Persistence is key: Investigating innovation and problem solving by Asian elephants using a novel multi-access box

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ABSTRACT

Innovative problem solving is considered a hallmark measure of behavioral flexibility as it describes behavior by which an animal uses previous experience to manipulate its environment to reach a goal. Elephants are a highly social taxa known for their ability to adapt to volatile environments. While innovation has been observed in elephants, one question is how behavioral traits associated with it vary at the individual level. To understand how individual differences in behavior impact expressions of innovation, we used a novel extractive foraging device comprised of three compartments to evaluate innovation in 14 captive Asian elephants. In the first phase of testing, elephants had an opportunity to learn one solution, while the second phase gave them an opportunity to innovate to open two other compartments with different solutions. We measured the behavioral traits of neophilia, persistence, motivation, and exploratory diversity, and hypothesized that higher levels of each would be associated with more innovation and success. Eight elephants innovated to solve three compartments, three solved two, and two solved only one. Consistent with studies in other species, we found that higher innovation scores and success were associated with greater persistence, but not with any other behavioral traits when analyzed per test session. Greater persistence and lower exploratory diversity were associated with success when analyzed at the level of each individual door. Further work is needed to understand how innovation varies both within and between species, with particular attention to the potential impact of anthropogenic change.

INTRODUCTION

The ability to adjust behavior flexibly is essential for survival when animals are faced with changes in their social and physical environments. This is particularly true for rapidly changing environments that are typical of the Anthropocene (Wong and Candolin 2015). Innovation is an important component of this behavioral flexibility that allows individuals to adapt to change. Kummer and Goodall (1985) first defined innovation in animals as a solution to a novel problem or a novel solution to an existing problem. More broadly, innovation has also been defined as a new or modified learned behavior (Reader and Laland 2003). These novel behaviors can allow animals to modify their niche or invade new habitats (Sol et al. 2016).

The effects of innovations on fitness are apparent in studies comparing behavior across species. For example, birds that are more innovative in an initial, home environment are more successful when establishing themselves in a new one compared to less innovative bird species (Sol et al. 2002, 2005). Innovation also may be more prevalent in bird species that reside in one area with seasonal variability year-round, as compared to those that migrate for seasonal consistency (Lefebvre et al. 2004). This supports the idea that innovative behaviors may be beneficial for coping with environmental change. Evolved cognitive mechanisms may also play an important role in innovation, as innovation rate in both birds and primates is also positively correlated with the volume of particular brain areas important for multimodal integration (Lefebvre et al. 2004), as well as overall relative brain volume in mammals (Sol et al. 2015).

The above-mentioned studies were based on rates of innovation across species documented from observations in the wild. Although this measure of innovation is beneficial at the species-level, it can be difficult to observe the process of innovation and therefore assess individual differences within a species using opportunistic, ethological methods in the wild (e.g., Fisher and

Hinde 1949; Smolker et al. 1997). This limitation has led researchers to begin evaluating innovation experimentally by introducing novel problems for animals to solve in captivity (e.g., Day et al. 2003) and in the wild (e.g., Benson-Amram and Holekamp 2012). Comparing problem solving in birds using a puzzle box, researchers found that success on the task was consistent with wild counts of innovation in the different avian families tested, suggesting that this was an ecologically meaningful assay for measuring variation in innovation (Webster and Lefebvre 2001). Using this type of experimental methodology as a proxy to study innovation, researchers have shown that innovation varies between species (kea, *Nestor notabilis* and New Caledonian crow, *Corvus moneduloides*: Auersperg et al. 2011; chimpanzees, *Pan troglodytes*, Western lowland gorillas, *Gorilla gorilla gorilla*, bonobos, *Pan paniscus* and orangutans, *Pongo abelii*: Manrique et al. 2013; Indian mynas, *Acridotheres tristis* and noisy miners, *Manorina melanocephala*: Griffin and Diquelou 2015) and between individuals within a species (Day et al. 2003; Benson-Amram and Holekamp 2012; Griffin et al. 2014; Daniels et al. 2019; Williams et al. 2021) tested on the same novel problems.

Individual variation in innovation may be driven by life history traits such as age and sex, with predictions involving sex varying widely by species (Griffin and Guez 2014). Interestingly, in primate studies, adults appear to be more innovative than juveniles (Reader and Laland 2001; Kendal et al. 2005), while other studies have shown either that juveniles are more innovative (perhaps due to their tendency for higher exploration: Aplin et al., 2013; Griffin et al., 2014), or that there is no effect of age at all (Cole et al., 2011; Benson-Amram and Holekamp 2012). Beyond sex and age, there are processes or phenotypes that may explain differences in innovation between individuals, including cognition, motivation and behavioral traits.

88 There are several behavioral traits that have been consistently tested for association with
89 individual variation in innovation, namely persistence, motivation, responses to novelty, and
90 diversity of motor actions. Some of these traits have more consistent relationships with
91 innovation while others differ depending on the species tested and how traits are measured
92 (reviewed by Griffin and Guez 2014). Persistence has been consistently associated with
93 successful problem solving and repeated innovation across species, such that individuals that
94 spend more time engaged with a task are more likely to solve it (e.g. Thornton and Samson 2012;
95 Griffin et al. 2014; Johnson-Ulrich et al. 2018). While persistence involves an animal's
96 motivation to work on a task, motivation has also been considered separately as an animal's
97 willingness to begin engaging with a task, and is often based on the desire for food rewards.
98 Even though the two measures may seem similar, persistence and motivation often do not
99 correlate, so they should be considered as separate constructs (Griffin and Guez 2014).
100 Motivation is thought to be influential in accordance with the “necessity drives innovation”
101 hypothesis, which suggests that innovations occur when individuals are in need of resources
102 (Reader and Laland 2003, Cooke et al. 2021). However, across studies reviewed by Griffin and
103 Guez (2014), motivation has not consistently correlated with problem solving when measured
104 using latencies to engage in a task (e.g., Keagy et al., 2009, 2011) or when using a morphology-
105 based measure of motivation (i.e., body condition, Bókony et al., 2014). Individuals' responses
106 to novelty, whether measured as fear of (neophobia) or attraction to (neophilia) it, are thought to
107 influence variation in innovation by influencing an individual's likelihood of engaging with
108 something novel in the first place. Some studies have shown clear relationships between these
109 variables within a species, such that individuals who are less fearful of novelty are more likely to
110 innovate (Benson-Amram and Holekamp 2012; Massen et al. 2013). However, this relationship

has also varied across contexts (e.g. Benson-Amram and Holekamp 2012; Bókonyi et al. 2014) and does not appear to present a consistent association across studies, potentially because there is such wide variation in how the response to novelty is measured (Griffin and Guez 2014). Problem solving with extractive foraging tasks (i.e., tasks that require the animal to use an appendage or tool to gain access to a hidden or obstructed food reward) is also thought to be influenced by the number of distinct motor actions (exploratory diversity) an animal uses when interacting with the task. This is because more diverse actions provide a raw source for behavioral variants. Many studies have found that increased exploratory diversity is associated with successful problem solving (e.g., chimpanzees, Massen et al. 2013; spotted hyenas, *Crocuta crocuta*: Johnson-Ulrich et al. 2018; raccoons, *Procyon lotor*: Daniels et al. 2019; yellow-bellied marmots, *Marmota flaviventer*: Williams et al. 2021).

One paradigm that has been used to test repeated innovation in multiple species is the multi-access device first developed by Auersperg et al. (2011) to compare innovation between two bird species. This paradigm provides an animal with an extractive foraging task that has multiple potential solutions available simultaneously and allows for mastered solutions to be progressively blocked. Therefore, researchers can assess an individual's ability to first solve a problem, and then to innovate beyond that first solution. Many studies have used this paradigm to assess innovative ability as well as the behavioral traits that influence it (Manrique et al. 2013; Huebner and Fichtel 2015; Johnson-Ulrich et al. 2018; Daniels et al. 2019; Williams et al. 2021; Cooke et al. 2021).

In the current study, we investigated innovative problem solving (hereafter “innovation”) as well as its associated behavioral traits in Asian elephants (*Elephas maximus*). Asian elephants have large brains (Shoshani et al. 2006), live in complex fission-fusion societies (de Silva et al.

2011), have demonstrated high levels of social behavioral flexibility through cooperation and consolation (Plotnik et al. 2011; Plotnik and de Waal 2014), and are capable of flexible decision making (Plotnik et al. 2019; Barrett and Benson-Amram 2020). Based on these observations in captivity and the wild, we believe elephants make strong candidates for demonstrating innovation experimentally. Elephants have been tested previously in a few problem-solving studies in which they have successfully solved novel tasks, although two of these studies have investigated social learning rather than individual innovation (African elephants: Greco et al. 2013; Asian elephants: Barrett and Benson-Amram 2020). At least one Asian elephant has demonstrated insightful problem solving, spontaneously solving a problem without trial and error learning (Foerder et al. 2011). Barrett and Benson-Amram (2021) assessed a number of personality traits potentially related to successful problem solving in both Asian and African elephants and found that aggressiveness and activity were important predictors for solving some tasks. We decided to investigate other behavioral differences in elephants that may be related to innovation in order to evaluate how individuals vary in, and the mechanisms underlying innovation. As Asian elephants represent an evolutionarily distant taxa from those species previously tested with a similar paradigm, our study will help determine whether relationships between behavioral traits and innovation are conserved across behaviorally flexible taxa and thus potentially the result of convergent cognitive evolution.

The goal of this study was to test zoo-housed Asian elephants using a modified version of the typical multi-access puzzle box (MAB) to investigate their capacity for innovation. Our MAB had three solutions which each required different motor actions typical to the elephant's behavioral repertoire. The elephants were provided with two different phases of this MAB in order to establish a single learned solution first, followed by novel opportunities to innovate.

Rather than have these solutions open to a single, common food reward (the typical methodology for this task in other species), our MAB consisted of three different compartments, each with its own food reward. We changed this fundamental aspect of the design in order to draw direct comparisons to parallel studies we are running with wild elephants using a similar MAB. Because this MAB will be deployed in a wild environment, immediate rebaiting will not be possible and thus providing multiple trials within a single box is most efficient. We assessed repeated innovation as the number of the three possible solutions discovered by the elephants over the course of the study. We investigated individual variation in innovation and the behavioral traits associated with it, as well as the elephants' overall success in opening MAB compartments. We hypothesized that greater motivation, persistence, neophilia, and exploratory diversity would be associated with a higher innovation score and higher overall success, similar to results found with other species. We also hypothesized that the elephants would demonstrate learning of the first phase solution over multiple sessions.

METHODS

Subjects and Study Sites

We tested 14 zoo-housed Asian elephants at two zoos: Oklahoma City Zoo in Oklahoma City, OK (OKCZ, N= 6) and Rosamond Gifford Zoo in Syracuse, NY (RGZ, N= 8). There were 5 males and 9 females, with ages ranging from 1-52 years old (Table 1). At both zoos, elephants were housed in large indoor and outdoor enclosures, with controlled but regular access between the two.

Table 1. Elephant subjects tested

Name	Sex	Age (years)	Location
Bamboo	F	51	OKCZ
Chandra	F	22	OKCZ
Rex	M	51	OKCZ
Asha*	F	24	OKCZ
Achara	F	4	OKCZ
Kandula	M	17	OKCZ
Ajay	M	1	RGZ
Batu	M	5	RGZ
Doc	M	23	RGZ
Kirina	F	25	RGZ
Mali	F	23	RGZ
Romani	F	43	RGZ
Siri	F	52	RGZ
Targa	F	37	RGZ

*This subject was removed from the dataset prior to analysis due to human error (discussed later).

Elephants were tested individually, except for one who was tested with her dependent calf (Asha). Although they were separated from their social group during testing, elephants had olfactory, auditory, and visual access to other elephants throughout the study. Testing took place in indoor enclosures at both zoos. At OKCZ the testing stall was 473.6 m² and at RGZ, the testing stall was 1,428 m². The elephants' diets were not altered during the study and they had access to water while they were tested.

ETHICS STATEMENT

This study was approved by the Hunter College Institutional Animal Care and Use Committee (Protocol # JP-Elephant Behavior 5/21) and the scientific review committees at both zoological institutions prior to the start of data collection.

THE APPARATUS

The puzzle box was a custom-made metal box consisting of three separate compartments connected with bolts. Each compartment measured 41.9 cm x 21.6 cm x 27.9 cm and was composed of steel grade-60/grade-80. All compartments had five 2.54 cm diameter holes drilled symmetrically into the door and each side of the box, with the intention of providing olfactory but not visual access to the food inside (see Figure 1). There were three types of compartments, and each featured a different solution door that an individual could interact with to open and obtain food. These solutions were designed to incorporate foraging behaviors that are typical for elephants (pulling down branches, stripping bark, and pushing with the trunk or body). Thus, while the behavioral action may be ecologically relevant to the elephant, we expected the innovation would result from the elephant's use of the action in a novel context. One solution was a push door which swung down into the box when pressure was applied. Another solution was a pull door which had a chain attached to its front and opened when pulled towards the elephant. This door was inset 20 cm inside the box. Both pull and push doors were secured shut with magnets. The last solution type was a slide door that could be opened by sliding it to the right (Fig. 1).

FIG. 1 ABOUT HERE

PROCEDURE

Elephants were tested at OKCZ from July to August 2019 and at RGZ from November 2019 to February 2020. The puzzle box was constructed in Oklahoma City and, after completion of the study there, shipped to Syracuse for testing in New York. Each elephant was given access to the puzzle box secured on the bollards of a stall at average elephant eye level (with the top of the box positioned 2.1 m off the ground) in either the morning or afternoon (Fig. 2). Each session

began (i.e., time was started) when an elephant entered the testing stall with their two front feet. Elephants had access to the box for an average of 13.7 minutes (range: 1.1-32.8 minutes, depending on whether there were delays between when doors were solved or when elephants no longer interacted with the box). A session was ended and the elephant shifted out of the stall when all MAB doors were opened, if 15 minutes passed without interaction with the box, or after 14 minutes without solving. This slight inconsistency in time before a session was ended was due to unexpected or sudden elephant husbandry needs (e.g., a need to shift elephants between stalls), but did not impact the elephants' propensity to solve due to the fact that solutions were reached early in sessions. The box always consisted of three compartments, but the types of compartments varied by phase (Fig. 1). Each compartment of the puzzle box was baited with high-quality food rewards approved by animal care staff (browser biscuits at OKCZ and marshmallows at RGZ) before the subject had access to the testing area. The puzzle box was cleaned between sessions. In cleaning the box, our goal was not to remove olfactory cues altogether, but to spread olfactory cues from other elephants across the surface of the box to eliminate any localized cues that may direct subjects to a particular solution.

FIG. 2 ABOUT HERE

All interactions were recorded from two viewpoints with a Canon Vixia HF R80 camcorder and a GoPro Hero 7 camera at OKCZ, and two GoPro Hero 7 cameras at RGZ to minimize instances where the view of the box was blocked by the subject, and thus to maximize opportunities to observe the elephants' complete interactions with the MAB. Staff and zookeepers were present during testing, but were not involved except to shift elephants in and out of the testing area.

The elephants were tested in two phases, with each phase consisting of two sessions with the puzzle box. Subjects only participated in one session per day, with at least two and no more than 13 days between sessions. This variability in time between sessions was due to the unpredictability of the elephants' schedules for research at the zoo. In Phase 1, the puzzle box was assembled with three push door compartments. Compartments of the box were baited with either one biscuit (OKCZ) or three marshmallows (RGZ) in the first session of Phase 1 (depending on the preferred rewards at each location), and the reward remained the same throughout the study unless the subject did not open all three compartments in the first session. In that case, the number of rewards was increased for subsequent sessions (three biscuits at OKCZ, six marshmallows at RGZ) to increase motivation. In Phase 2, the puzzle box was assembled with a push, pull and slide door compartment. The order of compartment presentation (i.e., top, middle, bottom) was randomized such that all six possible configurations were used across subjects and each subject received a different configuration in their second session than they did in their first session. If the subject solved all three doors in their first session of Phase 2, all three doors were baited for the second session. If they did not solve all three doors, only the unsolved doors were baited in the second session, with the solved doors open and empty. We did this to investigate whether elephants would innovate when their only option to retrieve a food reward required them to solve a new problem and open the previously-unsolved door(s). This should also increase motivation for attempting to open the challenging doors since they would not get any food rewards otherwise.

MEASURES

All videos were coded using BORIS software (Friard and Gamba 2016). Elephant interactions with the puzzle box were coded until the end of the session based on an ethogram we

developed which included behavioral modifiers for which part of the body was used, which feature and compartment of the box was touched, and if the compartment was baited at the time of the behavior (Supplementary Table 1). A session ended either when the subject solved the last available door, or was shifted out of the testing stall by animal care staff. Innovation score, success, and four behavioral traits (neophilia, motivation, persistence and exploratory diversity) were extracted from the coded videos (see Table 2). Innovation score was assigned based on an elephant's overall performance in the study (i.e., whether each subject ever opened one, two, or three types of doors). Success was the proportion of doors opened out of those available in each of the four sessions. For both of these measures, a door was considered solved when an elephant opened the door enough that their trunk could fit inside, even if they did not immediately reach in and retrieve the reward. Each subject's degree of neophilia was calculated as their latency to touch the box from the session start (once two feet were inside the testing stall) in their first session only. For one subject (Achara), due to an error, her first approach to the box was from behind it in a neighboring stall when another elephant (Asha) was being tested. Because her interactions from behind were slightly out of the camera's view, her access to the space was not completely captured on video. We made the assumption that she had access for the same amount of time as the other elephant in view to calculate her neophilia measure. This calculation was necessary to ensure we did not have to omit her data from the statistical models. Motivation was delineated as the latency to initially contact the box in each session. Due to the unique design of this puzzle box with three solutions available simultaneously, we decided to define some measures (persistence and exploratory diversity) considering both a session as a trial and each door as a trial (Table 2). This allowed us to assess how elephants approached the box as a whole and how they approached each problem within the box. Persistence was quantified as the

proportion of time spent interacting with the box by session or door. The exploratory diversity score (EDS) was measured as the number of unique action and body part combinations (out of 20 observed) that a subject exhibited in direct manipulation of the box either in each session, or for separate door trials.

Table 2. Behavioral measures calculated from coded videos of subjects

Behavioral measure	Session level	Door level
Innovation Score	Number of the 3 types of doors opened across the study (0,1,2 or 3)	
Success	Opened doors/total available doors	Whether door was opened (1) or not (0)
Persistence	Duration of interaction/total session time	Duration of interaction/total time between session start and first door solved, two door solves, or door solve and session end
Neophilia	Latency from session start (2 feet inside stall) to first contact with the box. Only measured for first session	
Motivation	Latency from session start to first contact with the box.	Not assessed at the door level because difficult to differentiate from persistence.
Exploratory Diversity Score (EDS)	Total number (out of 20 observed) of unique motor actions (based on different body parts) used to interact with the box per session.	Total number (out of 20 observed) of unique motor actions (based on different body parts) between session start and first door solved, two door solves, or door solve and session end.

See Supplementary List 1 for all 20 combinations of action and body part observed

ANALYSES

All sessions were coded by co-author A.P. 21% of these sessions were coded independently by first author S.L.J. for inter-rater reliability of measures included in the analyses. Sessions were pseudo-randomly selected for reliability coding such that each subject was coded at least once and all session and phase combinations were coded at each zoo. There was excellent agreement between coders for latencies (ICC (1)=0.99, F(44,45)= 136, p<0.001)

and durations ($ICC(1) = 0.99$, $F(13,14)=235$, $p<0.001$). There was good agreement for exploratory diversity scores ($ICC(1)=0.89$, $F(11,12)=17$, $p<0.001$).

While we tested 14 elephants, one subject (Asha) was excluded from the analysis because she was tested with her dependent calf and there was more interference from the calf than initially expected. Due to the calf's frequent interactions, we could not assess Asha's individual problem-solving ability. For the other 13 subjects, we tested whether multiple behavioral traits were associated with both innovation score and success when traits were measured at the session and door level. All analyses were conducted using R studio (R Studio Team, 2019) with R 4.0.3.

Behavioral traits associated with innovation

To test whether any behavioral traits were associated with innovation, we conducted linear models (LM) using the lme4 package (Bates et al., 2014) fitted with a normal distribution, with innovation as the response variable and behavioral traits as fixed effects. Since innovation was determined at the subject level, we converted the repeated, session and door-level measures (persistence, motivation, and EDS) to subject-level mean scores to include in this model. Before calculating these means, we wanted to confirm that a mean would be representative of the individual's behavior by determining whether each behavioral trait differed by individual and if the trait was repeatable. We used a likelihood ratio test to compare linear mixed models (LMMs) with subject ID as a random effect to LMs without the random effect (following Johnson-Ulrich et al. 2018), to determine whether there was significant variation in each response variable due to subject ID. Each of the repeated variables (persistence, motivation, EDS) was used as the response variable in its own model, with predictor variables of age, sex, zoo, trial number, and phase included to control for their effects. ICCs for repeatability were determined using rptR (Stoffel et al., 2017) for each of the variables that had significant variation based on subject ID.

Likelihood ratio tests and ICCs were calculated separately for session- and door-level measures. Means were only calculated for inclusion in the model predicting innovation for variables that had significant variation in ID and which were repeatable. Any measures that were not significant were excluded from the final model since these measures would not represent a behavioral trait that was consistent across sessions or doors, and therefore a mean would not be a good representation. We evaluated models of innovation separately for measures at the session and door level. Age, sex, and zoo were included in all models of innovation in order to control for their effects. We used stepwise elimination of terms from the full model based on Akaike's Information Criterion (AIC) to determine the best model for the data (Venables and Ripley 2002). Adjusted R^2 values are reported and plots of residuals were examined for all models to confirm that model assumptions of homogeneity and normality of residuals were met. We also ruled out collinearity of fixed effects by checking variance inflation factors (VIFs) using the car package (Fox and Weisberg, 2019) and only included variables with VIF values lower than 10 (Stine 1995).

Due to the wide range in session length for elephants that did not solve all available doors (5.6 to 32.8 minutes), we also wanted to determine whether there were any confounding effects of session length on innovation. Therefore, we conducted an LM with innovation as the response variable and session length as a fixed effect. Similarly, we also wanted to confirm that the elephants that did not open all available doors in a session were not subsequently prevented from exhibiting more exploratory diversity with shorter sessions. Thus, we conducted an LM with EDS as the response variable and session length as a fixed effect.

Behavioral traits associated with success

Beyond innovation, we were also interested in overall problem-solving success irrelevant of the types of doors opened. To evaluate whether behavioral traits were associated with problem-solving success across sessions, we used a binomial GLMM where our response variable was the number of doors successfully opened per session. For door-level analysis, we used a binomial GLMM where the response variable was success (1) or not (0) for each door. Since we were assessing success as a repeated measure (unlike innovation which was measured once) and accounting for individual variation, we did not limit our fixed effects to repeatable measures. We did however, eliminate other subject-level variables of age, sex, and zoo in order to avoid overfitting models with binary outcomes (Peduzzi et al. 1996) and to focus on the main fixed effects of interest. Therefore, all four behavioral measures were included in the models of success across sessions and all but motivation (since it was not defined at the door level) were included in models of success across doors. We checked that all models met assumptions of homogeneity and normality of residuals using the DHARMA package (Hartig, 2020) and ruled out collinearity using VIFs. We reported marginal and conditional R^2 values for each of the models.

Learning in phase 1

To assess whether the elephants learned the push door solution in Phase 1, we used an LMM to look at how latency to solve the first door changed between the two sessions. These latencies were calculated based on the duration of interaction with the box before a door was solved, in order to focus on the time a subject spent actively attempting to solve it. In the LMM, latency to solve was the response variable, session number was a fixed effect, and ID was a random effect. Because elephants were provided with multiple types of doors to solve in phase 2

and some were only provided, in session 2, with closed doors when they had not previously solved them, we were only able to assess learning across the two sessions of phase 1.

RESULTS

Of the 13 elephants which were included in the final analysis, eight elephants innovated to solve all three door types over the course of the study, three elephants solved only two door types, and two elephants only solved one door type. Thus, all 13 elephants solved at least one door type (see the video for an example of an elephant solving all three doors: Supplementary Video S1). Although the elephants sometimes blocked the camera view to the box, their interactions were only out of view on average 2% of each session. Across our elephant sample, we observed a mean persistence of 0.50 (SD: ± 0.28), a mean EDS of 7.64 (± 3.89), a mean motivation of 14.36 (± 25.34) seconds and mean neophilia of 32.38 (± 38.81) seconds as measured per session. For the measures that were also calculated per door, we observed a mean persistence of 0.59 (± 0.32), and mean EDS of 4.19 (± 3.63) (see Table 2 for units of measure for each trait).

Behavioral traits associated with innovation

To determine the traits to include in our model predicting innovation, we first checked for significant variation between subjects using likelihood ratio tests (N= 2-4 sessions). We also checked for repeatability within subjects for each behavioral trait. When evaluating session-level measures, persistence showed both significant variation between subjects across sessions and repeatability within subjects (Likelihood ratio test χ^2 (1, N=52) = 12.52, $p < 0.001$, ICC= 0.55). EDS did not vary significantly between subjects across all sessions (χ^2 (1, N=52) = 0.72, $p = 0.40$, ICC= 0.00). However, when considering only Phase 2 measures of EDS when subjects had the opportunity to exhibit all actions, there was variation between subjects and repeatability (χ^2 (1,

N=26) = 5.19, $p=0.022$, ICC= 0.66). Therefore, we included mean EDS measures for Phase 2 in our model for innovation. Motivation did not vary significantly between subjects across sessions (Likelihood ratio test χ^2 (1, N=39) = 0, $p=1$, ICC=0.00), so it was not included in the innovation model. Therefore, the innovation model for session level measures included mean persistence across all sessions and mean EDS in Phase 2, as well as the measures neophilia, age, sex and zoo.

Our best model included age, zoo, EDS and persistence (Table 3). Using this model, persistence was significantly associated with innovation such that as persistence increased, innovation also increased (Table 3, Fig. 3). No other variables were significantly associated with innovation (Table 3).

Table 3. Parameter estimates from best innovation model with session-level measures.

	Estimate	SE	95% CI	T value	p
Intercept	3.60	1.00	1.29, 5.91	3.59	0.007
Age	-0.02	0.01	-0.06, 0.002	-2.20	0.06
Zoo (RGZ)	-1.24	0.57	-2.54, 0.07	-2.18	0.06
Mean EDS	-0.17	0.12	-0.44, 0.09	-1.49	0.17
Mean Persistence	4.16	1.72	0.19, 8.13	2.42	0.04

N= 13, df= 8, adjusted $R^2=0.32$, AIC= 30.94. Significant results ($p<0.05$ are bolded).

FIG. 3 ABOUT HERE

When evaluating door-level measures, persistence showed significant variation between individuals and was repeatable (Likelihood ratio test χ^2 (1, N=149) = 26.56, $p<0.001$, ICC= 0.37) but EDS did not vary between individuals, even when only considering Phase 2 sessions (Likelihood ratio test χ^2 (1, N=71) = 0, $p=1.0$, ICC= 0.06). Therefore, the model for innovation

at the door level included mean persistence across doors, neophilia, age, sex, and zoo. The best model only included age and persistence, with neither variable being significantly associated with innovation (Supplementary Table 2).

To determine whether there were any confounding effects of variable session lengths for the elephants, we also modeled innovation based on session length. There was a significant effect of session length, such that longer sessions were associated with lower innovation scores (LM, $N=52$, $p=0.025$). Linear models with session length as the fixed effect and EDS as the response variable for elephants that did not open all doors in a session confirmed that session length was not associated with EDS (LM, $N=22$, $p=0.46$).

Behavioral traits associated with success

When considering success in problem solving per session as the response variable, persistence was positively and significantly associated with success (Fig. 4), such that as persistence increased by 0.1, the odds of success increased by a factor of 1.81. None of the other behavioral measures were significantly associated with success at the session level (Table 4).

The model assessing success at the door level showed that persistence and diversity were significantly associated with success (Table 5). As persistence increased by 0.1, the odds of success increased by a factor of 2.02 and as diversity increased by 1, the odds of success decreased by a factor of 0.73.

Table 4. Parameter estimates for GLMM for session level success

	Estimate	SE	Odds Ratio	Odds Ratio 95% CI	z value	p
Intercept	0.18	0.85	1.2	0.23, 7.97	0.215	0.83
Persistence	5.29	1.38	197.73	16.92, 4256.83	3.84	0.0001
Neophilia	-0.009	0.009	0.99	0.97, 1.01	-1.03	0.38

Diversity	-0.08	0.09	0.93	0.77, 1.09	-0.88	0.38
Motivation	0.01	0.01	0.82	0.97, 1.01	-1.10	0.27

N=52 , df= 46, R^2 (conditional= 0.47, marginal=0.43), AIC= 100.7. Significant results ($p < 0.05$ are bolded).

FIG. 4 ABOUT HERE

Table 5. Parameter estimates for GLMM for door level success

	Estimate	SE	OR	95% CI	Z value	p
Intercept	0.45	0.77	1.57	0.35, 7.14	0.585	0.56
Persistence	7.03	1.55	1127.80	54.08, 23520.8	4.54	<0.001
Neophilia	-0.02	0.01	0.98	0.96, 1.00	-1.7518	0.13
Diversity	-0.31	0.10	0.73	0.60, 0.89	-3.16	0.002

N= 149 , df= 144, R^2 (conditional= 0.72, marginal=0.63), Significant results ($p < 0.05$ are bolded).

Learning in phase 1

To assess learning, we used a linear mixed model to look at how latency to solve the first door of the box changed between session 1 and session 2. We found a significant effect of session number, such that in the second session there was a decreased latency to solve the door (Session 1: mean $\pm$ SD = 68.1 $\pm$ 72.2 s; Session 2: 31.6 $\pm$ 46.2 s; LMM: N=26, $p=0.048$).

DISCUSSION

In this study, we sought to explore elephant innovation and the behavioral traits that may influence innovative problem solving using a modified multi-access box (MAB) across two phases. Over the course of the entire study, all 13 elephants innovated to open at least one type of door in the MAB, three elephants were able to repeatedly innovate to open two types of doors,

and eight elephants were able to open all three types of doors. Therefore, we observed that all elephants in our sample were not only able to innovate, but that there was variation in how many times they innovated.

Behavioral traits associated with innovation

When evaluating the traits associated with innovation when measured at the session-level, we found that only persistence was associated as we had predicted. Higher persistence or a greater proportion of time spent in the session interacting with the MAB was associated with a higher innovation score. Studies with other species have found this same relationship (reviewed by Griffin & Guez, 2014), as animals that spend more time interacting with a task are more likely to discover one or more solutions to it. Contrary to the results with other species, however, we did not find an association between neophilia or EDS and innovation. In addition, we were unable to evaluate motivation in the model since the measure did not vary significantly between elephants.

There are a few possible explanations for why our results are not consistent with other species. Several other studies have measured neophilia/neophobia similarly (Johnson-Ulrich et al., 2018; Daniels et al., 2019; Benson-Amram et al., 2012) and have observed that individuals who are less afraid of novelty are more successful solving a novel problem. It is possible that our MAB was not novel enough to elicit varied responses from our sample of elephants; this variation would be necessary to demonstrate differences in attraction to novelty. Elephants in both zoos were continuously exposed to new enrichment items and much of the equipment used in their enclosures may look similar to the MAB (angular, metal structures). We also think that it would be more meaningful to measure neophilia as a personality trait by assessing each individual's latency to approach different novel items rather than only the single measurement taken with our MAB. Perhaps measuring the elephants' reactions to novelty across more than

one context or task would demonstrate that a relationship between neophilia and innovation does exist.

We were particularly surprised that we did not see the predicted relationship between increased exploratory diversity and higher innovation scores observed with other species (e.g., Indian myna: Griffin and Diquelou 2015; raccoon: Daniels et al. 2019). It is thought that a higher diversity of manipulative actions may lead to greater opportunities to learn the causal relationships of a novel object, particularly as it relates to a novel extractive foraging problem (Griffin and Guez 2014). However, it is possible that the design of our MAB with multiple rewards available simultaneously made the causal relationships more difficult to localize. This could have led to less-focused actions by the elephants, such that a higher diversity of actions would not necessarily lead an individual to discover a solution if its actions were not directed to the right part of the box.

Interestingly, when looking at these relationships using behavioral traits measured considering each available door as a trial, none of the traits were associated with innovation. Persistence measured at the door level may not be associated with innovation due to the variable amount of interaction that was required per door. For example, the push and slide doors could be solved with quicker touches, whereas the pull door required that the elephant grasped the chain and then pulled. It is possible that some elephants spent a lot of time attempting the pull solution, such that both successful and unsuccessful elephants would have high persistence scores, but the unsuccessful elephants would have low innovation scores. This is in contrast to the session-level persistence scores, where more interaction with the box overall led to more solutions discovered. This result suggests that there are recognizable differences in the relationships we observe based on how we choose to measure behavioral traits when using an MAB of this design.

Since all elephants were not provided with the same maximum session length due to animal husbandry requirements, we made sure to confirm that the variable session lengths elephants were subjected to did not limit the elephants' ability to innovate or exhibit more motor actions. We found that longer sessions were associated with lower innovation scores, suggesting that elephants that had shorter sessions were likely not prevented from innovating. This result may also indicate that the more innovative elephants could be faster problem solvers overall, since sessions were ended when they opened all doors of the MAB. When assessing sessions where elephants did not solve all available doors, we did not see a significant association between session time and EDS. Therefore, it is likely that the variability in session lengths between elephants is not confounding our results.

Behavioral traits associated with success

When considering overall success with the puzzle box per session, rather than innovation over the course of the study, we found the same relationship with persistence such that higher persistence was associated with greater likelihood of success per session. None of the other behavioral traits were significantly associated with success. When assessing door by door success, persistence was also associated with the likelihood of solving a door. Combining this with our innovation results at the door level, elephants are more likely to solve a door if they are persistent towards the box, but not necessarily more likely to be able to innovate new solutions.

We also found that exploratory diversity was associated with the likelihood of solving a door, but not in the direction we predicted. Our results showed that as EDS increased, the likelihood of solving a door decreased, whereas we predicted that higher EDS would lead to higher success. This could potentially be related to challenges individuals may have had performing particular actions that would have solved one of the doors. Therefore, if there were doors left on the box

that they had not yet been able to solve, a high EDS might be manifested as attempts to perform many different actions to solve the doors, without using the ones needed to open them. This would lead to higher EDS scores directed at doors that were not solved. Based on this result, which runs contrary to studies of other species that connect higher exploratory diversity to success and innovation (e.g., Benson-Amram and Holekamp 2012; Daniels et al. 2019), it is possible that an increase in the diversity of actions actually demonstrates a haphazard, trial-and-error driven attempt to open the box rather than a directed one. Elephants that had a better understanding of how to open the doors or had specific actions they used to manipulate objects in the past might be more selective in the actions they used to open a door and thus would be more successful at doing so. It is also possible that the definitions we used for EDS confounded these results. We attempted to cover all combinations of body parts (e.g., parts of trunk, mouth, head) and action types (e.g., push, pull, blow) observed when defining EDS (following Daniels et al., 2019), but perhaps a simpler categorization of behaviors would have led to different results.

Motivation measured per session was not associated with success in this study. Our measure of motivation was calculated as each elephant's latency to contact the box, which may not vary enough to reflect differences in motivation. We also recognize that our measures of motivation and neophilia were linked since latency to contact was used for both in the first session. It is possible that a relationship between motivational differences and innovation would be observed if techniques such as food deprivation were employed to create different motivational states (Cooke et al., 2021). It is not feasible to adjust the daily food intake of elephants for a study such as ours, but we might see more variation in motivation scores collected for wild elephants subjected to a similar MAB task, since there is natural variation in diet within a wild elephant population.

Our results supported our prediction that the elephants would learn to solve the push door in Phase 1 of this study, such that in the second session, individuals generally solved the first door more quickly than in the first session. In future studies, it would be interesting to provide more trials for the elephants in the Phase 2 configuration to see if learning occurred for the other door types when all doors remained available. Our MAB design including multiple available doors presented simultaneously is unique, and thus learning may need to be assessed differently. In Phase 2 in particular it might make more sense to investigate changes in the accuracy of behavior directed towards unsolved doors rather than changes in solving latency. This would require a detailed analysis of where and how elephants directed particular actions on the box, while leaving all doors available between sessions (rather than locking them once solved).

This study provides new insight into the traits associated with innovation and successful problem solving in zoo-housed Asian elephants, primarily emphasizing the key role of persistence. Overall, elephants were able to innovate when provided with a novel puzzle box demonstrating flexibility in their problem solving, and, for those elephants that interacted with the box longer, a greater likelihood of finding novel solutions. Further work is needed to disentangle whether some of the common relationships observed in other species between innovation and the behavioral traits of neophilia, motivation and exploratory diversity differed in this study due to species-level differences in ecology, cognition and behavior, or our modified experimental design.

In the wild, Asian elephants are endangered, and a major threat to their conservation is loss of habitat due to human-driven environmental disturbances (Leimgruber et al. 2003). Their environment is rapidly changing, and a capacity for innovation may explain how behavioral flexibility could help elephants adapt to anthropogenic change (Mumby and Plotnik 2018;

Barrett et al. 2018). In several elephant range countries, elephants often enter agricultural areas to forage on crops, and local communities have used a number of mitigation strategies to try to stop them. Anecdotally, elephants have been observed overcoming these strategies, which include physical barriers such as electric fences, by using tusks to snap wires or their feet to push down posts (Kioko et al. 2008; Mutinda et al. 2014). In addition to these potential examples of innovative problem solving in the wild, the simple adoption of crops as a novel food source could also be considered a foraging innovation. This has led us to expand our study of innovation in elephants, and, with work currently underway, we aim to investigate environmental impacts on wild Asian elephant cognition. In particular, we are interested in developing a clearer understanding of the relationship between innovation, personality and behavioral flexibility, and what mediates individual differences in their expression.

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726

727 **Fig 1.** The puzzle box in A) Phase 1 and B) Phase 2. The Phase 1 box on the left shows three
728 similar push doors stacked on top of each other. The phase 2 configuration shows all 3 types of
729 doors that subjects had an opportunity to solve (the configuration in the photo on the right is,
730 from top to bottom, slide, pull, push). Note that elephants did not all receive the same
731 configuration in Phase 2.

Fig 2. A sketch of a typical testing session, showing the elephant standing in front of the MAB. The MAB is bolted to bollards inside the testing area at eye-level. The sketch shows an open slide door (top), a closed push door (middle), and a closed pull door (bottom). Sketch by M. Rudolph.

Fig 3. Relationship between mean persistence and innovation scores with LM model fit (blue line with 95% confidence interval in grey). Persistence is the mean proportion of duration of interaction with the box out of total session time. Innovation score is the total number of types of doors opened (0,1,2,3) in the study. Each of the 13 subjects is represented by a black dot.

Fig 4. Relationship between persistence and success for session-level measures with GLMM model fit (blue line with 95% confidence interval in grey). Persistence is the proportion of duration of interaction with the box out of the total session time. Success is the number of doors solved out of available doors. Each black dot represents a session.