. geoffroyi*).

Skilled tail use, but not resting tail use, was highly lateralized in our sample of Colombian spider monkeys. All monkeys were 100% lateralized for the experimental tail tasks that required a great deal of dexterity and skill, with the exception of one young female who made three responses with the opposite tail side on one task. Five monkeys were left tail preferent across tasks, whereas two monkeys were right tail preferent. By comparison, observations on the full group of 14 monkeys found that no monkey had a bias for using the tail to wrap around the body at rest. The results for the experimental tail tasks are consistent with prior work in *A. geoffroyi*, which found that spider monkeys were 100% lateralized on a set of three tasks that required skilled tail use manipulation (Laska, 1998). Similarly, no population-level tail bias was reported; seven monkeys were left tail preferent and nine monkeys

were right tail preferent. In both studies, direction of tail use preference for manipulation was 100% consistent across tasks. However, the studies differed in that Laska (1998) reported similarly high levels of tail use bias for wrapping the tail at rest in both monkeys that used the tail for manipulation and monkeys who did not. The difference between the two studies may be attributable to the methods used to collect tail-wrapping data. Laska (1998) took two data points per day (midday and evening) per monkey for a total of 20 data points over 10 days. In the current study, we took one data point per monkey per day for a total of 30 data points over 30 days, with almost all data points collected during the early morning. It is possible that the difference in sampling may have resulted in the discrepancy between studies. Additional work is needed to replicate both the *A. f. rufiventris* and *A. geoffroyi* results to determine whether there is actually a robust effect for resting tail use, as well as to compare tail use patterns for manipulation versus rest in other prehensile-tailed monkeys.

Overall, our data suggest that task context and task complexity affect tail use laterality in Colombian spider monkeys, which is consistent with laterality theory regarding hand use in nonhuman primates (Fagot & Vaclair, 1991; MacNeilage, Studdert-Kennedy, & Lindblom, 1987), as well as prior work in elephant trunk laterality (Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Martin & Niemitz, 2003). Investigators working on human populations have also argued that the expression of laterality is dependent on task context and complexity (Seegelke, Hughes, & Schack, 2011). Moreover, a comparison of 23 species of parrots

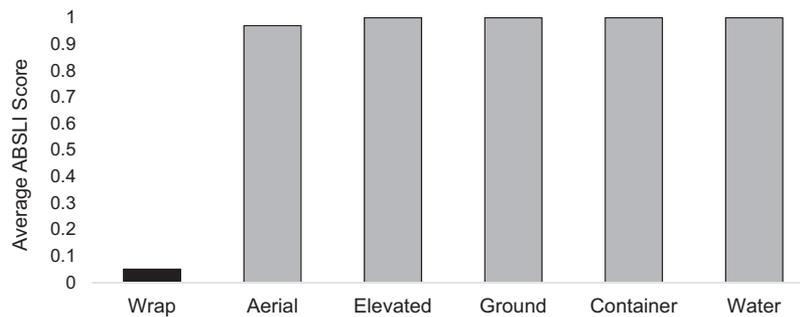


Figure 2. Average strength of tail use preference by task (absolute value of laterality index scores). Observational data denoted by black bars. Experimental data denoted by gray bars.

and cockatoos found that foot preference lateralization was strongly tied to ecology. Species that exhibited strong lateralization had diets consisting of large seeds that required manipulation to open, whereas species that were not lateralized ate smaller seeds and other food items that did not need to be manipulated (Brown & Magat, 2011). These findings across multiple taxa are convincing that context and complexity are critical variables in assessing behavioral laterality. A limitation of the current study is that we are unable to disentangle context from complexity, given that the tasks requiring the greatest skill were those involving feeding problems. Boeving, Belnap, and Nelson (2017) recently reported on laterality in spider monkey embraces, and social behavior may be another context distinct from feeding or resting for examining tail use asymmetries in future work. It is important to note that there is no standard definition of “complexity” either within primatology (for discussion, see Uomini, 2009) or across other domains of animal behavior. One reason may be that what can be considered a “complex” or “skilled” action varies by species. In the case of the spider monkey, the hands, feet, or tail can perform manipulation, and what constitutes “complex” may differ depending on what body part is used and in what manner it is used. In wild spider monkeys, reach attempts occur in this sequence, with monkeys first trying the hands, then the feet, and finally the tail (F. Aureli, personal communication). Thus, tail use for manipulation is not a consequence of captivity and has ecological relevance for the spider monkey. We urge investigators in laterality to consider species-specific factors in evaluating complexity as related to measurement in their studies.

There may also be individual-level factors to consider when weighing task complexity. We also hypothesized that experience in manipulating objects with the tail (as per our informal observations before the current study) would influence performance on the experimental tail use tasks. Our results were in line with our prediction in that only monkeys with tail manipulation experience were able to solve the novel problem-solving tasks, even though all monkeys were exposed to the tasks and could participate freely if they chose to do so. Furthermore, not every monkey with tail experience solved every task, suggesting that some of the tasks may have been more difficult than others. The two tasks that were solved by all monkeys involved picking up an object rather than picking up the food item directly. In the aerial task, monkeys were required to use the tail to pull a chain, and in the elevated task, monkeys were required to pick up a polyvinyl chloride bar that was baited with a sticky food substrate on one end. Surprisingly, one monkey did not solve the ground task, which involved picking up a peanut in the shell directly from a table at ground level with no other constraints. Anecdotally, the monkey who did not solve this task was not particularly fond of peanuts, which may or may not have influenced her performance. We kept the food item consistent within each task so that differences in size, shape, or texture did not affect the results. The other two tasks were only solved by half of the monkeys tested. These two tasks had one thing in common that differed from the other three tasks, which is that the food item moved freely inside an enclosed space during attempts to retrieve it. In the container task, the grape could roll around between two corners on the bottom of the container, given the 21° slant. In the water task, the marshmallow could be pushed below the water line and into any part of the container. The marshmallow texture was also different from the other food items

used in that it was malleable rather than hard. All monkeys put their tail into the water, whether they solved the task or not, so the substrate was not a factor in determining who was successful at solving. Laska (1998) also reported variability in success on caudal tasks across tasks and within individuals, with tasks involving retrieving food from a table (similar to our ground task) or while suspended (similar to our aerial task) having the highest mean percentages of success, whereas a task involving retrieving food from a restricted space with the most precision having the lowest mean percentage of success. Without additional data from other samples or more detailed data on attempts, we are hesitant to rank-order tail manipulation tasks on a scale from *least* to *most complex*, although we believe that the tasks were not equal in difficulty based on these two studies.

Interestingly, the three monkeys who solved both the container task and the water task in the current study were related through the maternal line. Paternity is not known in this group of spider monkeys, but ongoing fecal analyses may resolve this issue in the future. One of the outstanding questions left by this study is *how* do monkeys become skilled at using the tail for manipulation? On a related note, why do some monkeys not show this behavior at all? Prior work in *A. Geoffroyi* suggested that age might be a factor in tail use manipulation, given that eight monkeys of age <2 years old did not use the tail for extending reach, whereas all other group members did (Laska, 1998). In our own data, this age pattern does not hold. Monkeys that used the tail for manipulation in the current study ranged from 3 to 27 years old, and monkeys that did not use the tail for manipulation ranged from 3 to 50 years old. Ongoing studies in our laboratory are tracking early hand and tail use in infants born into the group to better address the question of how tail use manipulation ability and potentially tail use preferences develop.

In addition to *how* tail use becomes lateralized, another question that can be posed is *why* the tail would be lateralized for manipulation. In considering resting tail use, there is no consequence to the monkey from choosing to wrap the tail either to the left or the right of the body. By contrast, there are tangible consequences for mistakes made on the experimental tail tasks requiring manipulation. Here, monkeys could lose out on obtaining a high-value food item if their actions cause the food to drop into the sand below their elevated pan, or they are unable to solve the task. In this way, using the tail for manipulation is a goal-directed action requiring motor planning. To this end, there is a high cognitive demand placed on the monkey. A solution must be selected from many possible actions, executed with precision, and any errors made must be acknowledged to properly adjust future actions (Rosenbaum, 2005). Thus, there is a clear advantage for lateralization under these conditions in enhancing cognitive and behavioral efficiency (Vallortigara & Rogers, 2005).

In comparing tail use with prior data collected on hand use in our sample of Colombian spider monkeys, there was no relationship between resting tail and unimanual or bimanual task biases. Among the seven monkeys who used the tail for manipulation, three monkeys were consistent across caudal and manual testing, two monkeys matched direction on caudal and bimanual preferences but not unimanual preference, and no comparable hand data were available for the remaining two monkeys. It is not uncommon for investigators to report inconsistencies in hand use within individuals across tasks (Anderson, Degiorgio, Lamarque, & Fagot,

1996; Lilak & Phillips, 2008; Spinozzi & Truppa, 1999), which may suggest that individual monkeys show manual specialization for specific manual skills rather than true handedness (Marchant & McGrew, 2013; McGrew & Marchant, 1997). The lack of a robust pattern between tail and hand use preferences is comparable with prior work in Geoffroy's spider monkeys (Laska, 1998) and may be suggestive of different underlying neural mechanisms contributing to hand and tail laterality. Among humans, only roughly 50% are concordant in lateral preferences for handedness, footedness, eyedness, and earedness (Coren, 1993), lending further support for matching lateral preferences across body parts in some monkeys but not others. Moreover, Pubols and Pubols (1971) showed that the hands have twice the sensory cortical representation as the tail in *Ateles*. However, this study did not report on subjects' caudal abilities before the experiment. To the best of our knowledge, there are no data examining brain structure or function in monkeys that use the tail for manipulation as compared with those who do not. Such an approach linking behavioral asymmetries to brain asymmetries in the context of motor planning and laterality has been done in chimpanzees (Hopkins et al., 2017) and would be a logical next step in understanding laterality within brain-behavior relationships in spider monkeys.

Finally, probing the limits of the prehensile tail of spider monkeys and further characterizing how it is used in planning goal-directed actions are highly germane to investigators outside of laterality. For example, roboticists have been interested in building robots inspired by biological models such as the elephant trunk, octopus tentacle, and snake (for reviews, see Walker, 2013; Webster & Jones, 2010). These continuum or "soft robot" models are hyperredundant with many degrees of freedom compared with rigid human-arm models with joint limitations and have broad practical applications in fields like manufacturing and medicine for working alongside humans safely (Rus & Tolley, 2015). However, soft robots can be difficult to control, as well as to design and fabricate, which has led to an interest in merging soft and rigid components together (Drotman, Jadhav, Karimi, deZonia, & Trolley, 2017). We suggest that the prehensile tail of spider monkeys may be a yet untapped biological model that combines a rigid internal structure with a soft outer layer that may advance our understanding of how grasping is planned and executed.

In summary, we have shown that prehensile tail use in Colombian spider monkeys is sensitive to context and complexity—when skill is required for obtaining high-value food items, monkeys exhibit exclusive, or near exclusive, use of the tail with respect to one side of the body. By contrast, monkeys do not exhibit asymmetrical tail use when wrapping the tail around the body at rest, which does not require skill, nor is it associated with a cost based on execution. Although we are limited in the conclusions we can draw given our small sample size, we have shown how examining tail use biases can contribute to our understanding of behavioral laterality, as well as the aptitude for the spider monkey tail to grasp objects under different constraints, which may be valuable for roboticists and engineers working with biological models.

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