



Persistence is key: investigating innovative problem solving by Asian elephants using a novel multi-access box

Sarah L. Jacobson^{1,2} · Amanda Puitiza² · Rebecca J. Snyder³ · Ashley Sheppard⁴ · Joshua M. Plotnik^{1,2}

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Abstract

Innovative problem solving is considered a hallmark measure of behavioral flexibility as it describes behavior by which an animal manipulates its environment in a novel way to reach a goal. Elephants are a highly social taxa that have demonstrated a remarkable capacity for adapting to changing environments. 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 success in the second phase. 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 success was associated with greater persistence, but not with any other behavioral traits when analyzed per test session. Greater persistence and, unexpectedly, 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 changes in wild environments.

Keywords Innovation · Persistence · Problem solving · Cognition · Elephant · *Elephas maximus*

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 can be an important

component of 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 they later establish themselves in a new place, compared to less innovative 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 to maintain seasonal consistency (Lefebvre et al. 2004). These results support 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

✉ Sarah L. Jacobson
sjacobson1112@gmail.com

✉ Joshua M. Plotnik
Joshua.Plotnik@gmail.com

¹ Department of Psychology, The Graduate Center, City University of New York, 365 Fifth Avenue, New York, NY 10016, USA

² Department of Psychology, Hunter College, City University of New York, 695 Park Avenue, New York, NY 10065, USA

³ Oklahoma City Zoo and Botanical Garden, 2000 Remington, Place, Oklahoma City, OK 73111, USA

⁴ Rosamond Gifford Zoo, 1 Conservation Place, Syracuse, NY 13204, USA

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 orders tested, suggesting that this was an ecologically valid approach for investigating variation in innovation (Webster and Lefebvre 2001). A review of studies that have used experimental apparatuses from which food could be extracted (i.e., ‘extractive foraging tasks’) also concluded that the same processes influencing problem solving are associated with innovation in the wild, supporting the use of such tasks as experimental assays of innovation (Griffin and Guez 2014). Using this type of experimental methodology as a proxy to study innovation, researchers have shown that, using similar novel problems, 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; Johnson-Ulrich et al. 2018; Daniels et al. 2019; Williams et al. 2021).

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 in non-primates 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 and behavioral traits.

There are several behavioral traits that have been tested consistently for their association with individual variation in innovation, namely persistence, motivation, responses to novelty, and diversity of motor actions. Some of these traits have more consistent relationships with innovation while others differ depending on the species tested and how traits are measured (reviewed by Griffin and Guez 2014). Persistence has been consistently associated with successful problem solving and repeated innovation across species, such that individuals that spend more time engaged with a task are more likely to solve it (e.g. Thornton and Samson 2012; Griffin et al. 2014; Johnson-Ulrich et al. 2018). While persistence involves an animal’s motivation to work on a task, motivation has also been considered separately as an animal’s willingness to begin engaging with a task, and is often based on the desire for food rewards. Even though the two measures may seem similar, persistence and motivation often do not correlate, so they should be considered as separate constructs (Griffin and Guez 2014). Motivation is thought to be influential in accordance with the “necessity drives innovation” hypothesis, which suggests that innovations occur when individuals are in need of resources (Reader and Laland 2003; Cooke et al. 2021). However, across studies reviewed by Griffin and Guez (2014), motivation has not consistently correlated with problem solving when measured using latencies to engage in a task (e.g., Keagy et al. 2009, 2011) or when using a morphology-based measure of motivation (i.e., body condition, Bókonyi et al. 2014). Individuals’ responses to novelty, whether measured as fear of (neophobia) or attraction to (neophilia) it, are thought to influence variation in innovation by influencing an individual’s likelihood of engaging with something novel in the first place. While some studies have shown that individuals who are less fearful of novelty are more likely to innovate (Benson-Amram and Holekamp 2012; Massen et al. 2013), this relationship is neither consistent across contexts (e.g., Benson-Amram and Holekamp 2012; Bókonyi et al. 2014) nor between studies, likely due to the wide variation in how the response to novelty is measured (Griffin and Guez 2014). Problem solving with extractive foraging tasks—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/diversity of distinct motor actions an animal uses when interacting with the task (henceforth, we use the term ‘exploratory diversity’ to describe this quantity, but previous literature has also used terms such as behavioral (Williams et al. 2021) or motor (Johnson-Ulrich et al. 2018) diversity to describe the same trait). This relationship is thought to exist 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 innovation 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 relative to what is expected in mammalian species based on body mass (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 (Vidya and Sukumar 2005; Plotnik et al. 2011; Plotnik and de Waal 2014; Li et al. 2021), 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 examining innovation experimentally. Elephants have been tested previously in problem-solving studies in which the elephants have successfully solved novel tasks, although two of these studies investigated social learning rather than individual innovation (African elephants (*Loxodonta africana*): 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 (locomotion and exploration behaviors) were important predictors for solving some tasks. We decided to investigate other behavioral differences in elephants that may be related to innovation to evaluate the mechanisms underlying, and individual variation in innovation. As Asian elephants represent an evolutionarily distant taxa from those species previously tested with a similar paradigm, our study may contribute to our understanding of whether relationships between behavioral traits and innovation are consistent 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 device—a multi-access puzzle box (MAB)—to investigate their capacity for innovation. Our MAB had three solutions which each required different motor actions typical of the elephant's behavioral repertoire. 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 compartments, each with its own food reward. We changed this fundamental aspect of the design to draw future 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 provided the elephants with two different phases of this MAB. In the first phase, the three compartments were identical and thus could all be solved the same way; this allowed for the establishment of a single learned solution. In the second phase, two of the three compartments were novel and thus the elephants had an opportunity to innovate. We assessed innovation as the number of possible solutions discovered by the elephants over the course of the study. We investigated both individual variation in, and the behavioral traits associated with the elephants' success in opening the different compartments in the second phase. We hypothesized that greater motivation, persistence, neophilia, and exploratory diversity would be associated with higher success in the second phase, similar to results found with other species. We also hypothesized that the elephants would demonstrate an ability to learn the first phase solution across the two sessions of Phase 1.

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 five males and nine females, with ages ranging from 1 to 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.

Elephants were tested individually, except for one tested with her dependent calf (Asha). Although 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 1428 m². The elephants' diets were not altered during the study and they had access to water while they were tested.

Table 1 Elephant subjects tested

Name	Sex	Age (years)	Location
Bamboo	F	51	OKCZ
Chandra	F	22	OKCZ
Rex	M	51	OKCZ
Asha ^a	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

^aThis subject was removed from the dataset prior to analysis due to interference from her calf (discussed later)

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

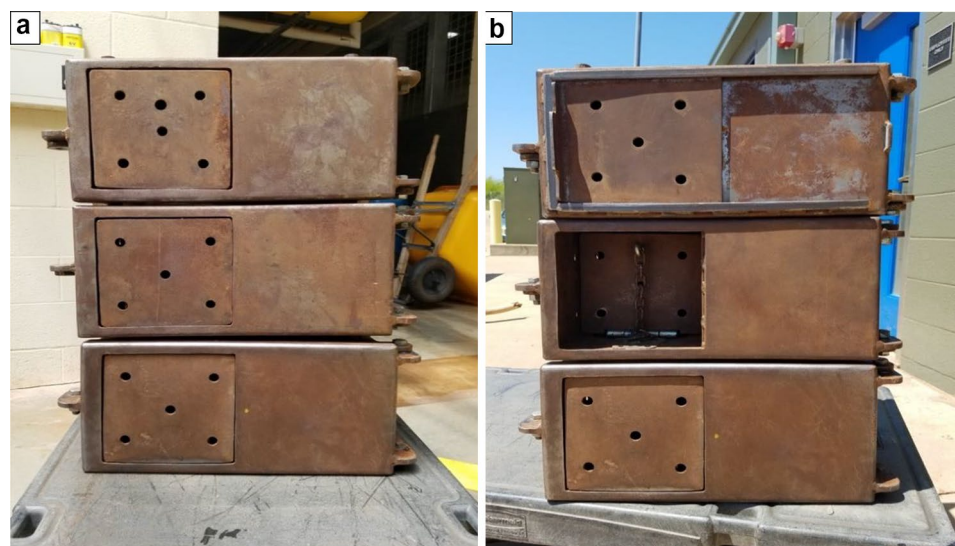
The puzzle box was a custom-made metal box consisting of three separate compartments connected with bolts. Each compartment measured 41.9 cm × 21.6 cm × 27.9 cm

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 Fig. 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 (inspired by Johnson-Ulrich et al. 2018). 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).

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.

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



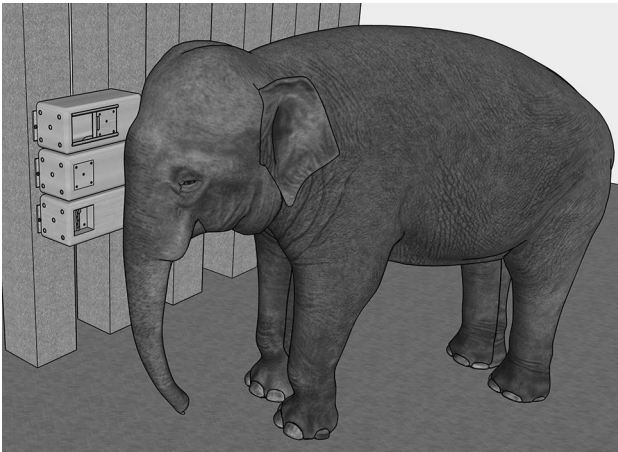


Fig. 2 A sketch of a typical testing session, showing the elephant standing in front of the MAB. The MAB is bolted to bollards inside the testing area at eye level. The sketch shows an open slide door (top), a closed push door (middle), and a closed pull door (bottom). Sketch by M. Rudolph

Elephants had access to the box for an average of 13.7 min (range 1.1–32.8 min, 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 min passed without interaction with the box, or after 14 min 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.

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. Zoo staff 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 identical push door compartments to give the elephants the opportunity to learn this solution. 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), similar to the "blocking" of solutions in other studies (e.g., Johnson-Ulrich et al. 2018; Daniels et al. 2019). This should also have increased 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 quantified as the proportion of doors opened out of those available in each of the two sessions of the second phase.

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 in Phase 2	Whether door was opened (1) or not (0) in Phase 2
Persistence	Duration of interaction/total session time in Phase 2	Duration of interaction/total time between session start and first door solved, two door solves, or door solve and session end in Phase 2
Neophilia	Latency from session start (2 feet inside stall) to first contact with the box. Only measured for first session of Phase 1	
Motivation	Latency from session start to first contact with the box in Phase 2	Not assessed at the door level because difficult to differentiate from persistence
Exploratory Diversity	Total number (out of 20 observed) of unique motor actions (based on different body parts) used to interact with the box per session in Phase 2	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 in Phase 2

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

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 of Phase 1 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 two 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. Exploratory diversity 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.

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, $F(11,12) = 17$, $p < 0.001$]. The same subset of sessions was also assessed by an independent coder who was not involved in data collection or study design to determine whether the number of doors opened was coded reliably. There was 100% agreement about the number and type of doors opened in these sessions.

While we tested 14 elephants, 1 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 success in Phase 2 when traits were measured at the session and door level. All analyses were conducted using R studio (RStudio Team 2020) with R 4.0.3.

Learning in Phase 1

To assess whether the elephants learned the push door solution in Phase 1, we used a linear mixed model (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 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 doors

were closed for some elephants in the phase's second session when they had not previously solved them, we were only able to assess learning across the two sessions of Phase 1.

Behavioral traits associated with success

To determine whether any behavioral traits were associated with innovation, we assessed problem-solving success in the second phase of the study when elephants had the opportunity to open all types of doors. To evaluate whether behavioral traits were associated with problem-solving success across the two sessions of Phase 2, we used a binomial generalized linear mixed model (GLMM) where our response variable was the proportion of doors successfully opened for each subject per session. We also evaluated success at the door level since we had multiple rewarded doors available. For this analysis, we used a binomial GLMM where the response variable was success (1) or no (0) for each door. To reduce the variables included in our models and to avoid overfitting models with binary outcomes (Peduzzi et al. 1996), we first checked for differences in success based on zoo, sex, and age class (juvenile = younger than 10 years old; adult = 10 years and older) using two-sample Mann–Whitney *U* tests. When no differences existed, we did not include these variables in the model. All four behavioral measures (persistence, exploratory diversity, motivation, and neophilia) were included in the models of success at the session level 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 2021). We ruled out collinearity of fixed effects using variance inflation factors in the car package (Fox and Weisberg 2019) and only included variables with values lower than three (Zuur et al. 2010). We reported marginal and conditional R^2 values for each of the models.

Due to the wide range in session length in Phase 2 for elephants that did not solve all available doors (17.35–32.8 min), we also wanted to determine whether there were any confounding effects of session length on success. Therefore, we conducted a linear model (LM) with success 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 exploratory diversity as the response variable and session length as a fixed effect.

Results

Of the 13 elephants included in the final analysis, 8 elephants innovated repeatedly to solve all 3 door types over the course of the study, 3 elephants solved only 2 door types, and 2 elephants only solved 1 door type. Thus, all 13 elephants solved at least 1 door type (see the video for an example of an elephant solving all 3 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 in Phase 2, we observed a mean persistence of 0.48 (SD: ± 0.28) of session time (i.e., 48% of the total session time was spent interacting with the MAB), a mean exploratory diversity of 9.31 (± 3.75) out of 20 behaviors observed, and a mean motivation of 5.92 (± 6.86) seconds as measured per session. The mean neophilia across elephants measured in their first session of Phase 1 was 32.39 (± 39.20) seconds. For the measures that were also calculated per door, we observed a mean persistence of 0.57 (± 0.30) of time between door solves (i.e., 57% of time between door solves is spent interacting with the MAB), and a mean exploratory diversity of 5.59 (± 3.96) out of 20 behaviors observed.

Learning in Phase 1

To assess learning, we used a LMM to look at how latency to solve the first door of the box changed between session 1 and session 2 of Phase 1. 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: $N=26$, $p=0.048$).

Behavioral traits associated with success

There were no differences in success in Phase 2 based on zoo ($U=84.5$, $p=0.82$), sex ($U=82$, $p=0.93$) and age class ($U=55.5$, $p=0.80$), and thus these variables were not included in the model. Using the model with persistence, exploratory diversity, motivation and neophilia as fixed effects and success in problem solving per session in Phase 2 as the response variable, persistence was positively and significantly associated with success (Fig. 3), such that as persistence increased by 0.1, the odds of success increased by a factor of 1.56. None of the other behavioral measures were significantly associated with success at the session level (Table 3).

The model assessing success at the door level in Phase 2 showed that persistence and diversity were significantly associated with success (Table 4, Fig. 4). As persistence increased by 0.1, the odds of success increased by a factor

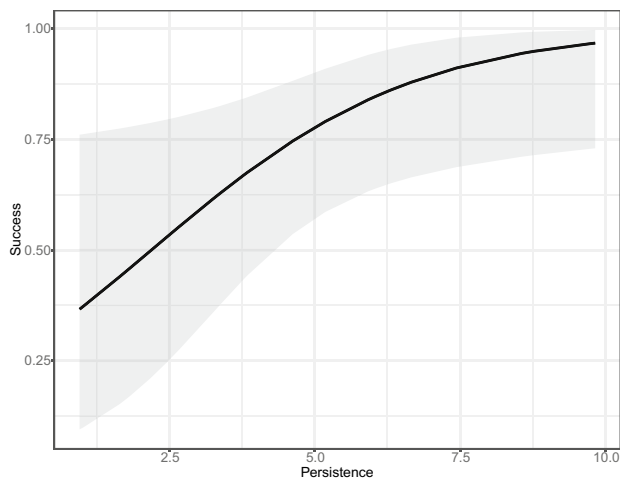


Fig. 3 Marginal predicted effect of persistence per session on success when holding other variables constant based on the GLMM model (black line with 95% confidence interval in grey). Persistence is the proportion of duration of interaction with the box out of the total session time and is scaled by a factor of 10. Success is the proportion of doors solved out of available doors

of 2.26 and as diversity increased by 1, the odds of success decreased by a factor of 0.67.

To determine whether there were any confounding effects of variable session length on the elephants’ performance, we also modeled success based on session length in Phase 2. There was a significant effect of session length, such that longer sessions were associated with lower success (LM, $N = 26$, $p < 0.001$). Linear models with session length as

the fixed effect and exploratory diversity as the response variable for elephants that did not open all doors in a session confirmed that session length was not associated with exploratory diversity (LM, $N = 14$, $p = 0.17$).

Discussion

In this study, we sought to explore elephant innovation and the behavioral traits that may influence innovative problem solving using a multi-access box (MAB) across two phases. Over the course of the study, all 13 elephants solved at least 1 type of door in the MAB, 3 elephants were able to repeatedly innovate to open only 2 types of doors, and 8 elephants were able to open all 3 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.

Our results support our prediction that the elephants would learn to solve the push door in Phase 1 of this study, such that in the second session of Phase 1, individuals generally solved the first door more quickly than in the first session. The elephants’ ability to learn the first solution in this phase when given repeated opportunities to do so demonstrates a baseline problem-solving ability necessary for the assessment of innovation in Phase 2. To efficiently assess innovation, we limited subjects’ access to doors in the second session of Phase 2 to those which they had not solved in the first session of Phase 2, unless they solved them all. Therefore, this meant that our ability to assess learning was limited in this phase. In future studies, it would be interesting to increase the number of trials in the

Table 3 Parameter estimates for GLMM for session level success in Phase 2

	Estimate	SE	Odds ratio	Odds ratio 95% CI	z value	p
Intercept	- 0.72	1.27	0.49	0.04, 5.87	- 0.57	0.57
Persistence^a	0.44	0.21	1.56	1.03, 2.35	2.12	0.03
Neophilia	- 0.01	0.01	1.0	0.97, 1.02	- 0.37	0.71
Diversity	0.02	0.14	1.02	0.77, 1.34	0.12	0.90
Motivation	- 0.04	0.05	0.96	0.87, 1.06	- 0.81	0.42

$N = 26$, $df = 20$, R^2 (conditional = 0.40, marginal = 0.32), significant results ($p < 0.05$ are bolded).

^aPersistence proportions were scaled so that a unit change in persistence is 0.1

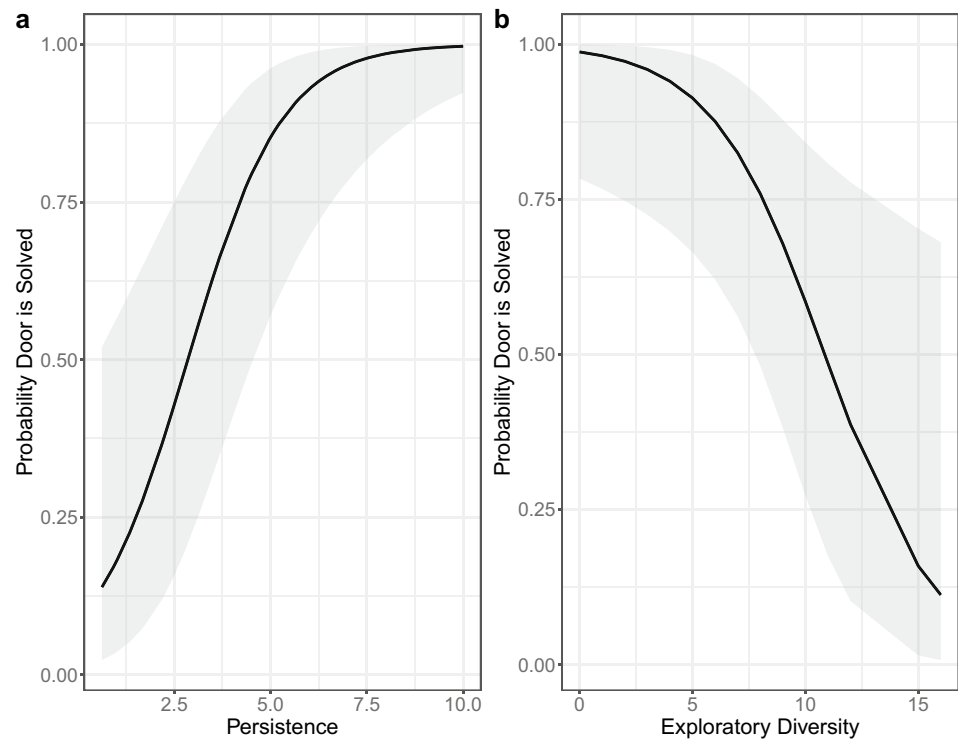
Table 4 Parameter estimates for GLMM for door level success in Phase 2

	Estimate	SE	OR	95% CI	z value	p
Intercept	- 0.23	1.20	0.80	0.08, 8.28	- 0.19	0.85
Persistence^a	0.82	0.24	2.26	1.40, 3.65	3.35	< 0.001
Neophilia	- 0.02	0.01	1.0	0.96, 1.03	- 0.18	0.86
Diversity	- 0.40	0.17	0.67	0.48, 0.94	- 2.34	0.002

$N = 71$, $df = 66$, R^2 (conditional = 0.75, marginal = 0.61), significant results ($p < 0.05$ are bolded)

^aPersistence proportions were scaled so that a unit change in persistence is 0.1

Fig. 4 Marginal predicted effect of persistence (a) and exploratory diversity (b) per door on the probability that the door is successfully opened when holding other variables constant based on the GLMM model (black line with 95% confidence interval in grey). Persistence is the proportion of duration of interaction with the box out of the total time between door solves and is scaled by a factor of 10. Exploratory diversity is the total number of unique motor actions between door solves



Phase 2 configuration to see if learning occurred for the other door types when all doors remained available. Unlike in other studies where all doors led to a single reward (e.g., Johnson-Ulrich et al. 2018; Daniels et al. 2019), our MAB design included multiple rewarding doors available simultaneously; this deviation made it more difficult to assess learning. 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).

Behavioral traits associated with success

Once elephants had experience with the push door solution in Phase 1, we assessed their ability to repeatedly innovate with two more possible solutions in Phase 2. When assessing their success per session with this more complicated puzzle box, we found that higher persistence, or a greater proportion of time spent interacting with the MAB, was associated with a greater likelihood of success per session. Studies with other species have found this same relationship (e.g., Thornton and Samson 2012; Griffin et al. 2014; reviewed by Griffin and Guez 2014), as animals that spend more time interacting with a task are more likely to discover one or more solutions to it. However, we did not find a significant association between neophilia, motivation or

exploratory diversity and success per session, which runs contrary to the results found for other species (e.g., Johnson-Ulrich et al. 2018; Daniels et al. 2019; reviewed by Griffin and Guez 2014).

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 and Holekamp 2012) and have observed that individuals who are less afraid of novelty are more successful novel problem solvers. 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 success per session observed with other species (e.g., Indian myna: Griffin and Diquelou 2015; hyena: Johnson-Ulrich et al. 2018; 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, which permitted the availability of multiple rewards 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.

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. Overall, the elephants in this study appeared to be highly motivated and neophilic, given their relatively short latencies to approach the MAB across all sessions. It is possible that we would observe a relationship between motivational differences and innovation 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 behavioral study, 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.

When assessing door by door success, greater persistence was associated with a greater likelihood of solving a door. 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 exploratory diversity decreased, the likelihood of solving a door increased, whereas we predicted that higher exploratory diversity 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 exploratory diversity might manifest as the performance of many different actions resulting in failure to solve the doors. This would lead to higher exploratory diversity 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; Johnson-Ulrich et al. 2018; 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 have been more selective in the actions they used to open a door (and thus used fewer motor actions), leading to greater success in solving the task. Therefore, some of our subjects may have innovated without much trial and error, potentially indicating some level of causal understanding about the doors. This would need to be investigated further in future studies.

Since elephants were not all provided with the same maximum session length due to animal husbandry requirements, we made sure to confirm that the variable session lengths did not limit the elephants' opportunities to successfully open doors or exhibit more exploratory diversity. We found that longer sessions were associated with lower success, 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 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 exploratory diversity. Therefore, it is likely that the variability in session lengths between elephants did not affect our results.

While we believe that these results provide insight into the relationships between behavioral traits and innovation in elephants, we recognize that there were several differences in our study design that limit comparisons with other species studied using MABs. We designed our MAB and the study protocol to be as simple as possible to implement a comparable study with wild elephants. This led us to only include three different solutions/opportunities for innovation, whereas other studies have provided four. It is possible that we would have seen more individual variation in innovation with the inclusion of a fourth solution since research with birds has demonstrated that fewer subjects were able to innovate four times, whereas many could innovate three times (Auersperg et al. 2011). However, research with hyenas did not find a difference between three and four solutions (Johnson-Ulrich et al. 2018). In the future, it would be interesting to push the limits of innovation for elephants with additional solutions and a larger sample size to investigate both individual variation in success and whether the relationships between innovation and behavior change with an increase in difficulty or the number of challenges. In this study, we defined an innovation as any opening of a door, without necessarily establishing that the elephants learned that particular solution through repeated successful solves. While some studies have emphasized that an innovation must be learned (Johnson-Ulrich et al. 2018; Daniels et al. 2019; but also see Williams et al. 2021), we aimed to assess innovation with fewer trials in order to compare with the more variable number of exposures to the apparatus that would occur in our parallel studies with wild elephants (currently in progress). Without establishing a learning process

for all the solution types, it is possible that some elephants discovered how to open a door without encoding the solution. However, because our analysis suggests that elephants did learn the push door solution after their first exposure—latencies to solve the first door decreased in their second session—it is likely that elephants would have demonstrated learning if given greater opportunity to interact with the other doors repeatedly as well.

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. Our results, along with those found in other species, suggest that these behaviors likely emerged multiple times through convergent evolution. This study also demonstrated that the relationship between exploratory diversity and successful problem solving is more complex than previously known. 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 may also be considered a foraging innovation (Prasher et al. 2019). 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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