

RESEARCH ARTICLE

Lateralization in seven lemur species when presented with a novel cognitive task

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Abstract

Objectives: Asymmetrical behavior patterns are observed in many animal species, but the potential adaptive significance of lateralization and the evolutionary forces driving it remain unclear. Most laterality studies have focused on a single species, which makes interspecies comparisons difficult. The aim of this study was to examine differences in the strength and direction of lateralization in multiple lemur species when engaged in a standardized, novel cognitive task.

Materials and Methods: We assessed laterality in seven lemur species at the Duke Lemur Center when using a novel puzzle-box. We recorded which hand opened the apparatus door and which hand picked up the food reward. We also recorded whether the mouth was used for either action instead of the hands. We then calculated handedness indices (HI), z-scores, and mouth-use rates.

Results: Overall, 62% of individuals were more lateralized than chance. However, within-genera, there were relatively equal numbers of individuals with a left- or right-hand bias, which resulted in ambipreference at the genus level. The hand a lemur used on its first success in the task predicted its overall HI value, and the strength of lateralization increased as the number of successes increased. *Varecia* had significantly higher mouth-use rates than all other genera.

Discussion: We found evidence of an individual learning trajectory in which the hand used on a lemur's first success was canalized as the preferred (and lateralized) hand, in support of the "cognitive simplicity" hypothesis. Individual variability in hand preference was high, which is consistent with previous research. Between-genera differences in mouth use appear to reflect species-specific feeding postures and differences in manual dexterity.

KEYWORDS

Eulemur, handedness, laterality, *Propithecus*, *Varecia*

1 | INTRODUCTION

Most animals show striking bilateral symmetry of their body plan, but this symmetrical form breaks down with function (i.e., behavior; Watson & Hanbury, 2007). Primates provide a good example of this asymmetry because they evolved grasping extremities that sometimes exhibit laterality, such as which hand they use more frequently to

groom or forage (McGrew & Marchant, 1997). Laterality may reflect larger hemispheric specialization in the brain or motor systems responsible for different behaviors and movements (Watson & Hanbury, 2007). The right-hand bias in humans is thought to reflect hemispheric specialization that is most closely associated with language functions (Papademetriou et al., 2005). There is also evidence that patterns of atypical individual handedness, particularly left-

handedness, are associated with many types of human pathological (e.g., dyslexia, autism, schizophrenia) and nonpathological (e.g., artistic skills, athletic prowess) conditions (Papademetriou et al., 2005). However, whether the population-level right-handedness exhibited by humans is the result of a unique coevolution of hemispheric lateralization and complex cognitive processes has led to extensive theoretical debate (Ward, Milliken, & Stafford, 1993).

These associations have led researchers to seek a nonhuman primate model for human handedness that could help elucidate the ultimate factors driving lateralization and the proximate mechanisms affecting its variability (Ward 2013). Postural origins (MacNeilage, Studdert-Kennedy, & Lindblom, 1987), cognitive simplicity (Flowers 1975; Papademetriou et al., 2005), task complexity (Fagot & Vauclair, 1991), and developmental hypotheses (Warren 1980, 1987) have been proposed to explain the evolution of lateralization. These hypotheses posit that postural positions, information-processing costs, the difficulty of a behavior, and age, respectively, drive lateralized behavior. These hypotheses are not mutually exclusive and are unlikely to uniformly explain the strength and direction of laterality across taxa that differ in morphology, development, and socioecology. By testing primate species that differ in these traits, we can attempt to parse whether certain factors, such as locomotor mode, diet, manual dexterity, and sociality, influence cognitive processes that manifest as lateralized behaviors. Beyond species differences, laterality may also vary throughout an individual's lifespan. For example, juveniles use their mouths more frequently because sensorimotor development of the mouth develops before manual motor development (Warren 1980, 1987).

Strepsirrhines are a notable primate lineage in which to investigate these evolutionary hypotheses. Lemurs represent a key mammalian lineage because they bridge primates with the rest of Mammalia but have remained biogeographically isolated on Madagascar for ~50 million years (Herrera & Dávalos, 2016). Lemur species are phylogenetically close but have radiated into a wide variety of socioecological niches. Therefore, lemurs can provide crucial evolutionary context for multiple aspects of primate behavior, including the evolution of lateralization. For example, Indriids and Lepilemurids are folivores, most Lemurids are frugivores, and some species are specialists (e.g., insects: *Daubentonia madagascariensis*; bamboo: *Haplemur* spp.). Lemur social organization is also diverse and includes solitary (*Microcebus* spp.) and pair-living species (some *Lepilemur* spp. and *Phaner* spp.) as well as those with small family groups (*Propithecus* spp.), large multimale-multifemale groups (*Lemur catta*), and groups characterized by fission-fusion dynamics (*Varecia* spp.). This intense niche partitioning is also evident in activity patterns (nocturnal, cathemeral, and diurnal), locomotor modes (vertical clinging and leaping, terrestrial and arboreal quadrupedalism, hind limb suspension), and forest strata utilized.

Laterality research in strepsirrhines has been widespread (see Table 1 for a review), but most studies have only tested one species or examined one behavior. Few studies have directly compared species using the same experimental design, and the majority of previous studies have used simple food-reaching or locomotive tasks to test for manual lateralization (Forsythe & Ward, 1988; Larson et al., 1989;

Leliveld et al., 2008; Stafford et al., 1993). Therefore, methodological differences preclude effectively comparing results between studies that have tested different species. Evidence supporting the four aforementioned lateralization hypotheses is present for some species but not others, and these differences likely reflect taxa-specific factors. Furthermore, none of these hypotheses consider the influence of the social learning processes that are integral to individual fitness in many primate species. Using an integrated learning and laterality experiment is a novel approach, but such an integration allows for a better understanding of the interaction between these two information-processing and decision-making cognitive abilities.

Therefore, the aim of this study was to use a standardized experimental protocol with a novel cognitive task to facilitate interspecies comparisons of manual lateralization. We tested manual lateralization of two behaviors (solving a task and food-reaching) within a social learning experimental paradigm. In a pilot study conducted prior to this study period, we observed that some individuals preferred to use their mouth rather than their hands to interact with the task apparatus. We thus added “mouth” as a retrieval option (in addition to left hand, right hand) and investigated whether there were species differences in mouth-use rate. We included lemur species with different diets, social structures, activity patterns, and locomotor modes to investigate the potential role of variable ecological factors and social learning processes in the evolution and development of lateralization (Baden 2011; Curtis 2004; McGoogan 2011; Sauther et al., 1999; Vasey 1997; Volampeno 2011; Wilson et al., 1989; Table S1). Because this study was part of a larger social learning experiment, we also examined whether individuals with prior knowledge of and experience with the apparatuses (i.e., the models) influenced the hand preferences of other group members (i.e., via observational learning).

First, we predicted species differences in the strength and direction of hand preference as well as mouth-use rate because species differences in socioecology and morphology should affect manual dexterity, spatial awareness, and cognitive abilities. Second, we predicted that younger individuals would show a weaker level of lateralization and use their mouth more frequently, which is consistent with the developmental hypothesis. Third, we predicted that the direction of hand preference of group members would be the same as the hand preference of the model individual due to observational learning on the part of group members. We further predicted that the strength of lateralization would increase over time to minimize energetic and temporal information-processing costs, consistent with the cognitive simplicity hypothesis (Flowers, 1975; Papademetriou et al., 2005).

2 | METHODS

This study was conducted at the Duke Lemur Center (DLC) in Durham, North Carolina from June 5 to September 1, 2017. Then, 66 lemurs across seven species (*E. coronatus*, *E. flavifrons*, *E. mongoz*, *L. catta*, *P. coquereli*, *V. rubra*, and *V. variegata*) and 16 groups were tested (Table S2). Free-ranging groups (eight groups total) lived in

TABLE 1 Previous studies examining lemur lateralization

Species	Manual bias	Task	n	Source
<i>D. madagascariensis</i>	Ambipreferent	Reaching, holding, tapping, probing	5	Lhota, Jůnek, and Bartoš (2009)
	Left-hand, right-hand	Food-holding, digit feeding	11	Feistner, Price, and Milliken (1994)
<i>E. albifrons</i>	Left-hand	Food reaching	15	Ward, Milliken, Dodson, Stafford, and Wallace (1990)
<i>E. collaris</i>	Left-hand	Routine activities	2	Schoek and Edds (2018)
	Left-hand	Food reaching	24	Ward et al. (1990)
<i>E. coronatus</i>	Left-hand	Food reaching	11	Ward et al. (1990)
<i>E. fulvus</i>	Right-hand	Food reaching	11	Ward et al. (1990)
<i>E. macaco</i>	Left-hand	Food reaching	33	Forsythe and Ward (1988)
	Left-hand	Food reaching	29	Ward et al. (1990)
<i>E. mongoz</i>	Right-hand	Food reaching	26	Ward et al. (1990)
<i>E. rubriventer</i>	Right-hand	Food reaching	5	Ward et al. (1990)
<i>E. ruffrons</i>	Ambipreferent	Routine behaviors and feeding apparatus	17	Schnoell, Huebner, Kappeler, and Fichtel (2014)
<i>E. rufus</i>	Left-hand	Food reaching	14	Ward et al. (1990)
<i>E. sanfordi</i>	Ambipreferent	Food reaching	17	Ward et al. (1990)
<i>G. moholi</i>	Right-hand	Food reaching, whole body turning	16	Dodson et al. (1992)
<i>G. senegalensis</i>	Left-hand	Eight conditions	10	Larson et al. (1989)
	Left-hand	Food reaching	8	Sanford and Ward (1986)
<i>H. griseus</i>	Left-hand	Food reaching, bamboo processing	13	Stafford, Milliken, and Ward (1993)
<i>L. catta</i>	Left-hand	Food reaching, chewing	21	Bennett, Ward, Milliken, and Stafford (1995)
	Left-hand	Feeding, grooming, agonism	22	Masataka (1989)
	Left-hand	Food reaching, feeding posture, chewing	13	Milliken, Forsythe, and Ward (1989)
	Left-hand	Routine activities	4	Schoek and Edds (2018)
	Left-hand	Bimanual food reaching	2	Schrauth (2007)
	Left-hand	Food reaching	42	Ward et al. (1990)
	Right-hand	Solving feeding apparatus	17	Regaiolli, Spiezio, and Hopkins (2016)
Sex-dependent	Routine activities	11	Shaw, Wolfe, and Panger (2004)	
<i>I. indri</i>	Contextually dependent	Food-reaching, postural grips	16	Rigamonti, Spiezio, Poli, and Fazio (2005)
<i>M. lehilahytsara</i>	Ambipreferent	Apparatus food reaching	19	Leliveld, Scheumann, and Zimmermann (2008)
<i>M. murinus</i>	Right-hand	Food reaching, whole body turning	8	Dodson et al. (1992)
	Ambipreferent/slight right	Apparatus food reaching	44	Leliveld et al. (2008)
	Ambipreferent/slight right	Apparatus food reaching	38	Scheumann and Zimmermann (2008)
	Ambipreferent/slight right	Apparatus food reaching	56	Scheumann, Joly-Radko, Leliveld, and Zimmermann (2011)
<i>O. garretti</i>	Right-hand	Food reaching	23	Milliken, Stafford, Dodson, Pinger, and Ward (1991) and Milliken, Ward, and Erickson (1991)
	Ambipreferent	Quadrupedal and bipedal food reaching	27	Ward and Cantalupo (1997)
	Contextually dependent slight left	Food reaching, body turning, tail wrapping, chewing	17	Hanbury et al. (2010)
<i>P. coquereli</i>	Ambipreferent	Feeding	15	Mason, Wolfe, and Johnson (1995)
	Mouth	Food-reaching, postural grips	11	Milliken, Ferra, Kraiter, and Ross (2005)
<i>P. tattersalli</i>	Mouth	Food-reaching, postural grips	3	Milliken et al. (2005)
<i>P. verreauxi</i>	Mouth	Food-reaching, postural grips	2	Milliken et al. (2005)
<i>V. variegata</i>	Left-hand	Food reaching in three different postures	5	Forsythe, Milliken, Stafford, and Ward (1988)

(Continues)

TABLE 1 (Continued)

Species	Manual bias	Task	n	Source
	Left-hand	Food reaching, head tilting	21	Nelson, O'Karma, Ruperti, and Novak (2009)
	Left-hand	Routine activities	2	Schoek and Edds (2018)

large, fenced-in tracts of forest ranging from 0.5 to 5.5 ha with indoor runs where the experimental trials were conducted. Indoor groups (eight groups total) lived in a series of two to four rooms ($3 \times 2.3 \times 2.2 \text{ m}^3$ per room) inside a building that were connected to corresponding outdoor runs ($3 \times 2.3 \times 4.3 \text{ m}^3$ per run). Three groups were also considered protected contact meaning that no one (even staff members) could be in the same enclosure as the lemurs, and the lemurs were shifted out of the enclosure before a staff member could enter to reset the apparatus. This sequence was repeated until an individual reached 10 successes or 10 min elapsed (time spent shifting animals in and out of the testing enclosure was subtracted from the total trial time).

This study was part of a larger project examining social learning across lemur species, and as such, we used a two-action paradigm apparatus similar to those used previously with other primate species (haplorrhines: Drea 2006; Dindo et al., 2008; van de Waal & Whiten 2012; Gunhold et al. 2015; strepsirrhines: Kendal et al., 2010; Stoinski, Drayton & Price, 2011; Schnoell, Dittman, & Fichtel 2014). The task goal for the lemur was to open the apparatus door and obtain a food reward. The apparatus (dimensions: $30 \times 15 \times 20 \text{ cm}^3$) was a plexi-glass box with one flap door (a hinge on the left side) that could be opened two different ways, either push or pull. The apparatus was baited with a single piece of food placed inside. The food item was whole peanuts for *P. coquereli* (because of their folivory-adapted gut) and grapes for all other species (grapes were cut in half so they did not roll). The apparatus was bolted onto a table (dimensions: $76 \times 51 \times 71 \text{ cm}^3$) because some of the species tested do not readily come to the ground. The legs of the table were fastened to the enclosure caging with zip ties during trials to secure the table and apparatus. The apparatus door had two stop levers on it: one on the inside of the door and one on the outside. These levers controlled how the door could be opened; if the inside lever was on, the door could only be pulled because the lever blocked it from being pushed open and vice versa for the outside lever.

Lemur groups with three individuals were provided three apparatuses (five groups total) and groups with four or more individuals were given all four apparatuses (11 groups total). The apparatuses were placed at least 1 m apart to minimize competition. Behavioral data were collected with a video camera (Nikon Coolpix L110) set up outside the enclosure for indoor groups and approximately three meters from the apparatuses for free-ranging groups.

2.1 | Experimental design

All groups were randomly assigned a group type (control, push, or pull) balanced within species. In other words, each species had at least one

control group and one or two experimental groups (there was only one *E. coronatus* group, which was designated as a control). This design enabled within-species comparisons as well as between-species comparisons. Control and experimental groups were designated using a random number generator. Where necessary, we pooled species data into broader genera to increase statistical power. The alpha female in each experimental group (the push or pull groups) was selected as the model individual; control groups did not have a model. Although this model selection created the potential for the alpha female to control access to the apparatuses, multiple apparatuses were available during the testing trials, which mitigated this issue.

Each group had at least one habituation trial that lasted approximately 15 minutes. During the habituation trial, unbaited and locked apparatuses were placed inside the enclosure to be visually and physically accessed by the lemur group. The video camera was also placed in its appropriate recording position outside of the enclosure (but was not recording). Directly following the habituation phase, the control groups began experimental trials and the model individuals from the push and pull groups began training trials. The intertrial day ranges differed between the indoor and free-ranging groups due to feeding and shifting schedules, but there was at least 1 day in between trials for all groups.

During the training phase for the push and pull groups, the model individual was shifted away from the group into a separate enclosure and given access to one apparatus. For models from pull groups, the inside stop lever on the apparatus was activated so the model could only pull the door open, and for models from push groups, the outside lever was activated so the model could only push the door open. Each training trial lasted 10 min or as long as it took the model to have 10 successes (whichever came first). The DLC used this success threshold to prevent overfeeding and minimize sugar intake. A success was defined as an individual opening the door and removing the food reward. We considered the training phase complete for each model once that individual reached 25 consecutive successes (a minimum of three training trials). Control groups did not have a model-training phase and therefore went directly from the habituation trial to the experimental trials.

We used an open-diffusion design during the experimental trials, in which all individuals in the group had access to the apparatus and the trained model if applicable (Hoppitt & Laland, 2013). Each group (across all conditions) participated in at least nine experimental trials each lasting 10 min or as long as it took one individual to reach 10 successes (whichever came first). This limit was established by the DLC to prevent over-feeding of particular individuals. During this phase, no stop levers were activated on the apparatus so a lemur could open the door using either a push or pull. The DLC staff shifted the group

out of the testing enclosure so the apparatuses could be secured inside, and then the group was released back into the testing enclosure through a shift door. All trials were video recorded starting when the shift door opened. After a success, a DLC staff member inside the enclosure reset the apparatus (replaced the food item and closed the apparatus door). Every effort was made to block the lemurs' view when the apparatus was reset.

2.2 | Data analysis

Video data from all 246 trials was coded. Coders recorded age and species of each individual in the trial, along with the method (left-hand, right-hand, or mouth) used to open the apparatus door and to retrieve the food item for each individual's successes. For "push" and "pull" groups, the model individual was also coded; the model's hand preference was then calculated as the "demonstrator" to assess the relationship between social learning and lateralization. Handedness was calculated separately for the hand that opened the apparatus door and the hand that grabbed the food reward. We calculated individual handedness indices (HI) based on the following equation: $HI = (RH - LH)/(RH + LH)$. In this equation, RH is the number of times the right hand was used, and LH is the number of times the left hand was used. A score of +1 indicated an individual was entirely right-handed, -1 indicated an individual was completely left-handed, and 0 indicated the individual was ambipreferent. We also calculated absolute HI values, which test the strength of lateralization but do not inform direction. In addition to HI values, we derived z-scores for each individual using the equation: $(x - (n/2))/(\sqrt{n \times 0.25})$ (McGrew & Marchant, 1997).

We calculated HI values for each individual in each trial and calculated overall individual averages and averages by genera (Table 2). We used the number of successes when the mouth was used as a proxy for mouth-use rate (calculated separately for opening the door and retrieving the food reward). HI values and ratios were not conducted on individuals who had fewer than 20 successes ($n = 37$ total individuals for analysis). The within-group sample size was relatively small due to the voluntary nature of the study (12 lemurs never touched the apparatuses), logistical circumstances, DLC-mandated rules, and cost. Where possible, we pooled species values into genus-level averages to further increase statistical power.

Table 2 shows descriptive summary statistics across individuals and genera. We analyzed all data in R (R Core Team, 2018). We ran a Gaussian generalized linear mixed model (GLMM) using the "glmer" function in the *lme4* package with genus, age, # successes using hands, and method used on first success as fixed-effects variables, HI as the response variable, and individual as a random-effects variable (Table S3). We used the same fixed and random effects in a second model with absolute HI as the response variable. The same relationships were significant when HI and absolute HI were replaced in these models with z-score and absolute z-score, respectively; therefore, we report the former models. A third model included the number of successes/trial grabbing the food with mouth as the response variable,

individual as a random-effects variable, and genus, age, and method used on first success as fixed effects variables (Table S3).

We tested all possible permutations of the fixed effects models using backwards-stepwise regression (*drop1* function in *lme4* package, which uses likelihood ratio tests to determine the best model), dredging (*dredge* function in *MuMIn* package, which uses restricted maximum likelihood to determine the best model), and analysis of variance (ANOVA; comparing each full model to the null model). Both the *dredge* and *drop1* methods derived the same conclusions regarding which variables were significant in each model and which models were best given an information criterion (i.e., Akaike's adjusted for small sample size [AICc]); the outputs of the best models obtained via dredging, per response variable, are documented in Table S3.

3 | RESULTS

We could not quantitatively test for a "demonstrator" effect given the small sample size in the experimental groups, but it did not appear that there was a relationship (2 of 13 individuals had the same preference as the demonstrator). Because social learning could not be tested, we tested individual learning through method-used-on-first-success as a proxy for trial-and-error learning. The majority of individuals attempted the task with both hands before achieving their first success; therefore, the hand used on first success may have been the hand they continued to use (this would be consistent with the cognitive simplicity hypothesis).

The average HI across all individuals and all trials was 0.06 ± 0.70 , and the average z-score was 1.04 ± 6.04 , meaning that the study population could collectively be categorized as ambipreferent (Table 2). However, ambipreference resulted from the extreme variability between individuals, which led to roughly even numbers of left-handed, ambipreferent, and right-handed lemurs (averaging together to be ~0). The z-scores and HI both showed that 23 of 37 individuals (62%) had a hand preference that was significantly different from chance (Figure 1) assessed by $(-1.96 \geq z \text{ or } 1.96 \leq z; -0.5 \geq HI \text{ or } 0.5 \leq HI)$. Of these individuals, 11 lemurs (30%) showed a left-hand preference, 12 (32%) showed a right-hand preference, 7 (19%) showed a mouth preference, and 7 (19%) were ambipreferent (Table 2).

The HI model with the lowest AICc score included the hand used on the first success (GLMM, *dredge*: z-value = 3.41, $p < .001$; *drop1*: LRT = 9.48, $p = .009$). This full model was significantly different from the null (ANOVA, $df = 10$, $\chi^2 = 16.72$, $p = .02$). The hand an individual used on their first success was the strongest predictor of HI (i.e., if an individual used their left hand on their first success, they were significantly more likely to show a significant left-hand preference in z-score and HI, see Figure 2). None of the other variables tested were significant. The strong individual HI variability within-genera resulted in a non-significant relationship because of equal numbers of strongly left- and right-handed lemurs. The model using absolute HI as a response variable included the number of successes performed as a significant predictor (GLMM, *dredge*: z-value = 2.25, $p = .01$; *drop1*: LRT = 4.55,

TABLE 2 Summary statistics for lemurs tested

Individual	z-score	HI	# Successes overall	# Successes (using either hand)	Preference
Aemilia			68	16	Mouth
AJ	0.65	0.168	30	21	Ambipreferent
Arche	0.9	0.319	60	31	Ambipreferent
Astro	-2.24	-0.357	33	20	Left
Bode	3.96	0.524	81	50	Right
Bonita			22	18	Mouth
Borealis	-3.78	-0.503	42	37	Left
Buzz			47	1	Mouth
Calpurnia			11	0	
Carolina ^a	3.96	0.448	110	107	Right
Cosmo			18	12	
Drusilla	-1.66	-0.122	68	52	Ambipreferent
Duggan	1.69	0.311	62	59	Ambipreferent
Gisela ^a	-4.39	-0.45	113	105	Left
Gretl ^a	9.9	1	101	98	Right
Griselda	-4.73	-0.55	67	58	Left
Halley ^a	8.46	-0.823	112	94	Left
Hedwig			8	5	
Hibernia	-6.79	-0.968	53	50	Left
Hiddleston	-9.11	-1	85	83	Left
Hostilian			58	0	Mouth
Julian	6.66	0.931	59	52	Right
Kalani	-1.03	-0.196	73	34	Ambipreferent
Kek	6.03	0.875	54	44	Right
Lincoln			40	0	Mouth
Lulu			11	9	
Maddie	0.13	0.072	61	57	Ambipreferent
Marcus			16	9	
Mico	-4.51	-0.446	100	91	Left
Narcissa			10	8	
Onyx	-7.04	-0.907	74	61	Left
Pandora ^a	2.33	-0.133	31	31	Right
PJ			60	14	Mouth
Pyxis			22	7	Mouth
Randy ^a	8.91	0.838	110	109	Right
Rodelinda ^a	10.00	1	103	100	Right
Sally	5.08	0.702	72	53	Right
Schroeder			8	8	
Seshat ^a	-8.55	-0.782	126	126	Left
Seshen	0.43	0.225	22	22	Ambipreferent
Sprite	6.00	0.804	64	64	Right
Stewart	-7.75	-1	60	60	Left
West ^a	10.49	0.979	114	114	Right
Wiig	7.23	0.852	60	60	Right

(Continues)

TABLE 2 (Continued)

Individual	z-score	HI	# Successes overall	# Successes (using either hand)	Preference
<i>Genus</i>					
<i>Eulemur</i>	0.779	0.154	856	781	Ambipreferent
<i>Lemur</i>	-0.214	-0.112	626	544	Ambipreferent
<i>Propithecus</i>	2.653	0.34	496	334	Ambipreferent
<i>Varecia</i>	1.592	-0.033	621	391	Mouth/ambipreferent

^aModel individual.

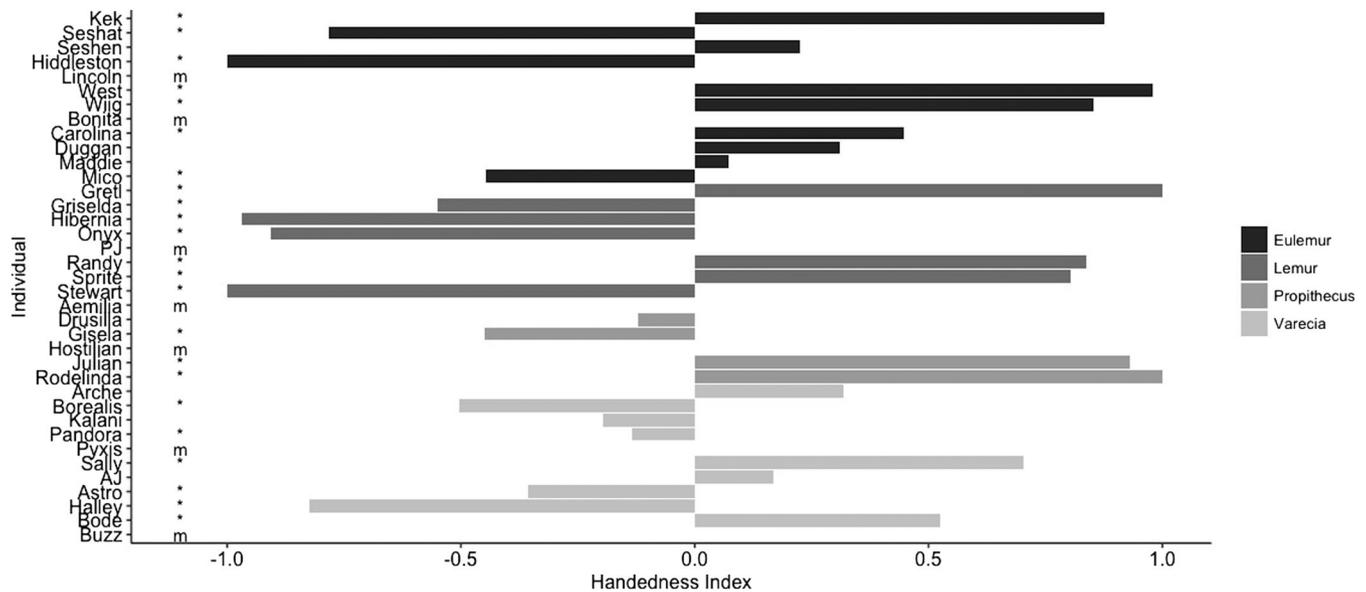


FIGURE 1 Handedness indices (HI) of all individuals in the study. A value of -1 is completely left-handed, 1 is completely right-handed. Colors denote genera. Stars indicate a significant difference from chance ($-1.96 \geq z$ or $1.96 \leq z$). “M” indicates a preference for mouth rather than either hand

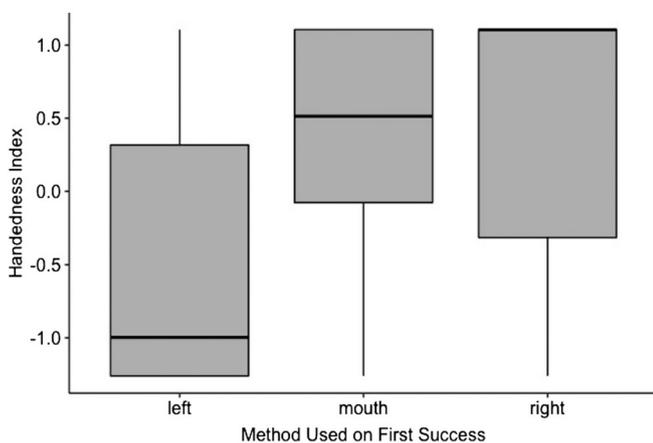


FIGURE 2 The hand an individual used for its first success significantly predicted their overall hand preference for all trials (i.e., handedness indices [HI]). A value of -1 is completely left-handed and 1 is completely right-handed

$p = .03$). There was a positive relationship between the number of overall successes and absolute HI, indicating that individuals became more lateralized as they became more familiar with the task over

successive trials (Figure 3). This full model was also significantly different from the null model (ANOVA, $df = 10$, $\chi^2 = 13.90$, $p = .05$).

The average mouth use across all individuals and all trials was 16% for opening the door and 35% for retrieving the food reward. The mouth-use rate (for grabbing the food) model with the lowest AICc score included genus as a significant predictor (GLMM, *dredge*: z -value = 3.13, $p = .002$; *drop1*: LRT = 17.01, $p < .001$). Again, this full model was significantly different from the null model (ANOVA, $df = 9$, $\chi^2 = 40.03$, $p < .0001$). *Varecia* had a significantly higher rate of mouth-use than *Propithecus*, *Eulemur*, and *Lemur* (Figure 4). There was also a trend for age with younger individuals showing higher rates of mouth-use ($p = .08$).

4 | DISCUSSION

In this study, 62% of lemurs were more lateralized than would be expected by chance confirming that lateralization, at least on an individual level, extends throughout the primate phylogeny. The lemurs in this study followed a “continue-with-the-hand-that-was-successful-first” heuristic, which appears to account for the difference between

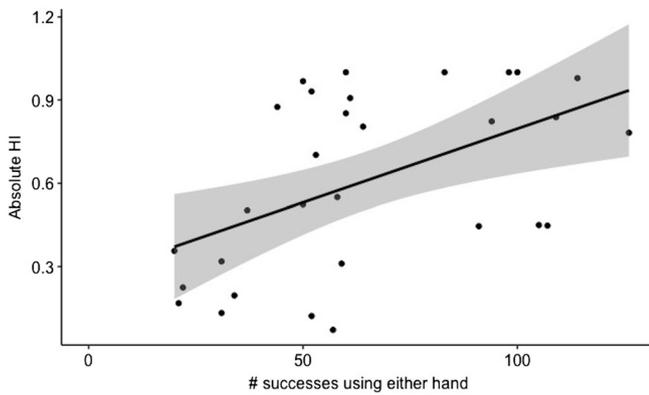


FIGURE 3 The strength of lateralization increased the more successes an individual had with either hand, suggesting canalization of preference through trials and over time

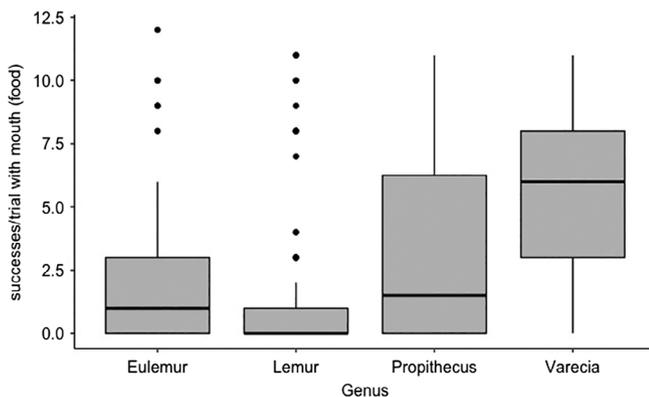


FIGURE 4 Between-genera differences in the number of successes per trial using the mouth to retrieve the food reward. *Varecia* had significantly higher percentages of mouth-use than all other species

strong individual hand preference and weak species and genus preferences. The 50% chance that an individual happened to first succeed with one hand over the other was perpetuated as the lemurs persisted with that initial hand. In other words, strong lateralization was canceled out at the genus level because of similar numbers of left- and right-preferent individuals. We also found species differences in the method (left-hand, right-hand, or mouth) used to solve the task. Finally, we found that individuals used the hand they first succeeded with and then became more lateralized over time. This is consistent with the Level 2 classification of strepsirrhines within McGrew and Marchant's (1997) lateralization framework, meaning that they show significant but incomplete individual-level lateralization and symmetrical population-level lateralization.

Genus-specific differences in hand lateralization are difficult to generalize because of the inherent individual-level variation present here. In other words, the differences observed between genera in this study were explained not by the evolutionary pressures of a niche, but rather by the high level of individual variability (we elaborate on genus-level differences in mouth-use below). Nearly all lemurs who

had a success had attempts beforehand using both hands. This individual variability appears to be rooted in the 50/50 chance an individual had their first success with either hand. This initial success was then used as a "template" to follow in future successes such that lemurs continued with that hand through the rest of the trials. The canalization of this initial bias was further exemplified by the positive relationship between the number of successes performed and strength of lateralization (i.e., absolute HI).

We therefore found support for the cognitive simplicity bias, as the hand an individual used for its first success was the hand it continued to use throughout the study, such that HI and z-score preferences matched the hand used on the first success. By sticking with the first-hand-to-succeed heuristic, the lemurs reduced temporal and energetic information-processing costs by avoiding having to make a decision about which hand to use for each success. Additionally, there was a positive relationship between the number of successes performed and absolute HI, indicating that individuals became more strongly lateralized over time. This canalization of an initial preference based on individual trial-and-error learning lends further support to the cognitive simplicity hypothesis.

Overall, more lemurs used their mouths consistently to retrieve the food than to open the door, which probably reflects the different actions required for these two steps. Compared to other species, ruffed lemurs (*Varecia*) used their mouths more frequently than their hands, and many of these individuals had trial successes while perched on top of the apparatus. These individuals would consistently perch on top of the puzzle box, reach down, and open the door with their head oriented upside down. This behavior likely reflects their natural foraging behavior in the high-canopy, terminal-branch niche that ruffed lemurs occupy, as they are accustomed to reaching down to grab fruit hanging below branches. In contrast to *Varecia*, *Eulemur* and *Lemur* do not regularly suspend during foraging, and typically maintain quadrupedal postures while feeding. Sifakas are vertical clingers/leapers and stay in orthograde postures while feeding.

Although the ruffed lemurs used their mouths more frequently, those who had upside down successes also had "normal" right-side-up successes. These mechanistic and postural differences may indicate some degree of behavioral flexibility. This is perhaps because the individuals who had both upside down and normal successes were all relatively young (all ≤ 4 years old), and more plastic in their behaviors. Our results lend some support to the developmental hypothesis in explaining manual lateralization in these lemur species. The age effects found in this study are consistent with previous studies that also found higher mouth-use rates among younger individuals and a gradual strengthening of lateralization with age (Mason et al., 1995).

This study contributes to the existing literature on strepsirrhine lateralization and emphasizes the individual variation inherent in these asymmetrical behavioral patterns. Using a social learning experiment to test lateralization complements the previous studies cited in Table 1 and allows for the integration of multiple cognitive processes (learning and lateralization). Explaining these individual-level differences using a learning-strategy lens is a novel approach in primate

lateralization research, which can be expanded upon in the future with other primate species.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

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