

# Preliminary comparisons of learning across four lemur genera at the Duke Lemur Center

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**Abstract** – Lemurs have been relatively understudied in cognitive research despite representing an adaptive radiation and occupying a key phylogenetic position as the most basal extant primate lineage. Many of the existing studies have focused on only one lemur species. We aimed to take a comparative approach by examining learning abilities in 66 lemurs from four genera at the Duke Lemur Center in North Carolina. We used a novel two-action puzzle box to assess inter-species variation in learning speed, task proficiency, and social tolerance during trials. We found differences between genera in the percentage of individuals who had successes, individuals' latency to touch the apparatus and the number of times an individual observed a group member's success. *Eulemur* and *Varecia* had shorter latencies and were observed more by conspecifics compared to *Propithecus* and *Lemur*. Shorter latencies may indicate reduced fear or increased motivation, while higher observation rates suggest more leniency or tolerance around the puzzle boxes. These results may be due to species differences in dominance and rank hierarchies; *Propithecus* and *Lemur* are more despotic than *Eulemur*, where some species exhibit sex co-dominance, and *Varecia*, which live in groups with high fission-fusion dynamics. We also show that even within these overall relationships, the different genera varied substantially in the temporal trajectory of these learning variables through the study trials. Overall, this comparative study provides preliminary insights into the taxon-specific learning trajectories of lemurs and contributes to the growing body of literature examining lemur cognition.

**Keywords** – cognition, *Eulemur*, *Propithecus*, social behavior, *Varecia*.

## Introduction

Lemurs are not well represented in primate cognition research compared to other taxa such as large-bodied apes, macaques, and baboons (Altschul et al., 2019). This bias towards the latter groups is likely the combined result of phylogenetic proximity to humans, brain size, presence of long-term field sites and longitudinal data, access to captive groups, and complexity of their social systems (Altschul et al., 2019;

Ramsay and Teichroeb, 2019; Hernandez et al., 2020). However, lemurs are integral to understanding the evolution of learning processes throughout the primate order as they are the most basal extant lineage within it (Perelman et al., 2011; Finstermeier et al., 2013). Lemurs are an ideal taxonomic group for conducting comparative studies because closely related species and genera have radiated into a diverse range of socioecological niches on Madagascar (Gould et al., 2007; Kappeler, 2012). This is particularly relevant to cognitive studies as there is

debate regarding the relative effects of ecological and social pressures on brain size and learning mechanisms (social brain hypothesis: Dunbar, 1998; ecological intelligence hypothesis: Gibson, 1986). For example, assessing different learning processes exhibited during experimental tasks with taxa that inhabit different social and ecological niches can shed light on the selective pressures acting on cognitive abilities.

To assess learning processes, variations of two-action paradigms have been widely used across primate and non-primate taxa (Galef et al., 1986; Heyes et al., 1992; Whiten et al., 2005; Dindo et al., 2008; van de Waal et al., 2015) including some lemurs (Schnoell et al., 2014; Stoinski et al., 2011; Kendal et al., 2010). This experimental design generally includes the use of an apparatus that can be opened or manipulated using two different methods (e.g., lift/slide, push/pull). There are then different groups of study subjects, some that have individuals already trained on one method or the other (experimental) and some without (control). These types of experiments have been used to assess information transmission among individuals in different group types (i.e., experimental vs control). More nuanced experimental designs can also be used to specifically test for particular social learning mechanisms, such as stimulus enhancement, imitation, or emulation (i.e., tasks with causally irrelevant actions, “ghost trials;” Clay and Tennie, 2018; Hopper, 2010; Tennie et al., 2010; Neadle et al., 2020).

The two-action apparatus has since been used for studies on various primate species (*Saginus* spp., Prescott and Buchanan-Smith, 1999; *Cebus apella*, Dindo et al., 2008; *Chlorocebus aethiops*, van de Waal et al., 2015; *Callithrix jacchus*, Gunhold et al., 2014), including some lemur species (*Eulemur rufifrons*, Schnoell and Fichtel, 2012; Schnoell et al., 2014; *Varecia variegata*, Stoinski et al., 2011; *Lemur catta*, Kendal et al., 2010). Use of the two-action apparatus with lemur species has yielded mixed evidence for social learning. In ring-tailed lemurs (*Lemur catta*), the use of a two-action apparatus indicated directed social learning of different methods in subgroups (Kendal et al., 2010).

Black-and-white ruffed lemurs (*Varecia variegata*) have also been found to socially learn in a two-action paradigm (Stoinski et al., 2011); however, a different study found inconclusive evidence for *Varecia* spp. (Dean et al., 2011). When presented with a two-action puzzle box, half of the individuals in four groups (two of which had a training period and two of which did not) of wild red-fronted lemurs (*Eulemur rufifrons*) maintained a behavioral preference for one action, whereas the others switched flexibly (essentially performing at chance, 50/50; Schnoell et al., 2014). Observations can also be biased, as was found in ring-tailed lemurs where individuals preferentially observed conspecifics that completed tasks more frequently (Kulahci et al., 2018). Ring-tailed lemurs seemed to perform best in food competition paradigms (Sandel et al., 2011), whereas more egalitarian species, such as red-fronted lemurs have shown higher social tolerance in proximity and observation (Fornasieri et al., 1990; Fichtel et al., 2018). Nevertheless, evidence for rank effects (such as females monopolizing access to apparatuses) have been mixed even within species (no effects with ring-tailed lemurs, Kappeler, 1987; effects exhibited with ring-tailed lemurs and black lemurs, *Eulemur macaco*, Fornasieri et al., 1990; no effects exhibited with brown lemurs, *Eulemur fulvus*, Fornasieri et al., 1990; effects exhibited with brown lemurs, *Eulemur fulvus*, Anderson and Fornasieri, 1992).

Many of these studies focused on one species or group; therefore, differences in apparatus, study settings, and experimental design make it difficult to directly compare results across taxa. Our goal with this preliminary study was to use a standardized apparatus and experimental design with seven lemur species housed in very similar conditions at the Duke Lemur Center (DLC). Controlling for methodology allowed us to make such inter-taxonomic comparisons and test for species differences in different learning metrics. This exploratory study comparatively examined the results of learning trials across genera to test for differences in experimental variables such as number of successful individuals, latency to touch apparatus, latency to success, task proficiency rate, and number

**Table 1.** Socioecological niche (in the wild) for the species tested.

Species	Diet (% fruit)	Avg. group size	Activity pattern	Locomotor mode	Natural habitat
<i>E. coronatus</i> <sup>1</sup>	Unknown (frugivore-folivore)	5-9	Cathemeral	Arboreal quadruped	Semi-deciduous forest
<i>E. flavifrons</i> <sup>2</sup>	~73% (frugivore)	6-10	Cathemeral	Arboreal quadruped	Transitional sub-humid forest
<i>E. mongoz</i> <sup>3</sup>	~65% (frugivore-folivore)	3-5	Cathemeral	Arboreal quadruped	Dry deciduous forest
<i>L. catta</i> <sup>4</sup>	30-60% (frugivore-folivore)	10-25	Cathemeral	Semi-terrestrial quadruped	Spiny forest
<i>P. coquereli</i> <sup>5</sup>	25-38% (folivore)	5-8	Diurnal	Vertical clinging/leaping	Dry deciduous forest
<i>V. rubra</i> <sup>6</sup>	75-90% (frugivore)	Community: 18-31 Core groups: 2-9	Diurnal	Arboreal quadruped/suspensory	Tropical rainforest
<i>V. variegata</i> <sup>7</sup>	82-92% (frugivore)	Community: 24-43 Core groups: 2-7	Diurnal	Arboreal quadruped/suspensory	Tropical and montane rainforest

<sup>1</sup>Wilson et al. (1989); <sup>2</sup>Digby and Kahlenberg (2002), Volampeno (2011); <sup>3</sup>Curtis (2004); <sup>4</sup>Sauther et al. (1999), Gould et al. (2003); <sup>5</sup>Kubzdela et al. (1992), McGoogan (2011); <sup>6</sup>Vasey (1997); <sup>7</sup>Overdorff et al. (2005), Baden (2011).

of successes an individual observed. We used latency to touch apparatus as a proxy for neophobia or curiosity, latency to success as a proxy for learning speed, proficiency rate as a proxy for learning efficiency, and successes observed as a proxy for social tolerance or observational influence. We also examined these experimental variables across the successive trials to assess task-solving skill over time and assess genus-level differences in learning trajectories and their temporal patterns.

To maximize our sample size at the DLC, we tested seven lemur species but pooled this data into broader genus-level groups to increase statistical power. The species we tested have different diets, social structures, and locomotor patterns (table 1), all of which may influence the manifestation of task-solving skills. For example, frugivorous primates have larger relative

brain sizes than folivorous primates (Maclean et al., 2009; Decasien et al., 2017). This is thought to be due to the spatial and temporal patchiness of fruits, which require complex navigation, planning, or memory (Gibson, 1986). Consistent with this reasoning, strictly frugivorous lemur species (*Varecia*) outperformed more generalist frugivores (*Lemur*, *Eulemur*) and folivores (sifakas, *Propithecus* spp.) on spatial memory tasks (Rosati et al., 2014). However, a recent study found no difference in spatial memory task performance on the Primate Cognition Test Battery between frugivorous *Varecia*, insectivorous-omnivorous *Microcebus* (mouse lemurs) and omnivorous *Lemur* (Fichtel et al., 2020). Further, *Varecia*, *Lemur*, *Propithecus* and *Eulemur* did not differ when tested on social inhibitory control abilities (Reddy et al., 2015). Partially due to dietary variation, lemur

species have also been found to differ in locomotor modes and positional behavior, which impacts body control and the manual dexterity needed in some cognitive tasks (Peckre et al., 2016; Batist and Mayhew, 2020). Species with less flexible or decreased manual dexterity may be unable to efficiently manipulate an apparatus. Strepsirrhine species that exhibit infant-clinging behaviors more frequently used manual grasping in a food manipulation test than species that carry infants orally (Peckre et al., 2016). In the context of our study, *Varecia* are the only taxon that orally carries infants, whereas the other species all have fur-grasping infants (Morland, 1990; Gould et al., 2007; Kappeler, 2012). Indeed, in a previous comparative study with these same genera, *Varecia* showed the highest rate of mouth use during a puzzle box task (Batist and Mayhew, 2020).

Unlike haplorrhines (apes, monkeys, and tarsiers), group size in strepsirrhines (lemurs, lorises, galagos, and pottos) did not correlate with relative brain size but did correlate with performance on social cognition tasks (Maclean et al., 2009; Maclean et al., 2013). Group size is thought to drive cognitive complexity because of the necessity to maintain social bonds, remember interactions with many conspecifics, and track fluid rank relationships (Dunbar, 1998). Previous studies indicated that *Lemur* (who live in large multi-male, multi-female groups) equaled and even outperformed some monkeys in cognitive tests (Sandel et al., 2011; Jones et al., 2014; Devaine et al., 2017; Fichtel et al., 2020). For example, ring-tailed lemurs (as well as mongooses, *Eulemur mongoz*, and blue-eyed black, *Eulemur flavifrons*, lemurs) showed similar numerical discrimination skills when compared with macaques (Jones et al., 2014).

Whereas most group-living lemur genera show strict female-dominated hierarchies (Wright, 1999), studies have shown that *Eulemur* exhibits “co-dominance” between the sexes and a more egalitarian social system overall (Pereira and McGlynn, 1997; Curtis, 2004; Fichtel et al., 2018; DLC staff, pers. comm.). Notably, *Lemur* and some *Propithecus* species

have more defined hierarchies and more pronounced female dominance or feeding priority (Sauther et al., 1999; Gould et al., 2003; Kappeler and Schaffler, 2008; McGoogan, 2011); however, *Propithecus* also shows overall low levels of aggression (Erhart and Overdorff, 1999).

Taken together, we aimed to determine whether there were differences in various learning metrics between lemur taxa using an exploratory puzzle box. We predicted that *Varecia* and *Lemur* would have quicker learning speeds and higher proficiency rates than *Propithecus* and *Eulemur*, whereas *Eulemur* would have the most successes observed. Our predictions are derived from several lines of information. Firstly, frugivorous taxa have larger relative brain sizes than folivorous taxa within primates (Maclean et al., 2009; Decasien et al., 2017). Further, *Varecia* exhibit strong fission-fusion dynamics where individuals move fluidly between subgroups of varying composition and duration (Vasey, 1998; Baden, 2011). Fission-fusion dynamics are thought to select for higher social cognitive abilities to keep track of fluid relationships, past interactions, and the identification of many individuals (Aureli et al., 2008). By contrast, *Propithecus* species tend to live in small family groups. *Lemur* live in large social groups, have a generalist diet, and have performed successfully in a number of previous cognitive studies. We predicted that the more egalitarian *Eulemur* would have a higher number of successes observed than the other genera tested, who have more pronounced ranks and dominance hierarchies. Although we were unable to systematically parse out social versus individual learning via the paradigm used in this study, these predictions (and their underlying reasoning) also suggest cross-taxa differences in the relative influence of observational learning and individuals’ trial-and-error.

## Materials and methods

### STUDY SITE AND SPECIES

We conducted this study from June–September 2017 at the Duke Lemur Center (DLC) in Durham, North Carolina. Sixty-six

lemurs from 7 species (*Eulemur coronatus*, *E. flavifrons*, *E. mongoz*, *L. catta*, *Propithecus coquereli*, *Varecia rubra*, and *V. variegata*) participated in the study (supplementary table S1). Most of these lemurs have been used in previous research, which may have impacted their performance in this study; however, because nearly all individuals were accustomed to experimental research and all lemurs receive novel enrichment (which includes puzzle feeders), we felt they had relatively comparable past experience. Lemurs were housed in 16 groups, including 8 free-ranging and 8 indoor groups. The free-ranging groups had access to large tracts of forest (0.5-5.5 ha) with indoor runs where the experimental trials were conducted. The indoor groups lived in a series of indoor rooms (2-4 rooms;  $3 \times 2.3 \times 2.2 \text{ m}^3$  per room) that were connected to outdoor runs ( $3 \times 2.3 \times 4.3 \text{ m}^3$  per run).

#### ETHICAL NOTE

This research complied with protocols approved by the Duke University (#A053-17-03) and Central Washington University (#A121601) Institutional Animal Care and Use Committees and adhered to the legal requirements of animal research in the United States of America. All experiments in this study were completely voluntary for the lemurs to participate in. Trials were ended immediately if any individuals began displaying signs of stress or agitation as assessed by DLC staff.

#### STUDY APPARATUS

We used multiple two-action apparatuses, which were modeled after those used in previous studies (Drea, 2006; Dindo et al., 2008; Kendal et al., 2010; Stoinski et al., 2011; van de Waal et al., 2012; Schnoell et al., 2014; Batist and Mayhew, 2020). The apparatus was a plexiglass box ( $\sim 30 \times 15 \times 20 \text{ cm}^3$ ) with one flap door hinged on the left side. The apparatus door had two stop levers (inside and outside), which controlled how the door could be opened. This door could be opened via two methods, push or pull, to retrieve a food reward inside (supplementary fig. S1). If the inside lever was

engaged, the door could only be pulled open, and if the outside lever was engaged, the door could only be pushed open. Grapes were used as a reward for all species except the folivorous *P. coquereli*, who were offered whole peanuts. The DLC does not allow sifakas to have sugar-rich foods, such as fruits, because of their fermentation-based digestive system and naturally folivorous diet. To accommodate some of the more arboreal lemur species tested and provide added durability, all apparatuses were bolted to a table ( $\sim 76 \times 51 \times 71 \text{ cm}$ ), which was then secured to the enclosure caging with zip ties during trials. Four apparatuses were used in total: lemur groups containing three individuals were provided three, and groups with four or more individuals were provided all four. To minimize conflict, the apparatuses were placed approximately one meter apart. All trials were video recorded (Nikon Coolpix L110) from outside the testing space.

#### EXPERIMENTAL DESIGN

This study was part of a larger project on lemur social learning, in which we assigned all groups randomly to a condition (control, experimental [push, pull]) balanced between genera (supplementary table S1). Each genus had at least one control group and one to three experimental groups, which differed based on the number of DLC lemur groups available to us for the study. Each group participated in at least one habituation session lasting approximately 15 minutes. During habituation, the video camera was placed in its recording position outside of the enclosure, and locked and unbaited apparatuses were placed inside the enclosure for visual and physical inspection by the lemurs. Following habituation, the control groups immediately began experimental trials, and the model individuals from the experimental groups began training trials. In each experimental group, we used the alpha female as the model individual except for Randy's group, whose dominant female was separated at the time for medical reasons. Although this created the potential for the alpha female to monopolize access, we used multiple apparatuses during the trials to help mitigate this issue. We were concerned that a

subordinate individual as the model may not want to “demonstrate” or interact with the apparatuses during experimental trials for fear of retaliation by the dominant animals (i.e., alpha female). Control groups did not have a model. There was at least one day between trials for all groups; however, because of feeding and shifting schedules, inter-trial day ranges differed between the indoor and free-ranging groups.

To train the model lemur in the experimental groups, the individual was shifted into a separate enclosure (other group members did not have visual access) and allowed access to one apparatus. To train models to pull, the inside stop lever was engaged so the door could only be pulled open. To train models to push, the outside lever was activated so the door could only be pushed open. We note that no manipulation was needed to train these behaviors, meaning that the actions needed for successes were within the individual learning capacities of the lemurs. Each training trial lasted ten minutes or until the model had ten successes (whichever came first). This success threshold was set by the DLC and used to prevent overfeeding. We defined a success as an individual opening the apparatus door and obtaining the reward. The training phase for a model was complete once that individual achieved twenty-five consecutive successes (a minimum of three training trials).

During the experimental trials, all individuals in the group had access to the apparatuses and the trained model (except for control groups who did not have a model). No stop levers were activated during these trials, so a lemur could use either the push or pull method to open the apparatus door. This open-diffusion approach allowed for some individuals to achieve a success before observing the model, which is why we chose to focus specifically on taxonomic differences for this study rather than individual vs social learning (which could not be done because of these experimental difficulties). Across all conditions, each group participated in at least nine experimental trials, which lasted either ten minutes or as long as it took one individual to achieve ten successes (whichever came first). All trials were video recorded, which started when the lemurs were

shifted into the testing enclosure after the apparatuses were baited. Following a success, a DLC staff member inside the enclosure replaced the food reward and closed the apparatus door. The lemurs’ view was obstructed by the staff member when the apparatus was reset.

## DATA ANALYSIS

In total, we recorded and coded 246 trials. We recorded multiple variables: the trial number for that group, each individual’s latency to touch the apparatus, latency to first attempt, latency to first success with the method used, the number of attempts, the number of successes, the method used for each success, and the lemurs present who observed each success. Latency to touch the apparatus was defined as the length of time from the start of the trial (when the door from the holding area to the experimental arena opened) to when an individual contacted the apparatus using any body part except the tail. Some lemurs would descend the caging towards the apparatus and their tail would graze the apparatus; this was not considered ‘contact’. Latency to first attempt was defined as the length of time from the start of the trial to the first time an individual interacted with the apparatus door. Latency to first success was defined as the length of time from the start of the trial to the first time an individual opened the apparatus door and retrieved the food item. We used head orientation as a proxy for observation as this has been observed to correlate with gaze following in lemurs (Shepherd and Platt, 2008; Ruiz et al., 2009), and there is evidence that lemurs attend to specific individuals (Kulahci et al., 2018). We then calculated an individual’s proficiency rate as the number of successes/the number of attempts. To test for inter-observer reliability, an external observer coded 20% of the trial videos (50 trials). The average Cohen’s kappa across all variables was 0.82.

We pooled data for all species into genera (*Lemur*, *Propithecus*, *Eulemur*, *Varecia*) because there was an uneven number of individuals per species, and the sample size was not large enough for a species-level analysis (supplementary table S1). To further maintain statistical power when conducting analyses related

to successes, we set a minimum success threshold for individuals of 15 successes across at least two trials. Individuals who had fewer than fifteen successes overall or only had successes during one trial were excluded from any analyses related to successes.

Because this study focused on examining the effect of taxa, we combined push and pull groups into ‘experimental’ and kept control groups as ‘control’. Although the apparatus had two ways of being opened (push, pull), the push method was overwhelmingly favored as it was (unintentionally) easier for the lemurs to do (easier for lemurs to accidentally push the door in and then realize that was a way to open the door). For overall method preference across trials, all but two individuals (the mongoose lemurs Maddie and Mico, same group) heavily favored the push method; even model individuals initially trained to pull favored pushing. The individuals that pulled on their first success quickly switched after discovering the easier, more dominant push method. Because of this, we believed combining push and pull groups into one ‘experimental’ condition was reasonable. As previously mentioned, our primary goal in this study was to assess species differences in learning trajectories, but we wanted to still include a ‘group type’ variable in our models to account for variation that may be attributed to group type rather than taxon (even though the 2-action paradigm itself did not work).

We analyzed all data in R (R Core Team, 2018). We had four response variables of interest: 1) latency to touch apparatus, 2) latency to success, 3) proficiency rate, and 4) the number of successes an individual observed. We used Spearman’s correlation tests to assess the relationships between these variables (1 and 2, 2 and 3, 1 and 3, 3 and 4). We then ran one generalized linear mixed model (GLMM) using the ‘lmer’ function in the *lme4* package (Bates et al., 2007) for each of the four response variables. The first three response variables were log-transformed to fit model assumptions on normality and heteroscedasticity. We used the Gaussian distribution for all models except those with counts (# successes observed), in

which we used a Poisson distribution (and ‘glmer’ rather than ‘lmer’). We included genus, trial number (1-9, as factor) and group type (experimental vs. control) as fixed effects for all models. We used ‘individual’ as a random effect in all models. Although it would have been interesting to include other explanatory variables such as rank or sex, the small sample size among factors and the exploratory nature of this study dictated that we adopt a conservative approach to maintain statistical power. We were primarily concerned with taxonomic differences and wanted to prioritize those variables in model testing.

We used both a null-hypothesis significance testing and information theoretic approach for assessing and interpreting models. We used two approaches to provide multiple lines of evidence and assess the robusticity of our results across approaches. We first assessed whether each full model was significantly better than the null model (i.e., response variable  $\sim 1 +$  random effect) and composite models (i.e., genus, genus + trial, etc.) using the Anova function in the *car* package (Fox and Weisberg, 2019). The Anova function uses Akaike’s Information Criterion (AIC) to compare models with the best fitting model being the one with the lowest AIC score (supplementary table S2). Hereafter we refer to this analysis as the Anova method.

We then also used an information theoretic approach to examine our models in a more nuanced way. This approach allows for the comparison of competing models simultaneously, and inferencing based on weighted support for explanatory variables across averaged candidate models (Grueber et al., 2011). In these types of analyses, a set of candidate models is generated from the global model (one for each of the 4 response variables described above). Candidate models reflect all possible combinations of explanatory terms and are compared using Akaike’s Information Criterion (AICc) adjusted for small sample size. The AICc is calculated by assessing the likelihood of the model and penalizing models for their respective number of parameters (Burnham and Anderson, 2002; Burnham et al., 2011; Grueber et al., 2011). The lower the AICc, the better the model fit is in

**Table 2.** Summary statistics of learning variables tested across genera, represented as the mean  $\pm$  the standard deviation. Number of individuals does not include the 4 clinging infants, who were all *Eulemur*.

	n	Ind's with $\geq 1$ success	Avg successes/ Ind.	Latency to touch (sec)	Latency to success (sec)	Proficiency rate (# attempts/ # successes)	Successes observed/ trial
<i>Eulemur</i>	17	13	46	23.2 $\pm$ 32.5	58.7 $\pm$ 94.2	4.1 $\pm$ 3.7	2.2 $\pm$ 2.1
<i>Lemur</i>	18	13	32	66.2 $\pm$ 87.3	105.1 $\pm$ 127.4	3.2 $\pm$ 3.0	0.4 $\pm$ 0.9
<i>Propithecus</i>	12	9	33	50.8 $\pm$ 77.9	66.3 $\pm$ 100.52	3.7 $\pm$ 2.9	0.3 $\pm$ 0.6
<i>Varecia</i>	15	14	38	29.9 $\pm$ 54.0	47.4 $\pm$ 81.6	5.1 $\pm$ 3.6	1.4 $\pm$ 1.5

explaining the variation of the data. The AICc score is used to rank models by their ‘weight’, which is the probability of a certain model having a better fit compared to other models in the candidate set (Burnham and Anderson, 2002; Burnham et al., 2011). Based on these weights, model averaging is used to generate parameter estimates and standard errors (Burnham and Anderson, 2002; Grueber et al., 2011). Model averages use the model with the lowest AICc and all other models within two AICc units.

We implemented this approach using the *model.avg* and *dredge* functions in the *MuMIn* R package (Barton, 2009). This approach has been used often in primatological research (Pasquaretta et al., 2014; Price et al., 2019; Tombak et al., 2019; Voyt et al., 2019; Troisi et al., 2021). We, like these authors, believe it to be a more nuanced way of interpreting model results, particularly in cases where two candidate models have very similar AICc scores (which occurred in this study). We evaluated top candidate models using the ‘DHARMA’ package, which assesses dispersion, zero-inflation, distribution of scaled residuals and overall model fit (Hartig, 2017). We emphasize that these models are exploratory; given the small sample size and significant intercept estimates these outputs are not as robust, but nonetheless provide preliminary indications of relationships.

## Results

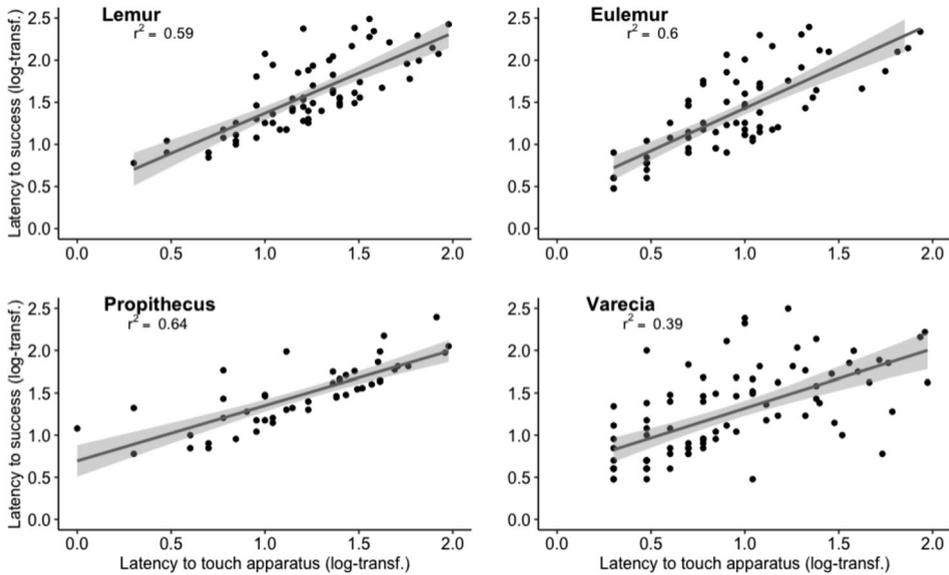
Of the 66 lemurs in this study, four were clinging infants that were excluded from analyses (although one, Poehler, did have a success towards the end of the study). There were 49

individuals (79%) that successfully opened the apparatus at least once during the nine experimental trials (table 2, supplementary table S1). Excluding model individuals ( $n = 9$ ), 40 of 53 lemurs (75%) had at least one success. For *Propithecus*, *Lemur*, and *Eulemur*, approximately one-quarter of individuals never had a success, whereas *Varecia* had only one unsuccessful individual. However, *Eulemur* had the highest rate of successes per individual (table 2). The rate of unsuccessful individuals was relatively equal between experimental and control groups. There were 11 successful individuals that did not meet our minimum success threshold (at least 15 successes across at least 2 trials) and were excluded from further analysis (supplementary table S1).

Within experimental groups, only 39% of individuals used their model’s trained method on their first success. As previously mentioned, all but two individuals heavily favored the push method. We acknowledge this was a flaw within our study, and therefore in this paper wanted to focus on the taxonomic differences rather than deciphering individual learning mechanisms. In all learning models below, there were no significant differences between the control and experimental groups.

## LEARNING VARIABLES

Across all lemurs, an individual’s latency to touch the apparatus was positively correlated with their latency to success (Spearman’s  $\rho = 0.80$ ,  $p < 0.001$ ; fig. 1). The strength of correlation between these variables differed when broken down by genus, with *Propithecus* showing the tightest correlation and *Varecia* exhibiting the most variation in either axis (fig. 1).



**Figure 1.** Differences in the correlation of latency to touch apparatus and latency to success for genera at the Duke Lemur Center. Variables have been log-transformed to make figures more easily interpretable. Solid line is the regression line ( $y \sim x$  formula), and shaded areas represent the 95% confidence interval of the line. *Propithecus* shows a tighter correlation than other genera, whereas *Varecia* has the lowest correlation coefficient.

Additionally, an individual's latency to success was negatively correlated with proficiency rate such that shorter latencies were related to higher proficiency rates (Spearman's  $\rho = -0.54$ ,  $p < 0.001$ ). In other words, the faster a lemur touched the apparatus, the faster they succeeded at the task and the better their proficiency rate. The number of successes an individual observed was not correlated to that individual's proficiency rate (Spearman's  $\rho = 0.05$ ,  $p = 0.392$ ).

#### LATENCY TO TOUCH APPARATUS

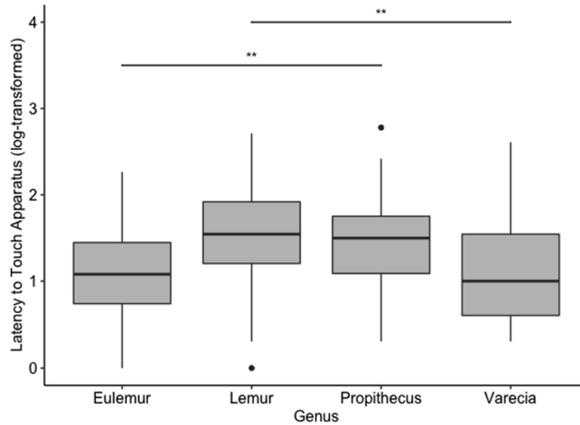
The full latency to touch apparatus model was significantly different from null or composite models using the Anova method (supplementary table S2). Using the model averaging method, the highest weighted model only included trial number and genus; however, the full model was within 2 AICc values and therefore also used in model averaging (supplementary table S3). These models show that *Propithecus* and *Lemur* each had significantly longer latencies than *Varecia* or *Eulemur* (fig. 2, table 3). Additionally, latencies decreased significantly through the trials (table 3).

#### LATENCY TO SUCCESS

The full latency to success model was significantly different from null or composite models using the Anova method (supplementary table S2). The highest weighted model in the model-averaging approach only included trial number; however, there were 3 other models within 2 AICc values and therefore also used in model averaging (supplementary table S3). Model-averaged estimates show that latencies decreased significantly through the trials (table 3).

#### PROFICIENCY RATE

Using the Anova method, the proficiency rate model with trial number and genus was significantly different from the null model, but the full model was not (supplementary table S2). Using the model averaging method, the highest weighted model only included trial number; no other model was within 2 AICc values (supplementary table S3). Estimates showed that proficiency rate increased through the trials (table 3). However, when broken down by genus, the trajectory of proficiency rate through



**Figure 2.** Differences in latency to touch the apparatus between genera at the Duke Lemur Center. *Eulemur* and *Varecia* both have significantly shorter latencies than either *Propithecus* or *Lemur* (\*\* indicate significant differences). The shaded boxes represent the inter-quartile range, thick midline shows the median. Lines extend out from the shaded boxes to show maximums, and the dots are outliers.

the trials showed variation (fig. 3). For example, *Propithecus* had constant values until a peak in trial 6 and then decrease after trial 7, whereas *Lemur* showed a sharp increase in trial 2 followed by a sharp decrease in trial 3. *Varecia* had a gradual increase in proficiency rate through all trials, and *Eulemur* had two similar increases in trials 1-4 and 5-7 (fig. 3).

#### NUMBER OF SUCCESSES OBSERVED

Using the Anova method, the successes-observed model with genus and trial number was significantly different from the null model, but the full model was not (supplementary table S2). Using the model-averaging method, the highest weighted model included genus and trial number; however, the full model was within 2 AICc values and therefore used in model averaging (supplementary table S3). Model-averaged estimates showed that *Eulemur* and *Varecia* observed more successes during the trials than both *Propithecus* and *Lemur* individuals (supplementary fig. S2, table 3). Along genus lines, the trajectory of successes observed through the trials was variable even within this relationship (fig. 4). For example, *Propithecus* had more successes observed (albeit still relatively low) in the latter half of trials. *Eulemur*

had a peak in successes observed in trials 3-6, with lower values on earlier and later trials (fig. 4).

We found further evidence of social tolerance in that we observed some mothers allowing their infants or juveniles to scrounge from them (i.e., the mother would open the door and then allow the infant/juvenile to grab the food item). The mothers Halley, Pyxis, and West were observed allowing this behavior, and all had offspring under  $\leq 1$  year. Notably this was only observed in *Varecia* and *Eulemur*. This mother-infant tolerance has also been observed in other primate species (Biro et al., 2006; Humle and Snowdon, 2008; Coelho et al., 2015).

#### Discussion/conclusion

By assessing four lemur genera using a standardized experiment, we were able to conduct exploratory cross-taxa comparisons on learning abilities and trajectories. We found relationships between genera and learning speed, success, proficiency, and leniency (i.e., allowing observations by other individuals, social tolerance). *Propithecus* fell at the bottom of all these metrics and *Eulemur* was consistently highest. *Varecia* and *Lemur* showed mixed results across the different learning metrics tested.

Across all group types and genera, there was a positive correlation between an individual's

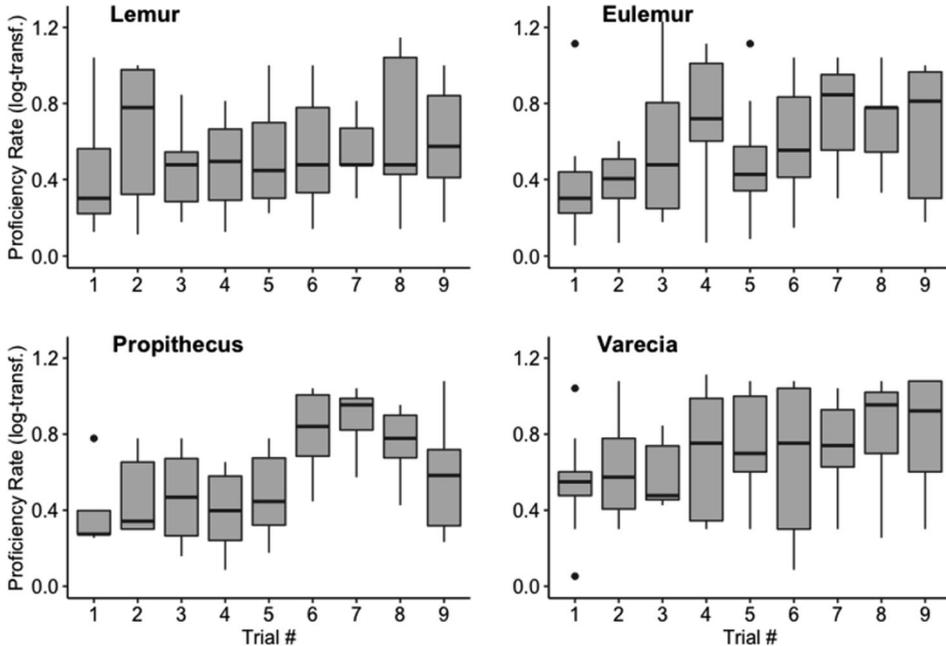
**Table 3.** Model-averaged coefficients are calculated by averaging the values from a subset of the candidate models (lowest AICc model and all models within 2 AICc). These subsets are given in supplementary table S3 (non-italicized rows). The estimate, standard error, z-value and p-value (from z scores) are listed for each level within the categorical explanatory variables.

	Estimate	Adjusted SE	z-value	p-value
<b>Latency to touch</b>				
(Intercept)	1.394	0.101	13.781	<2e-16***
Trial#	-0.049	0.008	6.477	<2e-16***
GenusLemur	0.266	0.100	2.661	0.008***
GenusPropithecus	0.350	0.110	3.186	0.001**
GenusVarecia	-0.072	0.103	0.702	0.482
GroupTypeExperimental	-0.078	0.098	0.790	0.429
<b>Latency to success</b>				
(Intercept)	2.052	0.109	18.738	<2e-16***
Trial#	-0.102	0.008	12.139	<2e-16***
GenusLemur	0.150	0.191	0.787	0.431
GenusPropithecus	0.093	0.1422	0.657	0.511
GenusVarecia	-0.040	0.094	0.427	0.669
GroupTypeExperimental	-0.057	0.101	0.568	0.570
<b>Proficiency rate</b>				
(Intercept)	0.405	0.039	10.262	<2e-16***
Trial#	0.036	0.005	7.015	<2e-16***
GenusLemur	-0.0002	0.005	0.035	0.972
GenusPropithecus	<-0.0001	0.005	0.016	0.988
GenusVarecia	0.0003	0.006	0.041	0.968
GroupTypeExperimental	0.0001	0.013	0.040	0.968
<b>Successes observed</b>				
(Intercept)	0.427	0.029	14.826	<2e-16***
Trial#	0.048	0.002	26.156	<2e-16***
GenusLemur	-1.741	0.002	937.869	<2e-16***
GenusPropithecus	-2.126	0.008	269.691	<2e-16***
GenusVarecia	-0.550	0.104	5.270	<0.0001***
GroupTypeExperimental	0.030	0.048	0.626	0.531

latency to touch the apparatus and latency to success. However, the genus-specific correlations differed, showing contrasting levels of variation. There was also a negative correlation between latency to success and proficiency rate, indicating that the sooner a lemur succeeded, the better its proficiency rate became. This is likely in part because the faster a lemur determined how to succeed, the more trials it then had to fine-tune its approach and therefore increase its proficiency rate.

Ring-tailed lemurs are one of the most ubiquitous lemur species represented in the primate cognition literature, sometimes equaling monkeys in their task performance (Sandel et al.,

2011; Maclean et al., 2013; Jones et al., 2014; Devaine et al., 2017; Fichtel et al., 2020). However, contrary to our prediction, *Lemur* did not outperform other taxa in learning speed or proficiency. We found that *Lemur* and *Propithecus* individuals had longer latencies to touch the apparatus and observed fewer of their group-mate's successes, making them less efficient than the other genera. These two species naturally have a more despotic social system compared to the more egalitarian *Eulemur* and *Varecia* species (Pereira and McGlynn, 1997; Digby and Kahlenberg, 2002; Gould et al., 2003; Curtis, 2004; Overdorff et al., 2005; Kappeler and Schäffler, 2008; Fichtel et al., 2018). This could



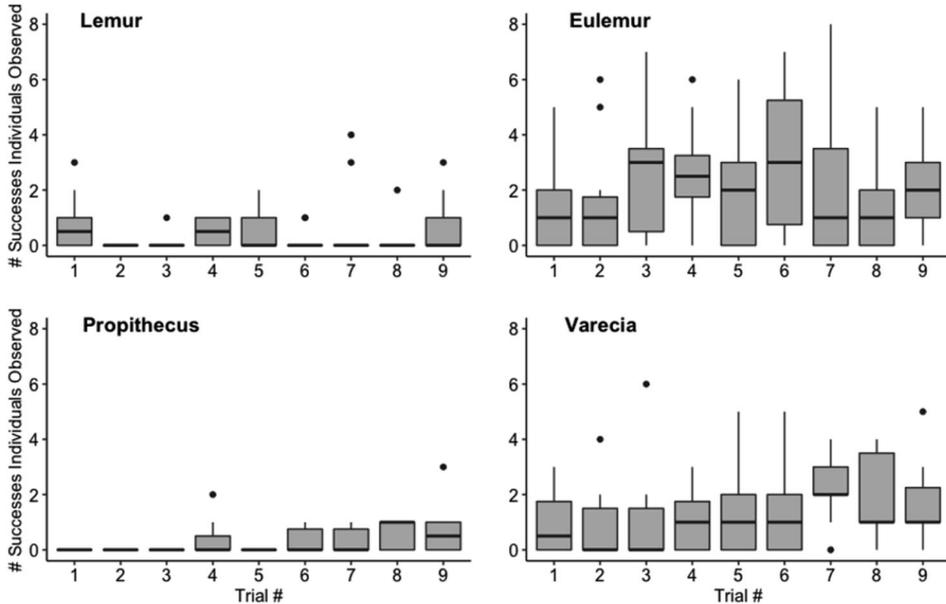
**Figure 3.** Differences in the trajectory of task proficiency through all trials between genera at the Duke Lemur Center. The shaded boxes represent the inter-quartile range, thick midline shows the median. Lines extend out from the shaded boxes to show maximums, and the dots are outliers. *Varecia* shows gradual increase in proficiency from trial 1-9, whereas *Propithecus* plateaus until trial 6+. Overall, *Lemur* shows a gradual increase except for the sharp increase in trial 2. *Eulemur* shows two gradual increases, in trials 1-4 and then again in trials 5-7 after which the rate plateaus.

explain the low number of successes observed in *Lemur* and *Propithecus* as high-ranking individuals may have been more likely to be intolerant of conspecifics in close proximity. The longer latencies for these two genera could also be explained by the stricter rank structure, as subordinate individuals may have been hesitant to try the apparatus for fear of retaliation by a dominant individual (who would have priority-of-access). Using the dominant female as the model individual in experimental groups may have exacerbated these differences; however, as previously mentioned, we were concerned that a subordinate model individual might not interact with the apparatuses during experimental trials for fear of retaliation by the dominant animals. Examining the effect of using models that are different sexes and/or ranks is an interesting avenue for future research.

*Eulemur* had the highest observation rate, supporting our prediction (and previous studies, e.g., Fichtel et al., 2018) that individuals

in this genus would be more socially tolerant of conspecifics in proximity to the apparatuses compared to other genera. Consistent with our predictions, *Varecia* had quicker learning speeds than *Propithecus*, but contrary to our expectation, there were no significant differences in proficiency rate between any of the genera tested. A previous social inhibitory control study also did not find differences in performance among the four lemur genera tested (Reddy et al., 2015). Similarly, *Varecia* and *Lemur* performed comparably on physical and social cognition tests in a recent study (Fichtel et al., 2020).

We also found interspecies temporal variation in the learning variables over the course of the consecutive trials. *Varecia* seemed to show gradual increases in task proficiency, speed, and ability through the trials, whereas *Propithecus* and *Eulemur* showed more stochastic steps (figs 3, 4). This may be due to the high percentage of



**Figure 4.** Differences in the trajectory of conspecific observations through all trials between genera at the Duke Lemur Center. The shaded boxes represent the inter-quartile range, thick midline shows the median. Lines extend out from the shaded boxes to show maximums, and the dots are outliers. *Lemur* and *Propithecus* had few conspecific observations throughout the trials. *Propithecus* show an increase in observation in the latter half of the trials. *Varecia* show a slight increase in observations after trial 3 and again after trial 6. *Eulemur* increase observations in trial 3 but revert back to fewer observations in trials 7-9.

individuals that had successes in *Varecia* compared to other genera (table 2), and the inherent larger variation that would potentially emerge from more individual-level variation (*Varecia* panel of fig. 1).

#### LIMITATIONS

We pooled the data across the *Eulemur* and *Varecia* species to generate more robust results; however, the subsequent coarse-grain analyses at the genus level could have overlooked more minute species differences. We emphasize that these are preliminary results from exploratory analyses, given the sample size and statistical power, but they do suggest a relationship between learning metrics and lemur taxon. Some notable caveats include that some lemurs had their first success before observing a conspecific's success and different individuals could succeed simultaneously albeit at different apparatuses. These caveats promote individual-based learning strategies and could influence the results. We did not test for the effect of other

demographic variables, such as rank or sex, as we were limited by the sample size in how many explanatory variables we could include without over-specifying the model and losing statistical power. It would be an interesting line of inquiry to include these additional variables in future studies.

As mentioned previously, all groups and species tested converged on one of the experimental methods (push). This may have been a result of individuals learning the easier method themselves through trial-and-error or could have been reinforced by a bias towards group conformity, as demonstrated previously with other primates (Dindo et al., 2009; van de Waal et al., 2012; van Leeuwen and Haun, 2013), but we are unable to adequately distinguish between the two with the present dataset. Future studies should pay particular attention to methodological considerations so they can avoid our pitfalls. Some studies have used multiple two-action apparatuses that each require tasks of varying difficulty within the same study to avoid

problems from any one task/device (Tennie et al., 2010). If interested in parsing out specific social learning mechanisms, such as emulation or imitation, other more nuanced experimental paradigms have been used previously to test for these (i.e., tasks with causally irrelevant actions, “ghost trials;” Hopper, 2010; Tennie et al., 2010; Clay and Tennie, 2018; Neadle et al., 2020).

## CONCLUSIONS

This study is one of only a few to comparatively examine learning across multiple lemur species using a standardized experimental protocol. We found evidence for genus-level differences in various learning metrics such as speed, success, and proficiency. Future research could expand upon this study by testing larger sample sizes to parse out the taxon-specific factors that influence learning. Lemurs offer a unique opportunity to examine how the socioecological niche impacts different aspects of behavioral complexity, given the variety of niches that closely related species have evolved to inhabit. More specifically, testing the social and ecological intelligence hypotheses with lemurs is thus an exciting area for future research. More generally, including lemurs in comparative cognition research can also further our understanding of the evolution of cognitive abilities throughout the Primate order.

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## Statement of ethics

Research permissions were obtained from the Duke University (#A053-17-03) and Central Washington University (#A121601) Institutional Animal Care and Use Committees.

## Conflict of interest statement

The authors declare that they have no conflict of interest.

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## Author contributions

CHB and JAM conceived and designed the study. CHB carried out data collection and conducted data analysis. CHB and JAM drafted the manuscript and approved the final version.

## Data availability statement

The R script is available at: <https://doi.org/10.6084/m9.figshare.17294156>. The full dataset is available in the supplementary material.

## Supplementary material

Supplementary material is available online at: <https://doi.org/10.6084/m9.figshare.19076675>

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