Fall 12-21-2020

Exploring Behavioral Flexibility, Problem-Solving, and Innovation in Captive Asian Elephants (Elephas maximus)

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Exploring Behavioral Flexibility, Problem-Solving, and Innovation

in Captive Asian Elephants (*Elephas maximus*)

by

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Submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Animal Behavior and Conservation, Hunter College,
The City University of New York

2020

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Table of Contents

Dedication

To Mami and Papi: Thank you for always being there for me and supporting me even if you

didn't always agree with me. I love you both very much!

To Daniella: Thanks for helping me take a breather once in a while.

To my family in Peru: Thank you for all the love and support despite being far away.

To Jerry

Acknowledgments

Abstract

Many intelligent and socially complex species, such as the Asian elephant, have been shown to adapt well to environments impacted by anthropogenic changes, likely due to a capacity for behavioral flexibility. This flexibility, coupled with habitat loss and fragmentation, has contributed to an increase in conflict between humans and wildlife. Cognition, behavior, and individual variation research has the potential to improve conservation efforts, as well as conditions for animals living under human care, and advance the study of convergent cognitive evolution. To investigate individual variation in cognition in elephants, we studied Asian elephants in a zoo to identify behavioral measures of problem-solving and innovation. We presented six elephants at the Oklahoma City Zoo with an extractive foraging device comprised of three compartments over two testing phases. We measured persistence, motivation, neophilic responses, exploratory motor diversity, latency to solve, success, and repeated innovation. Four of the six elephants were able to solve all three doors while the other two were able to solve two doors. We found a positive correlation between persistence and success within a session ($r = 0.458$, $p < 0.01$). Using linear mixed effects modeling, the model with only persistence as a predictor of success was the best-fit model ($\chi^2(1) = 15.918$, $p<0.001$), with probability of success at 0.85 at the mean persistence level. We did find individual variation across our behavioral measures that could potentially be explained by differences in life history, age, rank, and sex. These findings help contribute to our understanding of problem-solving ability, innovative capacity, and overall behavioral flexibility in Asian elephants.

Keywords: *Elephas maximus*, innovation, problem-solving, puzzle box, behavioral flexibility, persistence, exploratory motor diversity, zoo research

Introduction

In recent years, interest has grown in the study of applied animal cognition research, with a focus on understanding how behavior and cognition impact human-animal relationships both in captivity and in the wild. In addition, comparative cognitive research can tell us more about how complex cognitive capabilities evolved both within the primate taxa and convergently across evolutionarily distinct nonhuman animals. Anthropogenic impact has led to major environmental changes and many species have learned to adapt and modify their behavior in order to survive in rapidly changing environments (Ditchkoff, Saalfeld, & Gibson, 2006). This flexibility in behavior allows an individual to adapt, through learning or innovation, to new conditions (Sol and Lefebvre, 2000). Incorporating behavioral data into wildlife management programs could provide a strong framework for future research (Berger-Tal et.al., 2011), as it has been shown to be useful in reintroduction programs (Berger-Tal & Saltz, 2014) and assessing anthropogenic disturbances (Tadesse & Kotler, 2012; Payne, van der Meulen, Suthers, Gray, & Taylor, 2015).

Several species have been shown to exhibit flexibility in many aspects of behavior. Foraging flexibility, for example, has been found in trap-building spiders that alter their web architecture based on the cues of available prey (Blamires, Chao, Liao, & Tso, 2011). Northern gannets were also shown to alter their foraging behavior when the abundance of one of their most common prey declined by changing feeding locations (Montevecchi, Benvenuti, Garthe, Davoren, & Fifield, 2009). Spotted sand lizards similarly altered their foraging strategies in response to prey availability and if they were in a degraded vs. non-degraded habitat (Blumroeder, Eccard, & Blaum, 2012).

Many species living in close proximity to humans employ foraging behavior flexibility, taking advantage of the anthropogenic changes in the surrounding area. Certain species have

developed "raiding" behaviors that exploit resources while minimizing the risk associated with interacting with humans. For example, some baboons in South Africa raid crops in nearby urban areas, and appear to have greater reproductive success despite the obvious risk of the behavior (Fehlmann et al., 2017). Asian elephants in Cambodia also participate in crop raiding, with varying rates dependent on crop type and season (Webber, Sereivathana, Maltby, & Lee, 2011).

Certain cognitive processes, such as problem-solving, have been linked to a species' adaptability to human-altered environments and their response to the resulting conflict (Barrett, Stanton, & Benson-Amram, 2019). By acknowledging and understanding the potential for individual animals to express different levels of behavioral flexibility in their response to the environment, conservation and management efforts could be better directed at the individuals involved. Other factors–such as how animals learn and respond to novelty (i.e., neophilia)–are associated with behavioral flexibility as they may play a role in the inhibition of previous behavior and the expression of novel behaviors. Barrett and colleagues (2019) also highlighted a possible link between behavioral flexibility and innovation, which is seen in the innovative behavior found in species living in urban environments who take advantage of human activities by, for example, crop-raiding and stealing food.

Innovation, as defined by Reader and Laland (2003), is the development of new or modified learned behavior. Being innovative increases an individual's—or a population's— potential ecological expansion through the use of new foraging methods or navigation of human-constructed obstacles. There have been many documented, potential examples of innovation in the wild, including potato washing in Japanese macaques (Kawai, 1965), mollusk diving in Norway rats (Gandolfi and Parisi, 1973), foraging using sponges in bottlenose dolphins

(Smolker, Richards, Connor, Mann, & Berggren, 1997), and the manipulation of sugar packets in noisy miners (Delgado-V & Correa-H, 2015).

Researchers began studying innovation in more controlled settings, as naturally occurring instances of innovation are infrequent and it is usually difficult to determine the original innovator. Webster and Lefebvre (2001) looked at innovative ability in five avian species using a foraging puzzle box; individuals were captured from the wild and temporarily housed for the study. This was the first time this problem-solving assay was used to study innovation. The authors found correlations between ability to solve the puzzle box and documented capacity for innovation in the wild, supporting the assay's ecological relevance. Since then, many foraging puzzle boxes have been used to study innovation in a number of different species, including African lions, *Panthera leo* (Borrego & Dowling, 2016), meerkats, *Suricata suricatta* (Thornton & Samson, 2012), chimpanzees, *Pan troglodytes*, bonobos, *Pan paniscus*, gorillas, *Gorilla gorilla*, & Sumatran orangutans, *Pongo abelii* (Manrique, Völter, & Call, 2013), and two species of mouse lemurs, *Microcebus murinus* and *Microcebus berthae* (Henke-von der Malsburg & Fichtel, 2018). Beyond establishing the ability to innovate, Benson-Amram and Holekamp (2012) also used a puzzle box to demonstrate that individual wild spotted hyenas that showed a greater diversity of initial exploratory behaviors were more successful at problem-solving.

Auersperg, Von Bayern, Gajdon, Huber, & Kacelnik (2011) developed the multi-access box (MAB) paradigm to further investigate innovation. The MAB offered several simultaneous tasks and allowed for mastered solutions to be progressively removed as an option. This MAB paradigm allows the researcher to assess which solutions are approached first, how many solutions are found, behavioral flexibility, neophilic responses, exploration techniques, motivation, and many other factors. The authors applied this paradigm to compare problem

solving in two extractive foraging species, keas (*Nestor notabilis*) and New Caledonian crows (*Corvus moneduloides*). They found differences in exploration technique, affordance learning, neophobia, and object manipulation across individuals and between the parrot and corvid species (Auersperg et. al., 2011).

Johnson-Ulrich, Johnson-Ulrich, and Holekamp (2018) used the MAB paradigm to study repeated innovation in 10 captive spotted hyenas. Their MAB was comprised of a push, slide, and two different pull doors that all opened up into the interior of the box, which was baited with a food reward; once a solution was learned, that particular door was bolted shut in subsequent trials. The authors measured the hyenas' persistence, motivation, motor diversity, activity, efficiency, inhibitory control, and neophobia when interacting with the box. High persistence, high motor diversity, high activity, and low neophobia were found to predict repeated innovation, or the number of unique innovations learned across trials. Four hyenas were able to find all four possible solutions.

Daniels, Fanelli, Gilbert, & Benson-Amram (2019) similarly used the MAB paradigm to assess cognitive and behavioral traits that may determine behavioral flexibility. The MAB used had three possible solutions on which 20 captive raccoons were tested. Successful raccoons showed high motor diversity, high persistence, low neophobia, and evidence of learning across trials. Seven raccoons were able to find all three possible solutions.

To advance the goals of comparative cognition research, we chose to apply a similar paradigm to study innovation and associated problem-solving behaviors in a different species, the Asian elephant. By using similar methods to study cognition across different species, we can learn more about the convergent evolution of cognition across evolutionary distant species.

Asian elephants

Asian elephants (*Elephas maximus*) are a particularly important animal to study because of their endangered conservation status (Choudhury et al., 2008), complex cognition (Irie & Hasegawa, 2009; Byrne, Bates, & Moss, 2009; Jacobson and Plotnik, 2020), and fission-fusion social dynamics (Vidya & Sukumar, 2005; de Silva, Ranjeewa, & Kryazhimskiy, 2011). They live in habitats that are rapidly changing due in large part to human encroachment, and they now only inhabit about 10% of their historical range (WCS, 2019). Instances of Asian elephants bypassing a variety of human barriers intended to deter crop raiding (Zhang & Wang, 2003; Wilson, Davies, Hazarika, & Zimmermann, 2015) suggest that a better understanding of their decision-making processes, and the flexibility they exhibit when adapting to anthropogenic change, could have significant implications for human-elephant conflict mitigation and conservation. Learning more about how individuals approach new problems in their environment could be more productive towards mitigating elephant disturbances in place of using ineffective and fear-based conditioning tactics to deter or alter elephant behavior (Mumby and Plotnik, 2018).

In addition to observed problem-solving in the wild, cognitive studies with Asian elephants have shown them capable of visual discrimination and long-term memory (Rensch, 1957), olfactory quantity discrimination (Plotnik et. al., 2019), human cue discrimination (Polla, Grueter, & Smith, 2018), mirror self-recognition (Plotnik, De Waal, & Reiss, 2006), numerical competence (Irie, Hiraiwa-Hasegawa, & Kutsukake, 2019), cooperation (Plotnik, Lair, Suphachoksahakun, & De Waal, 2011), consolation (Plotnik, & de Waal, 2014), tool use and modification (Chevalier-Skolnikoff & Liska, 1993; Hart & Hart, 1994; Hart, Hart, McCoy, &

Sarath, 2001), body self-awareness (Dale & Plotnik, 2017), and understanding means-end relations (Irie-Sugimoto, Kobayashi, Sato, & Hasegawa, 2008).

Only two previous studies looked at insightful problem-solving in zoo housed Asian elephants. In Foerder et al. (2011), one elephant spontaneously moved a large cube to stand upon to reach a food item that was otherwise beyond reach; this same elephant also went on to generalize this tool use to other objects, indicating a capacity for insightful problem-solving. Barrett & Benson-Amram (2020) showed that one elephant could solve a floating object task without any training, using water as a tool to reach a food reward inside a tube.

Asian elephants' complex cognition may be a result of having the largest absolute brain size of terrestrial mammals, with an encephalization quotient of 2.0 on average and a well-developed olfactory system (Shoshani, Kupsky, & Marchant, 2006). The similarities between human and elephant brain structure could explain analogous cognitive functions, although the composition of neurons in specific brain sections has been shown to be quite different between humans and elephants (Herculano-Houzel et al., 2014).

Innovation, which is potentially equivalent to creativity in humans, is considered one of the most complex cognitive functions (Reader, 2003). A few studies have compared brain size and complex cognitive abilities. Sol, Bacher, Reader, & Lefebvre (2008) analyzed 400 documented human-mediated introductions of mammals to new environments and showed that mammal species with larger brains tended to be more successful at establishing themselves in novel environments. Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp (2016) found that brain size predicted problem-solving ability across related species of carnivores.

The complex social relationships Asian elephants form may also influence their cognitive abilities. They are known to live in complex fission-fusion groups with individuals typically

forming long-term bonds with a small, stable group, while also forming extensive yet fluid social affiliations across groups (de Silva et al., 2011). Females lead these multigenerational, family groups, with males dispersing locally (Vidya & Sukumar, 2005). Due to anthropogenic disturbance, different matrilines have coalesced (Vidya, et al., 2007) and stable, long-term all-male groups have formed (Srinivasaiah, Kumar, Vaidyanathan, Sukumar, & Sinha, 2019). Access to many diverse social relationships can offer individuals a chance to learn and pass knowledge within a group (Reader, 2003), as it is expected that groups contain a diverse set of individuals with their own set of skills (Griffin & Guez, 2015).

It is likely that similar behaviors may arise among group members through learning and/or social facilitation. Social learning may occur from observing members within the group, particularly by younger elephants. Petraccione, Root-Gutteridge, Cusano, and Parks (2017) found that a zoo-housed calf's level of dexterity, behavioral repertoire, and fine motor skills increased over time; the calf was seen spending over 98% of his time in association with other members of the herd at a zoo, and his associations were not defined by his genetic relatedness. Another zoo study found that elephants that observed another solving a task showed increased interest in the task even if they could not solve it, possibly suggesting social learning through stimulus enhancement (Barrett & Benson-Amram, 2020). Although I did not assess social learning experimentally in the present study, I considered social access when reviewing similarities in behavior between subjects.

Hypothesis, objectives, and predictions

Cognitive research can further inform management and conservation efforts for Asian elephants, both under human care and in the wild, which is vital for the continued survival of this endangered species. Although there is a long history of zoo elephant research, these studies have

mostly focused on pharmacology, nutrition, reproduction, sensory biology and diseases like elephant endotheliotropic herpesvirus (for a review, see Bechert et al., 2019). Zoos provide a great avenue for cognitive studies because they allow for a controlled, safe research environment and the involvement of expert zoo staff. Studying cognition in zoos can have both basic and applied science applications. For the former, this work allows for a greater understanding of how elephants navigate their physical and social worlds. For the latter, studying cognition in zoos can foster public understanding of science, provide additional physical and mental stimulation for animals, reduce stereotypical behaviors, and could lead to improvements in zoo education and management protocols (Plotnik, de Waal, Moore III, & Reiss, 2010; Hopper, 2017). Providing individuals with challenges similar to those they would experience in the wild in the form of cognition tests encourages stimulation and can contribute positively to animal welfare (Plotnik et al., 2010). When cognitive testing was implemented with a group of zoo-housed primates, for example, researchers found a decrease in aggressive interactions due to testing and an increase in associations among group members during testing days; these findings lead researchers to infer that cognitive testing can contribute to stronger group cohesion (Whitehouse, Micheletta, Powell, Bordier, & Waller, 2013).

The current study looked at the behavioral flexibility and innovative techniques zoo housed Asian elephants (*Elephas maximus*) used to solve a custom-made, multi-solution puzzle box across two testing phases. The first testing phase examined individual elephants' problem-solving techniques in three simultaneous trials each with the same solution. The second testing phase assessed an individual's ability to innovate when faced with other possible solutions. From previous puzzle box studies with hyenas (Johnson-Ulrich et al., 2018) and raccoons (Daniels et al., 2019), multi-access box paradigms were used to measure repeated innovation successfully in

a behaviorally flexible species. Although it has been shown that captive animals show different innovative problem-solving capabilities from their wild counterparts (Benson-Amram, Weldele, & Holekamp, 2013), the current study provides a baseline for investigating the behavioral flexibility of Asian elephants.

This is the first examination of problem-solving in elephants with a multi-solution puzzle box. We expected the elephants to demonstrate innovation, behavioral flexibility, learning, and high neophilia because they often encounter and adapt to changing environments, although we did expect this to vary among individuals. Based on previous problem-solving research, we predicted that greater exploratory motor diversity, persistence, motivation, and neophilic responses would be associated with higher success, as well as a higher number of solutions found. Elephants were also expected to solve the box faster in later sessions as a result of learning. We expected to find the greatest similarities in motor diversity patterns between individuals within the related female herd, as they generally have the greatest opportunity to learn from each other when interacting socially or when interacting with enrichment items. Non-related members of the herd (one female and one male) with limited access to the herd were still expected to exhibit more similar behaviors to the related females than to the single male typically housed alone.

Methods

Subjects

This study included six Asian elephants (males: $n = 2$, females: $n = 4$) from the Oklahoma City Zoo in Oklahoma City, OK (see Table 1). Ages of subjects ranged from 4 years to 51 years old at the start of the study. Achara is the offspring of Asha and Rex. Asha and

Chandra, the matriarch (noted with an asterisk in Table 1), are half-sisters. All elephants were born in zoos, except for Bamboo and Rex, who were wild-born and brought into human care soon after. During the period of this study from July 2019 to August 2019, the elephants were housed in various combinations of indoor and outdoor enclosures. These include the elephant barn, which has seven stalls and a large sand enclosure, and three outdoor enclosures. The total area of all the enclosures within the barn is 2.64 km^2. The four related females were always housed together in the elephant barn, except for brief separations for training sessions and experimental trials for this study. Bamboo and Kandula were typically housed with the herd in the outdoor enclosures during the day and several times a week overnight. During this study, Rex was housed alone.

Table 1. Descriptive information for the subjects in the study

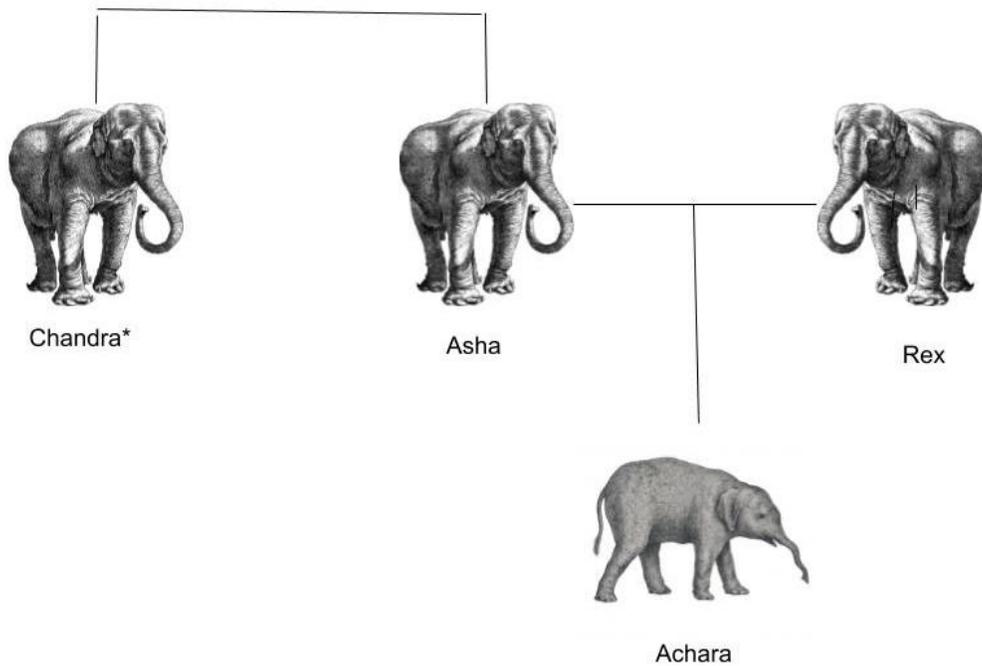| Name	Sex	Birthplace	Age (years)	Years at OKC Zoo
Bamboo	F	Thailand (wild)	51	4
Chandra*	F	Dickerson Park Zoo in Springfield, MO	22	21
Rex	M	India (wild)	51	8
Asha	F	Dickerson Park Zoo in Springfield, MO	24	21
Achara	F	Oklahoma City Zoo in Oklahoma City, OK	4	4
Kandula	M	National Zoo in Washington D.C.	17	4

Figure 1. Family tree showing only those elephants with a genetic relationship.

Husbandry and Testing Enclosure

Elephants were tested individually, except for Asha, who was tested with her dependent (10-month-old) calf. All the testing took place in one of the barn stalls, which measured 5.87 m by 6.88 m and had an area of 473.62 m^2 (see Figure 2 and 3). The puzzle box was attached to the metal bollards used to divide the stalls. The height from the bottom of the box to the floor was 1.54 m. When an elephant was in this testing stall, she/he had access to two water dispensers in the right and left front corners of the stall. Conspecifics were not allowed in the stall adjacent to the testing stall during testing. Conspecifics were occasionally placed in a nearby maternity stall, where they had a partial view of the puzzle box, but only if they had already been tested on that

particular phase. Diet was not altered for the purpose of the study, although the elephants did not

have access to hay during testing.

Figure 2. Photos of the stall door (blue) leading from the maternity stall into the testing stall
(LEFT), and a view from this door of where the puzzle box (red) was installed (RIGHT).

Figure 3. Photos of the stall door (blue) leading from the adjacent stall into the testing stall (LEFT), and a view from this door of where the puzzle box (red) was installed (RIGHT).

Ethical Approval

This study was approved and reviewed by the Hunter College Institutional Animal Care and Use Committee (Protocol # JP-Elephant Behavior 5/21), as well as the Scientific Review Committee at the Oklahoma City Zoo prior to the start of data collection.

Apparatus

The custom-made metal box consisted of three separate compartments that were 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. Each compartment had five 2.54 cm diameter holes placed

symmetrically on the door and on each side of the box (see Figures 4-6). Compartments weighed between 20 to 21.5 kg each. Each compartment featured a different solution door.

Push Door Compartment. When pressure was applied to the door, the door swung down flat into the box (see Figure 4). Magnets were used to create mild resistance to ensure the door would not accidentally fall open. There was an inside lip that kept the food reward from rolling forward and getting trapped by the opened door. Once this door was opened, it could not be re-closed by the elephant.

Pull Door Compartment. A chain was attached to the top center of the door. This chain needed to be pulled towards the elephant to open the door (see Figure 5). This door was also in-set 20 cm inside the box and there were an additional three holes on the inside panel. This door could be re-closed by pushing the door up and back into place.

Slide Door Compartment. This door opened when it was slid to the right (see Figure 6). There was a lip that stuck out on the left edge of the door that could be grasped. This door could be re-closed by moving the door back to the starting position.

Figure 4. The puzzle box showing the push door compartment closed (LEFT image), and the door pushed opened allowing access to the reward behind the lip inside (RIGHT image).

Figure 5. The puzzle box showing the pull door compartment closed (LEFT image), and the door pulled opened allowing access to the reward inside (RIGHT image).

Figure 6. The puzzle box showing the slide door compartment closed (LEFT image), and the opened door slid across which allowed access to the reward inside (RIGHT image).

Procedure

Each subject was given access to the custom puzzle box either in the morning or afternoon, and the behavior of each subject was recorded for a maximum of 30 minutes. The box was always composed of three compartments. Each compartment was baited with a food reward. The box was secured to the bollards of the stall at average elephant-eye level–the top of the puzzle box was 2.108 m above the ground–while the focal subject was physically away from the testing area in a separate stall. The food rewards were part of the elephants' daily diet and were

chosen by the caretakers. The reward items were commercially available browser biscuits. At the

start of each trial, the focal subject was released into the testing enclosure via the sliding stall

door from the maternity stall (Figure 2) or adjacent stall (Figure 3). The puzzle box was cleaned

with rubbing alcohol between trials.

Trials were videotaped with a Canon Vixia HF R80 camcorder and a GoPro Hero 7 set up

on a tripod. The video camera was set on the outside of the enclosure looking down into the

testing enclosure from the top of a stairway (Figure 7); the GoPro was set on a raised shelf on the

ground floor looking into the stall from a side angle of the box (Figure 8). Staff and zookeepers

were present but not involved during trials.

Figure 7. This photograph shows the camcorder's view of the puzzle box in the testing stall as
well as the entrance from the maternity stall.

Figure 8. This photograph shows the view of the puzzle box in the testing stall and the adjacent stall from the GoPro.

Subjects were tested in two phases, and their progression onto the second phase was dependent on their performance in the first phase. Each phase consisted of two sessions with the puzzle box. A subject successfully passed Phase 1 by opening at least one push door out of the total six push doors available over their two sessions. This was done to establish a baseline method for solving the puzzle box. Subjects that succeeded moved on to Phase 2. If a subject failed, testing was discontinued.

Subjects participated in one session per day. The session began when the subject entered the testing stall. The session ended when the subject opened all three compartments of the puzzle box or after 15 minutes elapsed without any interaction with the box. Compartments were baited with one biscuit each. If the subject did not open all three compartments in a session, compartments were, from then on, baited with three biscuits each to increase motivation. At the

end of each trial, the subject was shifted to a stall where she/he would not have access to the puzzle box and the puzzle box was removed from the enclosure or cleaned and prepared for the next subject.

Phase 1 (2 sessions): The puzzle box was assembled with three push-door compartments that were baited with the food reward.

Phase 2 (2 sessions): The puzzle box was assembled with a push-door compartment, a pull-door compartment, and a slide-door compartment in random order. The order of compartments (from top to bottom) was randomized before testing began and each subject had a different order for their two sessions. If the subject solved all three doors in the first session, all three compartments were baited for the second session. If the subject solved two doors in the first session, only the unsolved door was baited in the second session; the other doors were left open and empty. If the subject solved one door in the first session, only the unsolved doors were baited in the second session. The other door was left open and empty.

Behavioral Assays

We used the following measures to examine problem solving and innovation (see Table 2): (1) persistence, (2) motivation, (3) exploratory motor diversity, (4) neophilia, and (5) latency to solve. Behavioral assays were measured at the session- and/or subject-level for all individuals.

Table 2. Summary of behavioral measures used in analysis.

Measure	Definition
Persistence	Ratio of the total time spent interacting with the box to total session time, measured once per session[a]
Motivation	Latency from start of session to first contact with the box, measured once per session[a]
Exploratory motor diversity	Score of unique behaviors an individual exhibited when interacting with the box, measured once per session[a,b,c]
Neophilia	Latency from start of first session to first contact with the box, measured once per subject[b,c]
Repeated innovation	Number of solutions learned: possible score between 0-3, measured once per subject[a]
Success	Ratio of solutions found out of total solutions possible, measured once per session as well as once per subject
Latency to solve first door	Latency from first contact to first solution, only counting the time interacting with the box, measured once per session

[a]Johnson-Ulrich et al., 2018
[b]Bensom-Amram and Holekamp, 2012
[c]Daniels et al., 2019

Behavioral Coding

All videos were coded for behaviors using BORIS, a free, open-source event-logging software for video/audio coding and live observations created by students from the University of Torino (Friard & Gamba, 2016). An ethogram was created to code for behaviors (see Table 3). Behavioral modifiers were added to make note of the part of the body used, the feature of the box touched, the compartment of the box touched, and if the compartment was baited at the time of the behavior. The total session duration was measured from when the elephant first placed two legs over the stall threshold until the session was stopped because 1) the elephant solved the final door & retrieved the reward or 2) the elephant was shifted out of the testing stall without having solved all the doors.

Table 3. Ethogram of all observed behaviors exhibited by elephants during puzzle box sessions, including possible body part used when there was more than one option.

Behavior	Possible Body Part Used	Definition
Pushing	1) trunk tip, 2) trunk middle, 3) trunk base, 4) head, 5) body	Touching with visible pressure on box surface, typically accompanied by a swift approach and/or a noisy impact
Sliding	1) trunk tip, 2) trunk middle, 3) trunk base, 4) head, 5) body	Moving door either left or right
Rubbing	1) trunk tip, 2) trunk middle, 3) trunk base, 4) head, 5) body	Directed pressure moving in one direction across half of the width of the box or the height of the box; continuous, repetitive back and forth pressure on the box
Hitting bout	1) trunk tip, 2) trunk middle, 3) trunk base, 4) head, 5) body	Forceful rhythmic contact, separated by no more than 2 seconds, on approximately the same location of the surface of the box
Blowing		Releasing air audibly from the trunk when interacting with box
Grasping		Using trunk to curl around or using trunk tip to grip an extended feature of the box
Reaching		Extending trunk over the top/around the side or under the bottom towards the back of the box
Bipedal		Elephant is in upright position on back two legs
Mouthing		Using mouth or tongue to apply pressure on to surface of the box
Pulling		Elephant moves trunk inwards towards themselves and/or downward while grasping chain
Playing bout		Elephant manipulates door in a repetitive motion until movement stops for 4 seconds; this applies to an empty compartment door
Interaction with the box		Time from when individual first contacts the box until contact stops for at least 4 seconds

Reliability

A 20% random sample of the videos were re-coded by another observer to check inter-rater reliability using intraclass correlations (ICC). There was excellent agreement between coders for latencies (ICC(1)=0.92, $F(17,18) = 24.4$, $p<0.001$) and durations (ICC(1)=0.99, $F(6,7)$

= 130, p<0.001). Good agreement for all other behaviors coded was determined using Cohen's

kappa (kappa = 0.69, p <.0.001).

Analyses

All data were analyzed using SPSS v. 25 software and R v. 4.0.3. We used non-

parametric tests to take into account a small sample size and non-normal distribution. We ran

Kendall tau rank correlations in SPSS to assess the association between behavioral measures at

the session-level and success, as well as to determine whether behavioral measures were

independent. We could not look for correlations on a subject-level due to an insufficient number

of observations.

We also ran linear mixed effects models in R using the lme4 package to assess if success

could be predicted by one or more of the behavioral assays, accounting for interdependency

between the measures simultaneously. This method was used to account for non-independence

and missing values in the session-level data. Each model included subjects as a random effect

and behavioral assays as fixed effects. For successive models, we removed the behavioral assays

with the least significance on the previous model. Chi-square tests were used to check the

validity of each successive model created after the removal of a behavioral assay.

To examine whether social access may affect problem-solving technique, we looked at

the similarities in exploratory motor diversity across the related female herd and the extended

social group. We created social networks based on the physical access the elephants had to each

other in their enclosures.

To assess learning, we compared latency to solve the first door in the first session to the

second session in Phase 1 in which all elephants received the same fully-baited puzzle box. We

also compared time interacting with the box between the second session of Phase 1 and the first

session of Phase 2 to determine whether the elephants took more time when faced with the new puzzle box.

Results

All subjects opened at least one of the push doors in Phase 1, which permitted them to move on to Phase 2. Throughout Phase 2, six (100%) elephants opened the push and slide doors while only four (66.7%) elephants opened all three, including the pull door. When looking at the elephants' first solutions, five (83.3%) initially opened the push door and one (16.7%) initially opened the pull door. The second solution for four (66.7%) of the elephants was the slide door, for one (16.7%) was the pull door, and for another one (16.7%) was the push door. Two elephants did not solve the pull door in their first session; when tested solely on this door in their second session, both failed to solve it.

The data are incomplete for a few elephants. One elephant, Asha, did not solve any of the doors for her initial two Phase 2 sessions, although her dependent calf opened some of the doors. She was given an additional third session in which she opened the push, slide, and pull door in that order. Due to an error moving elephants between stalls, Achara and Asha participated in their first session of Phase 1 together in the stall adjacent to the box. Therefore, both Achara and Asha do not have neophilia scores and are missing a motivation score for their first session.

Table 4. Descriptive statistics for the session-level measures.

	Minimum	Maximum	Mean	Standard Deviation
Persistence (Time interacting with box/session time, N=25)	0.087	0.838	0.393	0.239
Motivation (sec, N=23)	0.500	35.757	7.930	11.195
Exploratory Motor Diversity (N=25)	3	17	9.76	3.897
Success (Doors solved/total doors available, N=25)	0	1	0.707	0.400
Latency to Solve First Door (sec, N=19)	1.248	103	26.126	25.100

Boxplots were used to examine our continuous variables: motivation (see Figure 8) and latency to solve the first door in a session (see Figure 9). Motivation scores do not appear normally distributed, with a skew towards shorter time values. Although we found outliers for both measures, these data points were not removed in order to maintain statistical power. There was also variation in exploratory motor diversity across subjects and between phases (see Figure 10). Neophilia measures (see Figure 11) were not included in any statistical analysis because we had so few observations.
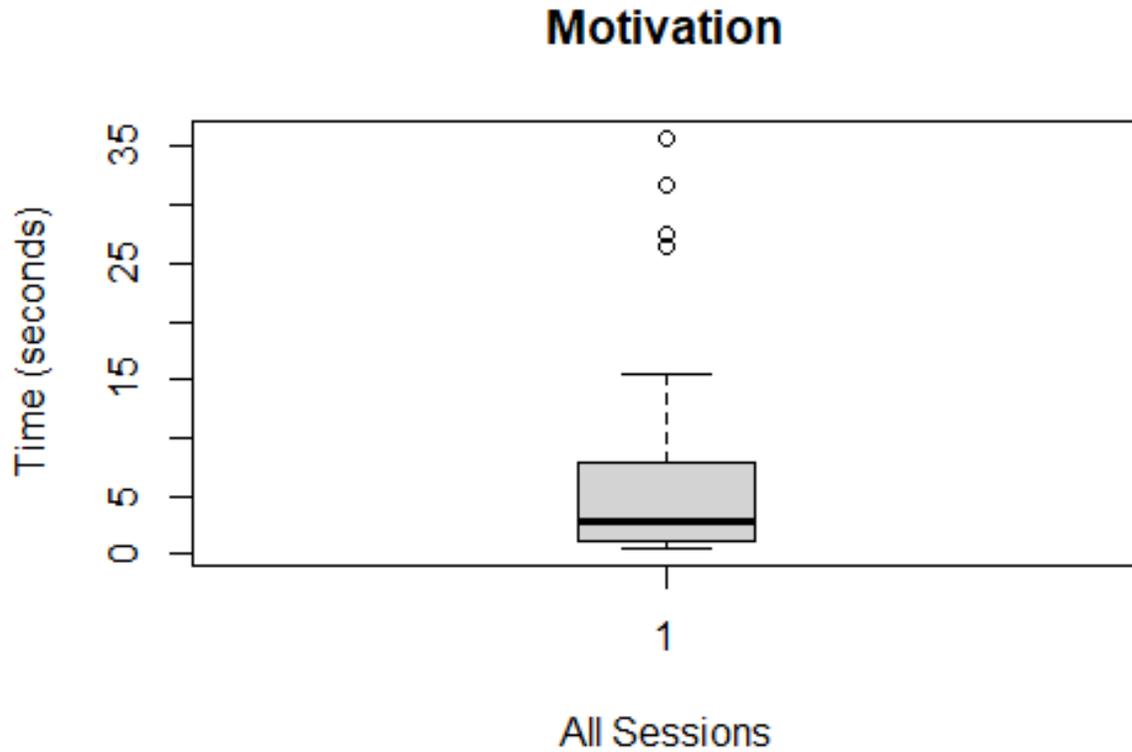
Figure 8. Boxplot of session-level motivation scores. The bold line within the box represents the median at 2.749, with the lower (Q1) and upper (Q3) quartiles below and above this line, respectively. The minimum and maximum scores are indicated by the bottom and top whisker edge, respectively. Four outliers are represented by circles.
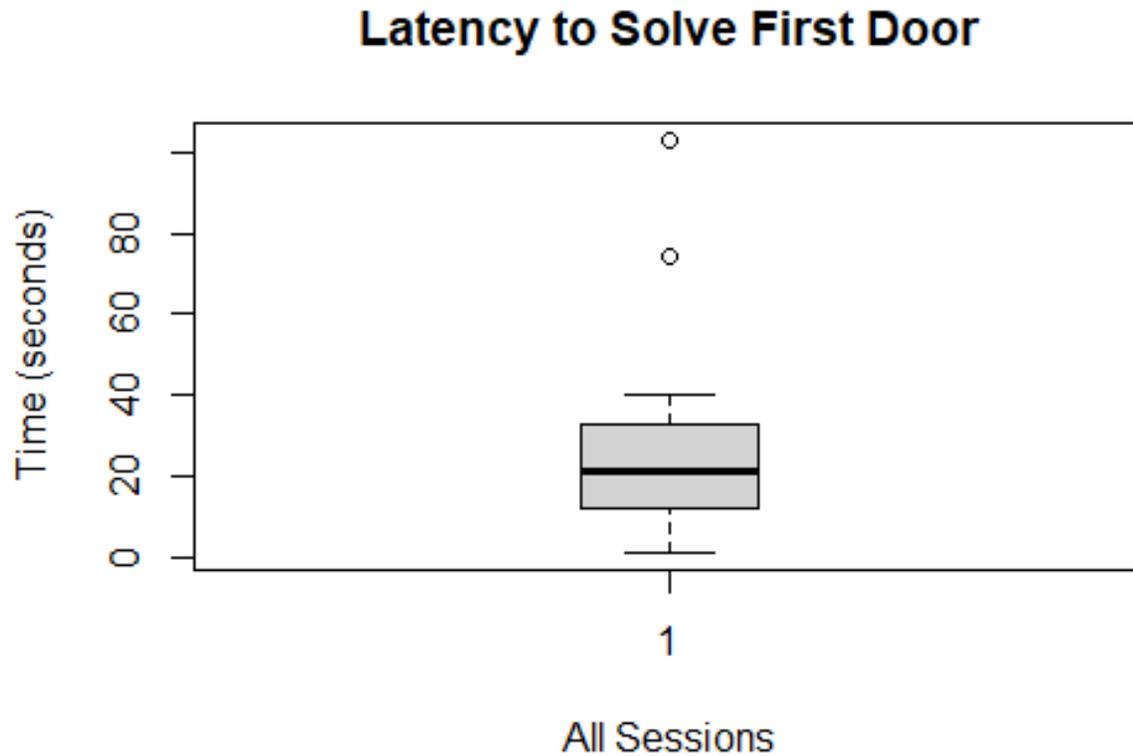
Latency to Solve First Door

Figure 9. Boxplot of latencies to solve the first door in a session. The bold line within the box represents the median at 21.5, with the lower (Q1) and upper (Q3) quartiles below and above this line, respectively. The minimum and maximum scores are indicated by the bottom and top whisker end, respectively. Two outliers are represented by circles.
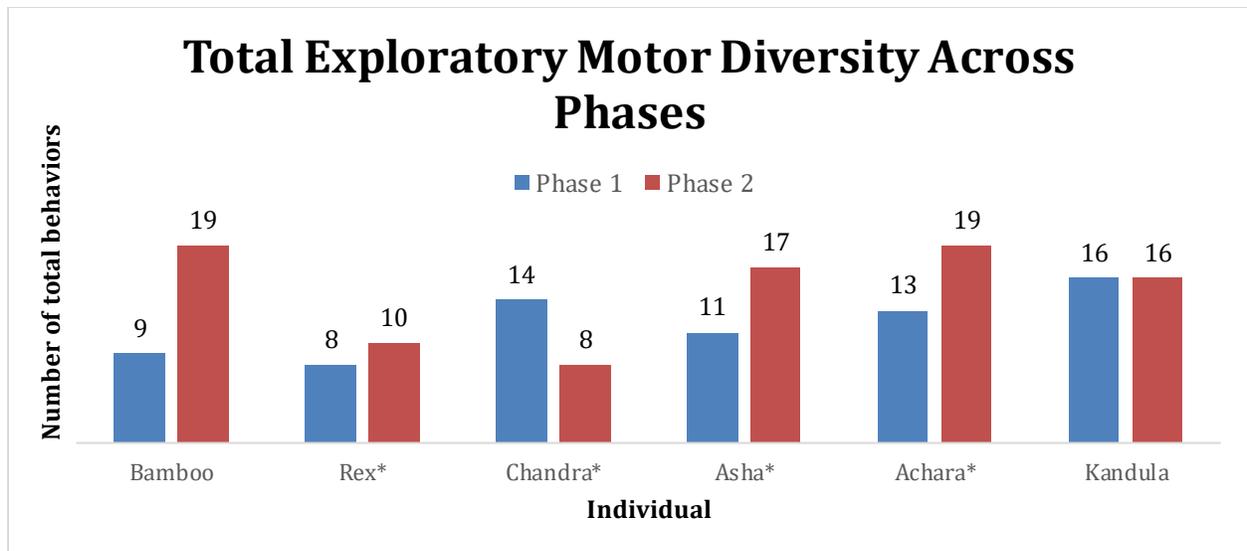
Figure 10. Exploratory motor diversity for all subjects for both phases. Elephants that achieved the highest innovation score of 3 are noted with an asterisk.
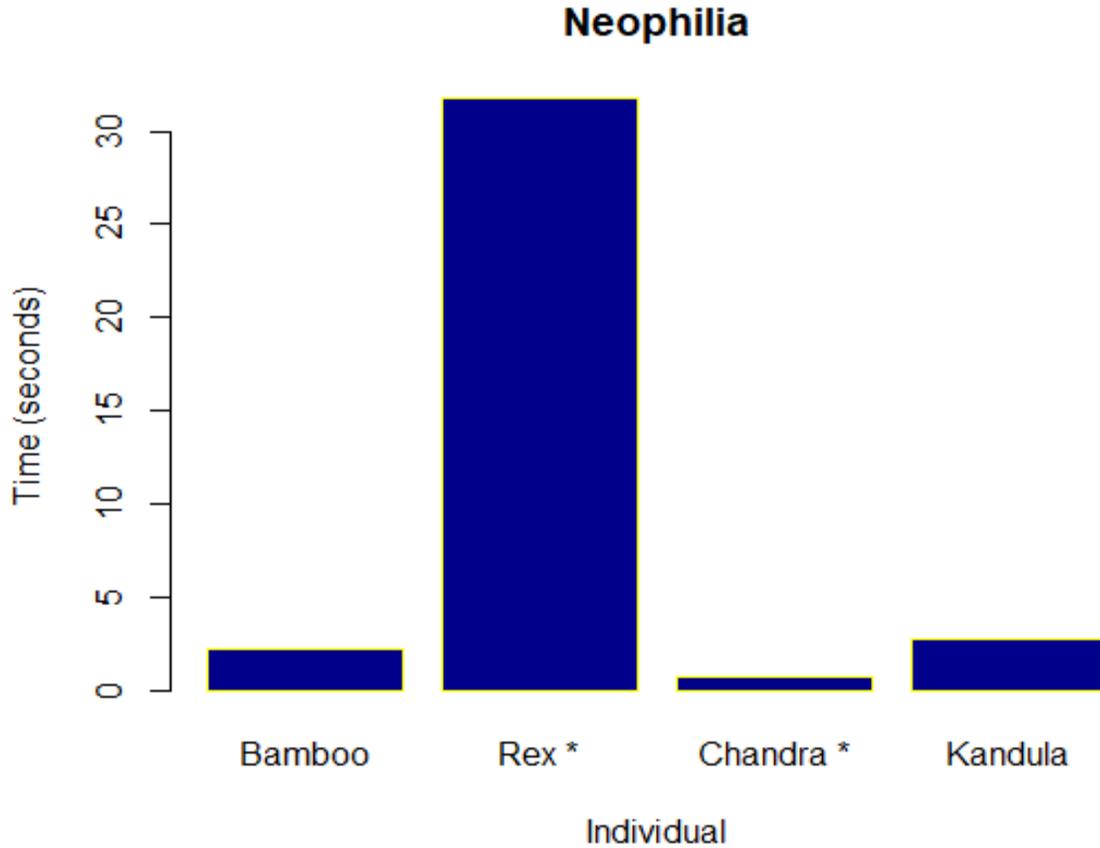
Figure 11. Neophilia scores for four of the elephants. Elephants that achieved the highest innovation score of 3 are noted with an asterisk.

To assess the behavioral assays and their degree of independence, we examined Kendall tau rank correlations between the session-level measures of persistence, motivation, exploration diversity, and success (see Table 5). After adjusting significance levels using the Bonferroni correction, we found a significant correlation between persistence and success (r = 0.458, p < 0.01; see Figure 11).

Table 5. Correlation matrix of raw per session behavioral measures from Table 2.

	Persistence	Motivation	Exploratory Motor Diversity	Success	Latency to Solve 1st Door
Persistence	1.00	-.343	.014	.458*	.036
Motivation		1.00	-.233	-.066	-.073
Exploratory Motor Diversity			1.00	-.144	-.037
Success				1.00	.067
Latency to Solve 1st Door					1.00

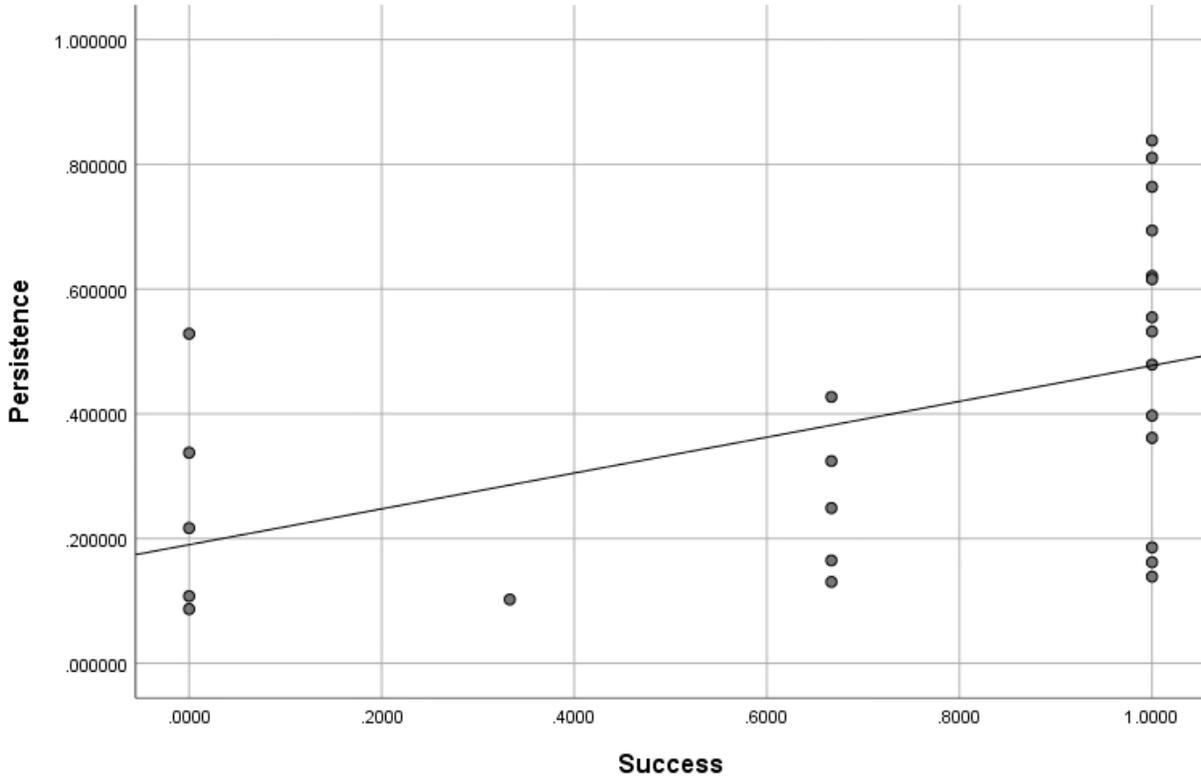*Indicates $p < 0.01$, Kendall's tau rank correlation

Figure 11. Session-level relationship between persistence and success ($p < 0.01$)

We used linear mixed effects modeling to test whether one or multiple behavioral

measures could predict success on a session-level. Our first model (PMDL) included persistence,

motivation, exploratory motor diversity, and latency to solve the first door as fixed effects. Due to a lack of a significant effect, the next model (PMD) was created dropping the measure of latency to solve the first door (p_r = 0.297). In the PMD model, there was a slightly significant positive effect from persistence (p_r = 0.095). The next model (PD) dropped the measure of motivation (p_r = 0.3491). In the PD model, persistence had a significant positive effect (p_r = 0.00493) while exploratory motor diversity had a negative effect but this was not significant (p_r = 0.06928). For the final model (P), exploratory motor diversity was dropped, and persistence had a significant positive effect on success (p_r = 0.00975). Model reduction was justified using chi-square testing to compare the removal of each behavioral measure. Removing latency to solve first door ($\chi^2(1)$ = 1.026, p=0.3124; see Figure 12), motivation ($\chi^2(1)$ = 0.0593, p=0.8075; see Figure 13), and exploratory motor diversity ($\chi^2 (1)$ = 0.0986, p=0.7535; see Figure 14) did not significantly make the simpler model worse. When persistence was removed, the simpler model was significantly worse ($\chi^2(1)$ = 15.918, p<0.001).

To visualize the significance persistence had on the odds of success, the z-transform of persistence as the predictor was used to construct a graph of the final Pz model (see Figure 15). The graph displays data points that are the log odds of success for each elephant in each session. The intercept of the regression line represents the log-odds of success, which was 1.751 when persistence was at its mean value (z = 0). The slope of the regression line represents the log-odds of success, which increased by 2.032 for each increase of 1 standard deviation in persistence. At the mean persistence level, the estimated probability of success is 0.85; when the persistence level is +1 SD, it is 0.98; and when persistence level is -1 SD, it is 0.43.
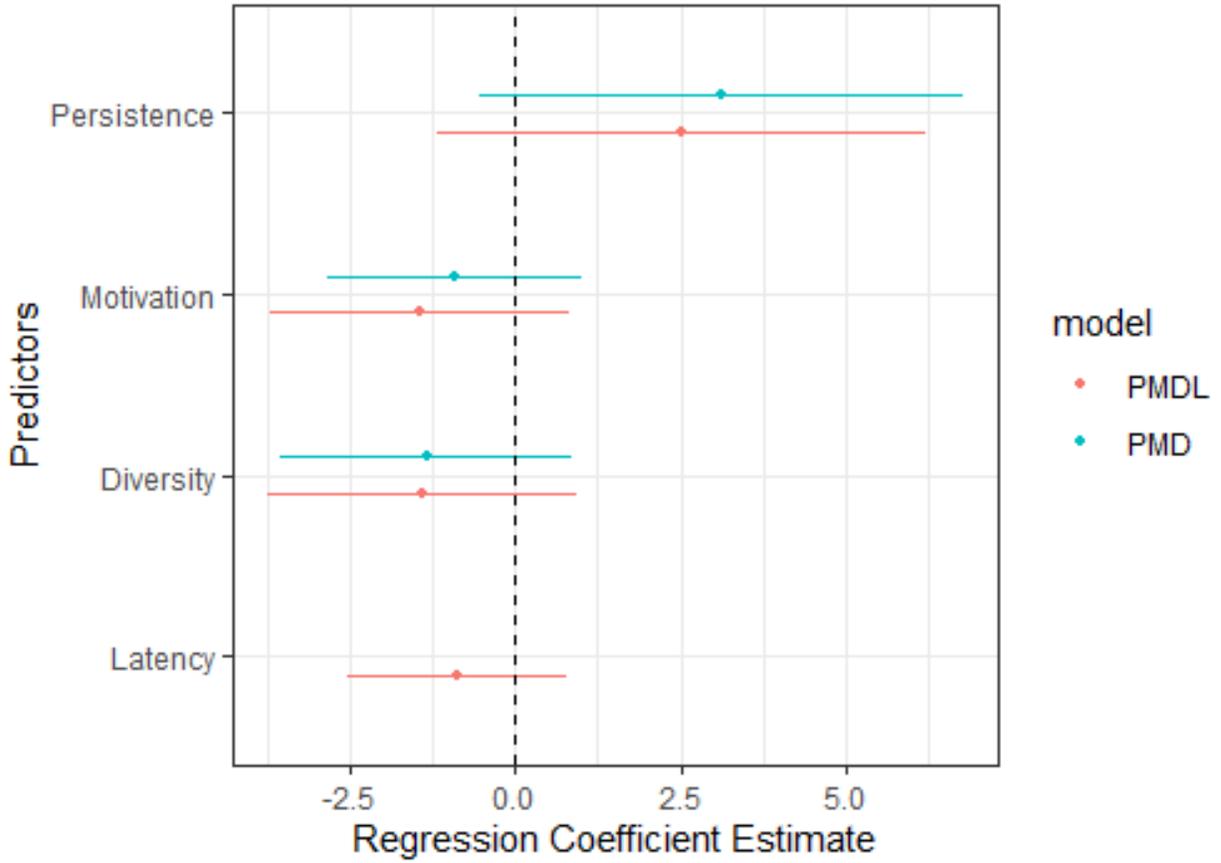
Figure 12. Odds ratio comparison of the first model built using persistence, motivation, exploratory motor diversity, and latency to solve first door (PMDL) and the second model (PMD) dropped latency to solve first door. There are no significant effects from either model.
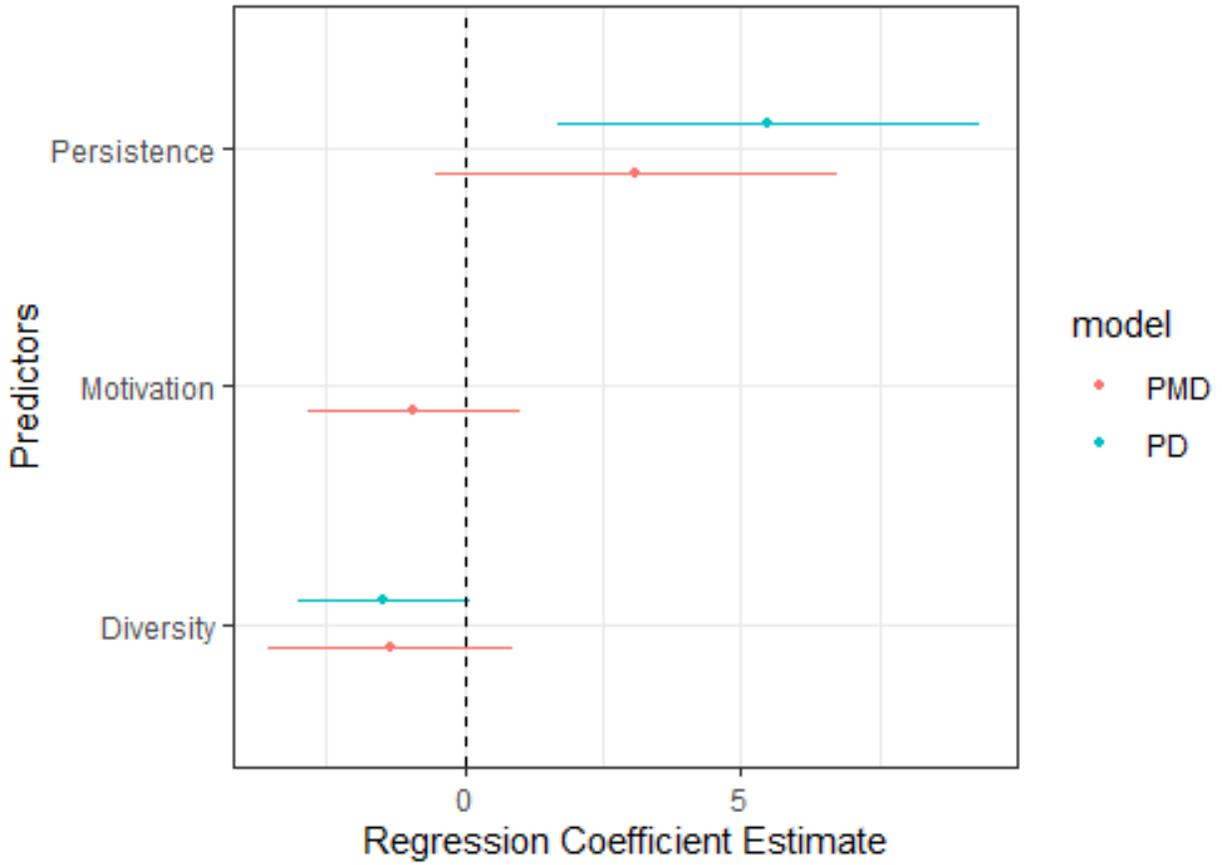
Figure 13. Odds ratio comparison of the second model (PMD) and the second model (PD) dropped motivation. There is a positive effect from persistence, as well as a slight negative effect from exploratory motor diversity in the PD model.
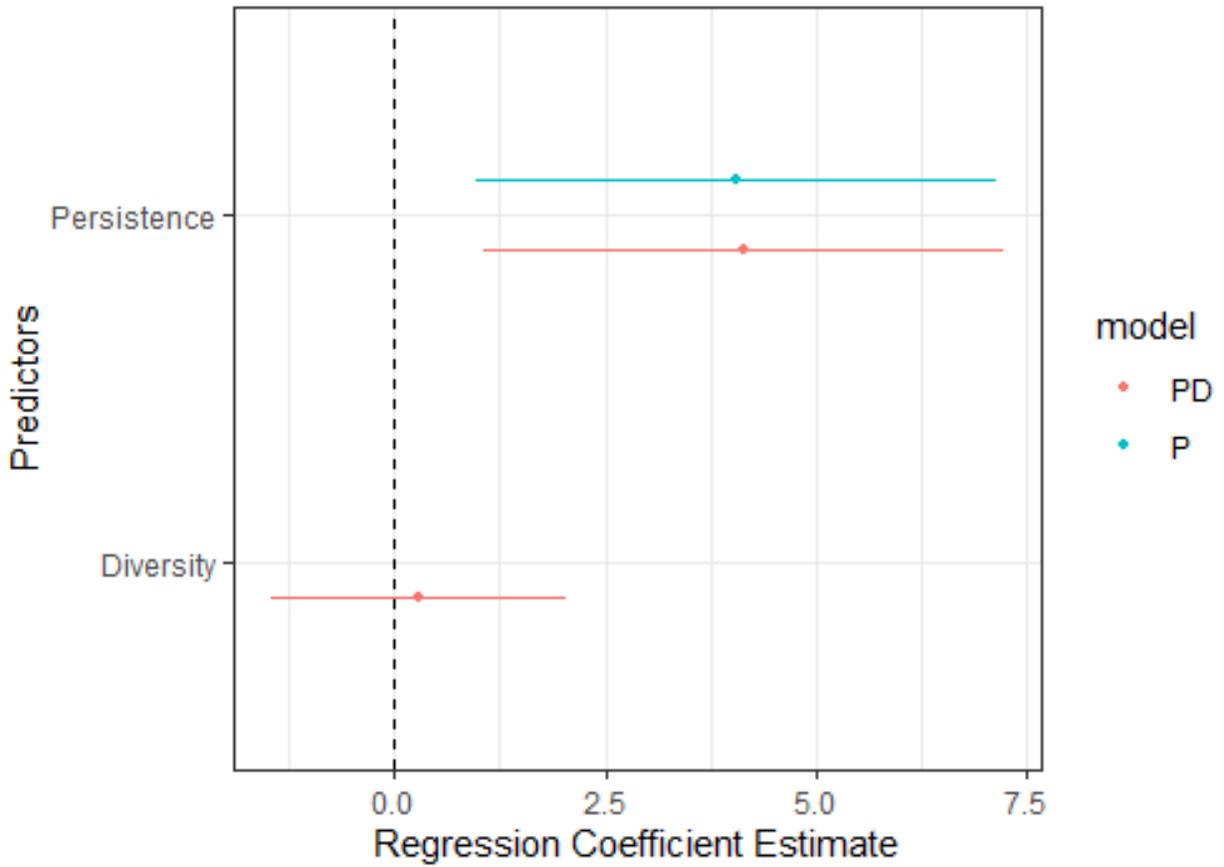
Figure 14. Odds ratio comparison of the third model (PD) and the fourth model (P) dropped exploratory motor diversity. There is a positive effect from persistence in the P model.
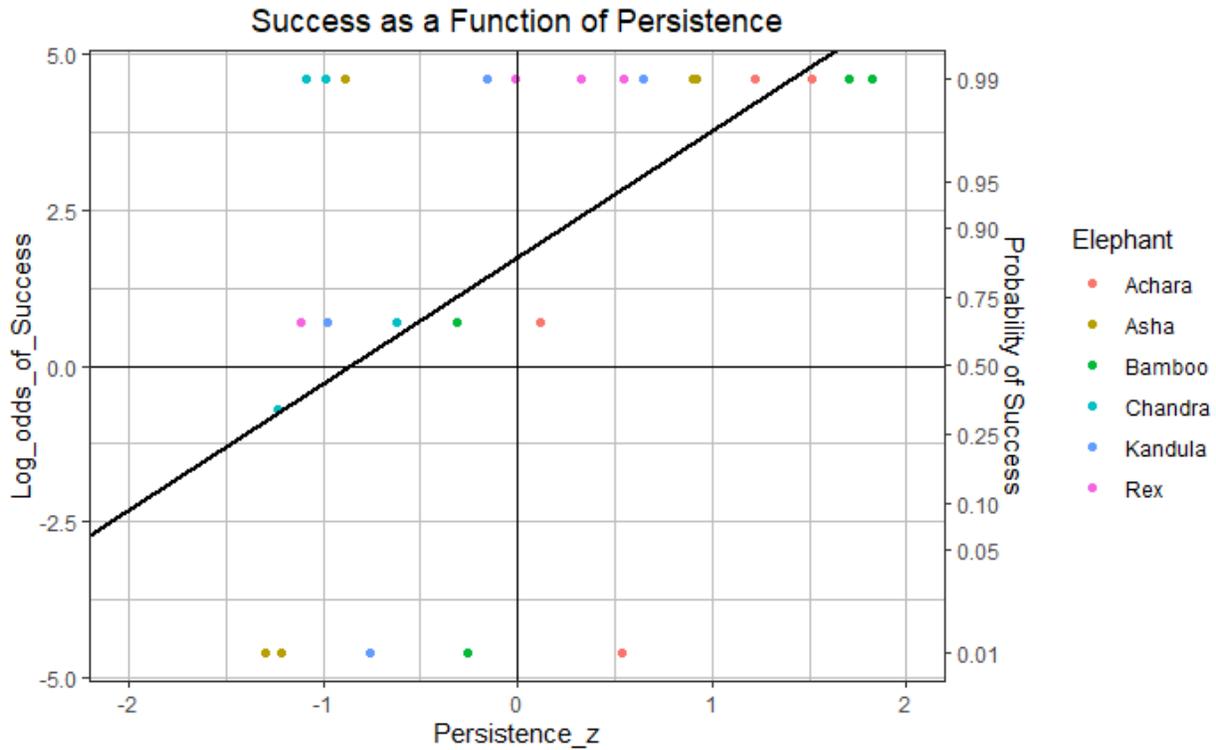
Figure 15. One-predictor model (Pz) using z-scored persistence values. The estimated probability of success was 0.85 at the mean persistence level.

We could not test the effect of sex or place of origin on success with the limited sample size. Descriptively, there was one wild-born female and one captive-born male who were unable to solve the pull door. All the related individuals living together were able to achieve the highest innovation score, as well as the related male subject living alone. The two individuals with social access but no kinship to the herd both reached a maximum innovation score of 2. Social networks showing shared exploratory behaviors were created with nodes representing individual elephants and edge width indicating the possibility of interaction (0.5 or 1) for Phase 1 (Figure 16) and Phase 2 (Figure 17). The edges are labeled with the number of matching exploratory behaviors.

Figure 16. Social network examining similar behaviors across social groupings for Phase 1. Color of node represents social group (yellow: member of related female herd; red: non-related member of the herd; green: typically housed alone). Shape of node represents innovation score (red: 2; yellow: 3).
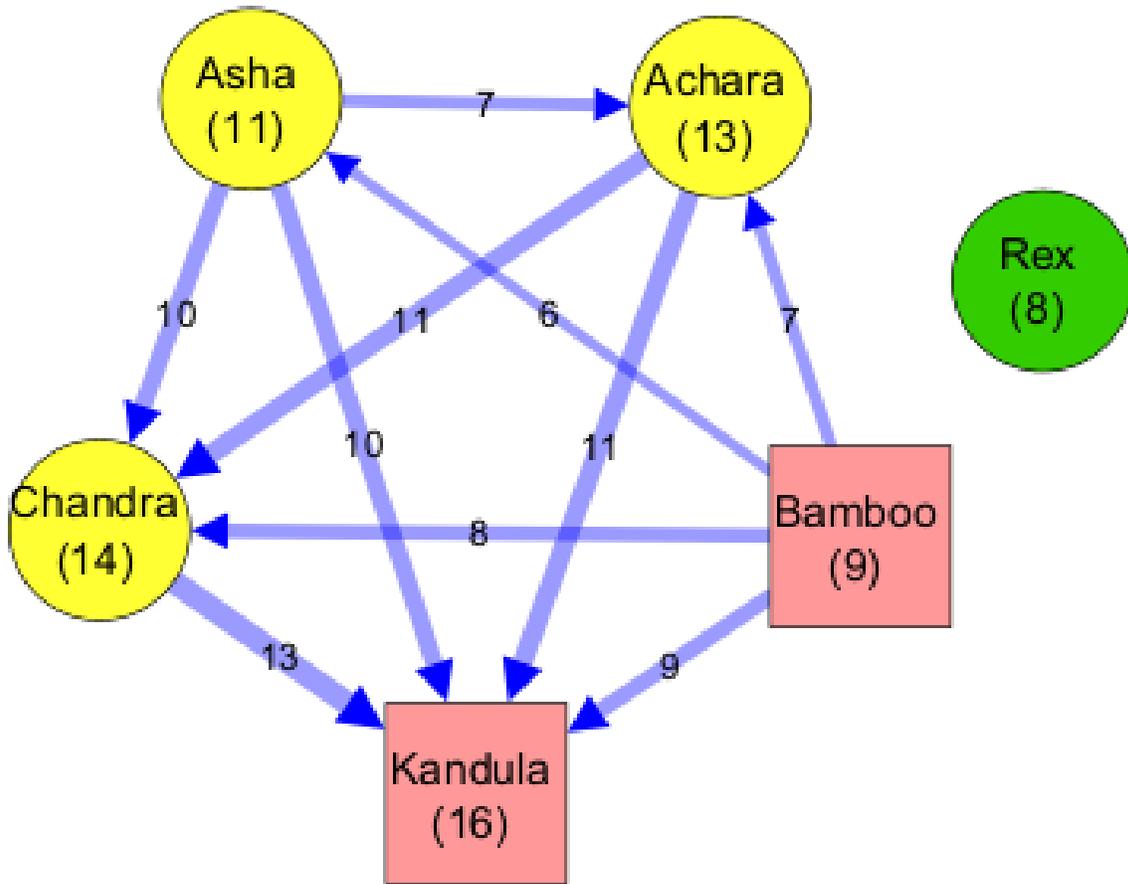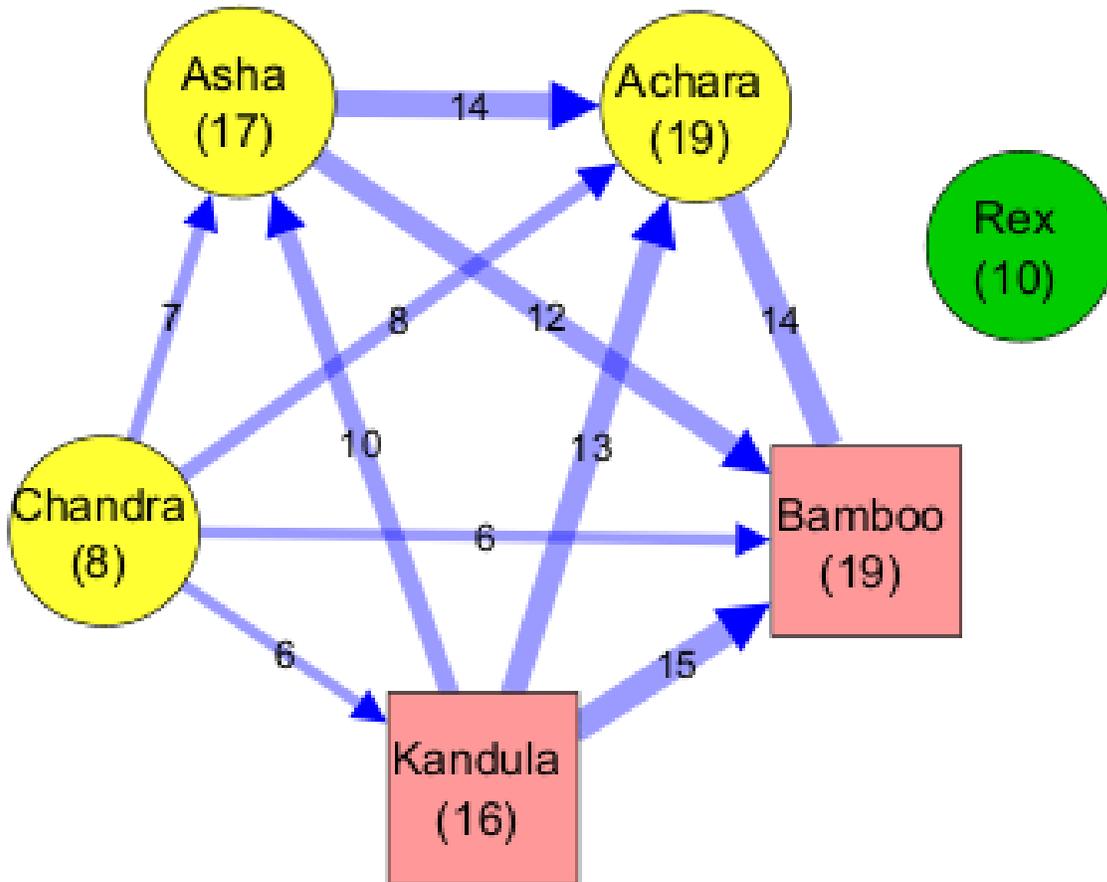
Figure 17. Social network examining similar behaviors across social groupings for Phase 2. Color of node represents social group (yellow: member of related female herd; red: non-related member of the herd; green: typically housed alone). Shape of node represents innovation score (red: 2; yellow: 3).

Elephants showed inter-individual differences in how quickly they were able to solve each compartment. Three out of the four elephants with complete data showed a decrease in latency to solve the first door in Phase 1 (see Figure 18). Excluding Asha, all three elephants given the fully baited box for both Phase 2 sessions showed a decrease in latency to solve the first door (see Figure 19).
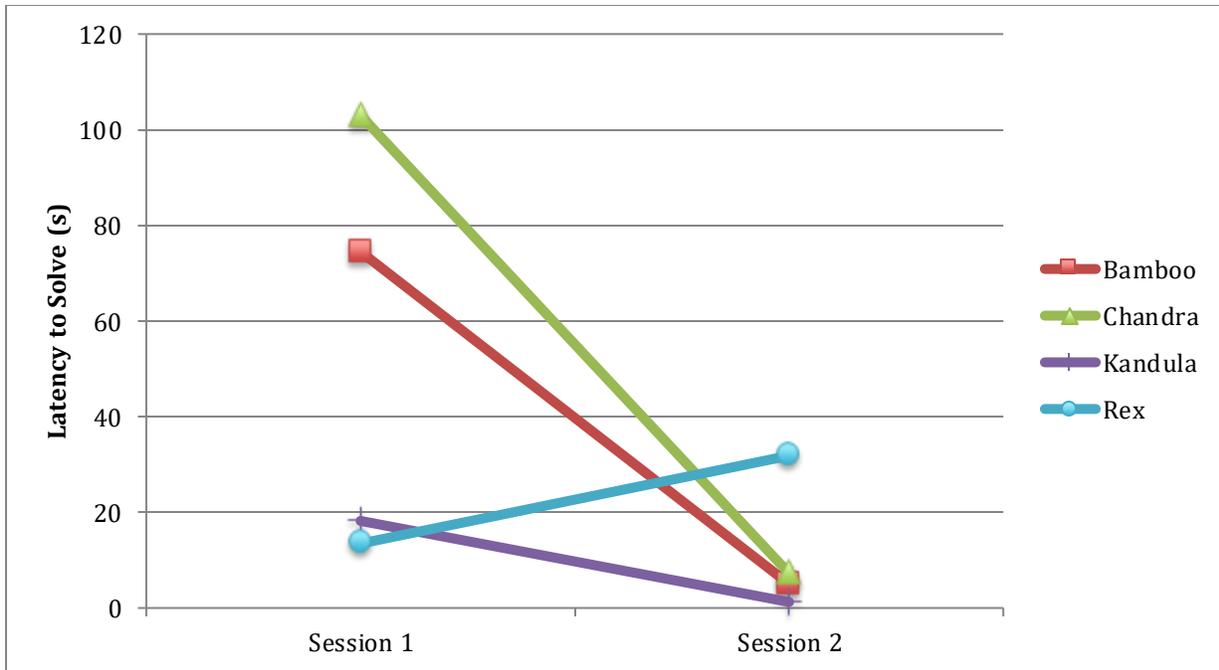
Figure 18. Latency to solve the first door in each session of Phase 1.
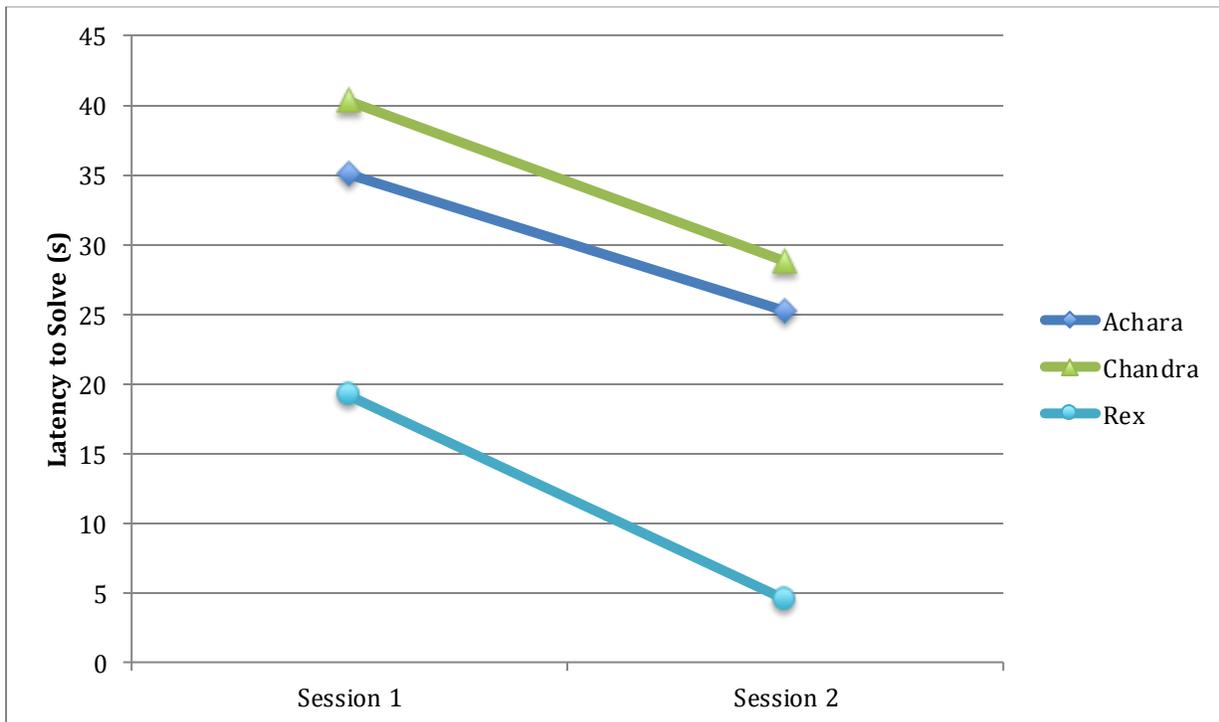
Figure 19. Latency to solve the first door in each session of Phase 2.

Time interacting with the box, or working time, also differed across elephants between the end of Phase 1 and the beginning of Phase 2 (see Figure 20). Two out of the three elephants that solved the entire box in the first session of Phase 2 showed an increase in working time from the second session of Phase 1. The two elephants that failed to open the pull door showed a decrease in working time. The elephant that solved zero doors in her first session of Phase 2 also showed a decrease in working time.
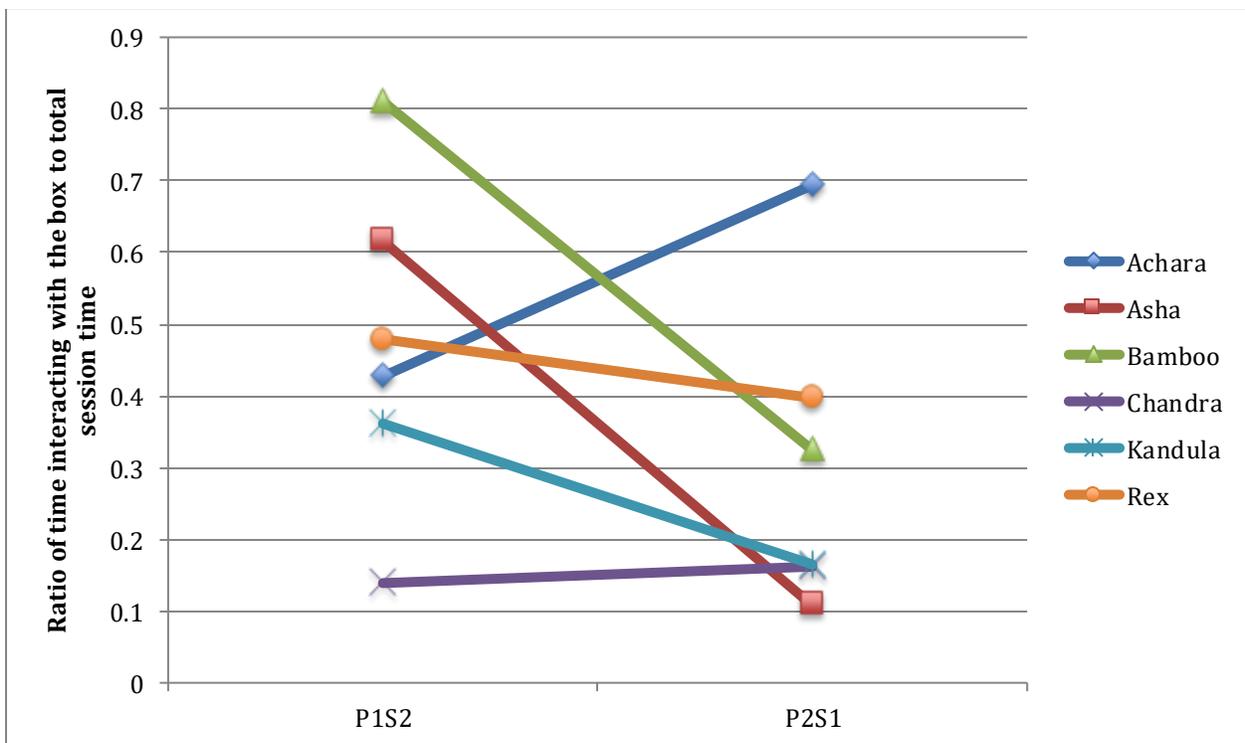
Figure 20. Time interacting with the box from the end of Phase 1 (P1S2: Phase 1 Session 2) to the beginning of Phase 2 (P2S1: Phase 2 Session 1). Achara, Chandra, and Rex solved all three doors in P2S1; Bamboo and Kandula failed to open the pull door in P2S1. Asha failed to open any door in P2S1.

Discussion

This study demonstrated the first empirical evidence that Asian elephants can repeatedly innovate, with four individuals opening all three types of doors. Persistence was positively correlated with success within a session, such that success on a task increased with greater persistence. This association should be considered with caution considering our small sample size and multiple observations from the same individual, but it does give insight into which behavioral measure may serve as a possible predictor for success in Asian elephants.

The simplest model created using mixed effects analysis also showed persistence as the sole behavioral assay that predicted success, with an estimated probability of success of 0.85 at the mean persistence level (see Figure 15). This supports previous research that found persistence to be a positive predictor of success (Benson-Amram and Holekamp, 2012) and repeated innovation (Johnson-Ulrich et al., 2018). Although not significant in the final model, there was an interesting interaction found in the PD model (see Figure 15) between persistence and exploratory motor diversity. When persistence was controlled for, a lower exploratory motor diversity was predictive of success. This is surprising as it contradicts previous research that found greater motor diversity predicted success (Benson-Amram and Holekamp, 2012; Benson-Amram et al., 2013; Griffin, Diquelou, and Perea, 2014; Griffin and Diquelou, 2015), although it may be a result specific to our small study group. It is possible that individual elephants used a more precise & deliberate technique when interacting with the box and thus, did not need to resort to more general behaviors such as pushing the entire box with the body.

When comparing similar behaviors for Phase 1, individuals shared the most behaviors with the elephant with the highest motor diversity, Kandula, who had a score of 16. When examining the behaviors used to actually solve the push door in Phase 1, we saw both Asha and

Chandra successfully exhibit trunk hitting and body pushing. In Phase 2, however, we did see a split between the related female herd and the two non-related individuals with more restrictive access to the main herd. Both Achara (a member of the related female herd) and Bamboo had a motor diversity score of 19, which was the highest observed in Phase 2. The other members of the herd (Asha and Chandra) shared more similar behaviors with Achara while Kandula shared more similarities with Bamboo. Across solving methods in Phase 2, we did see some similarities within the herd: Chandra and Achara both used the trunk middle to grasp the chain and solve the pull door; Asha, Achara, and Kandula opened the slide door with a swinging trunk motion. It must be restated here that both Bamboo and Kandula were unable to open the pull door, and this may be the reason for their highly similar behavior. It is interesting to note that Rex–the only elephant usually kept alone–showed the lowest motor diversity and was the only elephant not seen exhibiting mouthing behavior on the box, yet he was able to solve all three types of doors.

The indirect method used to assess the influence of social interaction on problem-solving technique was clearly not as robust as specifically testing for social facilitation and/or learning. For instance, a study was conducted with African elephants at the San Diego Zoo who participated in an observer-demonstrator experiment using a multi-solution feeding apparatus (Greco, Brown, Andrews, Swaisgood, & Caine, 2013). The researchers did not find support for elephants copying the methods used by the model elephant; they did, however, see greater initial interest and focus on the foraging apparatus in the modeled condition vs. unmodeled condition. For the present study, it is possible that members of the related female herd could hear/smell each other interacting with the box, and this reassured and/or motivated individuals to interact with the box themselves. Research on the social organization of elephants in zoos has shown that social interactions are related to age, personality, presence of calves, and relatedness to others in

the herd; findings such as these support the idea that elephants under human care should be provided with the most appropriate social environment possible (Williams, Carter, Hall, & Bremner-Harrison, 2019). Such an environment could allow for species-typical behaviors to emerge and persist within social groups.

The results of this study support the prediction that elephants were learning during this experiment. All elephants with latencies to solve the first door in a session–except Rex in Phase 1–showed a decrease from the first to the second session within a phase. Unlike the results found when studying octopus problem-solving (Richter, Hochner, & Kuba, 2016), elephants' working time did not increase when they were presented with a new puzzle in Phase 2. It did appear that the two elephants, Achara and Chandra, who solved all three doors in their first Phase 2 session, spent slightly more time interacting with the box than they did in the second session of Phase 1.

During coding, we also noticed "nonsense behaviors" (e.g., pushing on the pull door), or actions that could not be used to open a specific door, similar to Auersperg et al (2011)'s classification of ITAs, or ineffective tool actions. The number of "nonsense behaviors" on slide and pull doors in the present study decreased for three elephants from Phase 2's first session to the second session; these nonsense behaviors were, for the most part, centered on still-baited compartments. Elephants were mainly using trial-and-error learning, exhibiting multiple different methods to solve the doors; although a particular method might have worked in the first session, this was not necessarily repeated in the second session. Some elephants solved the door with one direct move, however, we could not infer that this was insightful problem-solving as we did not know the history of each elephant.

Because the sample size was limited, it is possible to discuss each individual's pattern of behaviors in relation to the puzzle box. Age, rank, and sex, as well as an individual's life history,

may all affect problem-solving and innovation ability. It must be noted that Kandula was entering the hormonal state of musth (see Poole, 1987 for more information) during Phase 2 testing; because this state is associated with significant behavioral changes, this could have resulted in more rubbing and behaviors using the head.

Behavioral flexibility was found among all subjects, notably in the different ways they solved the doors as well as the variation in exploratory motor diversity across the four sessions. Referring to Figure 10, we can see that most of the elephants increased in exploratory motor diversity from Phase 1 to Phase 2. Achara and Bamboo, the elephants with the highest motor diversity scores, added six and ten behaviors to their repertoire from Phase 1 to Phase 2, respectively. Not counting slide or pull behaviors, Asha dropped two behaviors and added five new behaviors from Phase 1 to Phase 2; Kandula dropped two behaviors and added one behavior; Rex dropped two behaviors and added two behaviors. Chandra decreased in exploratory behaviors from Phase 1 to Phase 2, and only added slide and pull behaviors in Phase 2. Within this sample, individual variation was found across all our behavioral assays and favored behaviors as well as solving behaviors described in Table 8.

Elephants have been documented using tools on occasion, including modifying branches to swat flies (Hart et al., 2001) and manipulating water to reach food (Barrett & Benson-Amram, 2020). The elephants in this study did not have access to any external tools, but a few individuals used blowing to move treats within the compartment. Elephants have been shown to use blowing to acquire inaccessible food as well as position food for easy grasping (Mizuno, Irie, Hiraiwa-Hasegawa, & Kutsukake, 2016), so it is not surprising that we observed this tactic in this study. One elephant, Bamboo, blew open one of the push doors while another elephant, Asha, used blowing extensively while interacting with the box from behind.

When coding behaviors, the variability in trunk tip morphology was particularly striking. Asha specifically had a noticeable slit on her left nostril due to an injury she suffered as a calf, which may possibly contribute to greater trunk stiffness. According to her caretakers, she cannot completely close the slit when grabbing items; however, that does not seem to affect her precision when opening, grabbing, and manipulating objects but does seem to affect her ability to "vacuum" food off the ground. These sorts of differences would very likely affect how the elephant went about solving the door, particularly the pull door that required precise trunk tip movement within a tight space. Asha, notably, opened the pull door by using her trunk tip to grasp the chain unlike the other elephants who used the trunk middle. It is difficult to say how much of a role trunk-tip morphology may have had on how elephants attempted to open doors, but based on the observed variation (e.g., some elephants placed their trunk opening flat on the box while others used more of a pursed position when investigating), it is likely it was important.

Table 8. Summary table of individual variation among six subjects.

Individual	Most Commonly Used Behaviors	Solving Behaviors	Stereotypical Behavior	Highlights
Bamboo	Grasping, mouthing, pushing, blowing, hitting, and rubbing; twisting bolts; investigating with trunk tip flat on	Trunk tip pushing; trunk tip/middle hitting blowing; trunk base rubbing on slide door	Some circling with head shaking	Highest motor diversity; failed to open pull door; highest persistence in a session
Rex	Pushing, blowing, and rubbing; pulling bolts; light tapping; investigating with pursued trunk tip; controlled trunk entrance into opened compartments; no mouthing behavior	Opened from behind; trunk tip/middle/base pushing; grasping lip and sliding; sliding lip with trunk tip edge; pull with trunk middle	Swaying	Least neophilic response; lowest motor diversity; most successful subject (91.7%)
Chandra	Lots of finger activity including reaching between compartments and tapping all over; investigating with trunk tip flat on	Trunk middle hitting; trunk tip/middle and body pushing; pull with trunk middle	Some immobility and circling	Most neophilic response; lowest motivation in a session; longest latency to solve first door in a session
Asha	Blowing, hitting, and pushing; investigating with pursed trunk tip (V-shape)	Opened from behind; blowing; trunk tip and body pushing; trunk base hitting; swinging trunk middle opened slide	Recurring motion of touching trunk tip to box bottom corner	Least successful subject; highest motivation in a session; lowest persistence in a session
Achara	Blowing, mouthing, rubbing, and pushing; some interaction with box from behind; finger tapping and inserting between compartments; standing	Trunk tip/middle pushing; opened from behind; swinging trunk middle opened slide; pull with trunk middle	N/A	Highest motor diversity; exhibited playing behavior with pull door, as well as charging and spinning
Kandula	Pushing, rubbing, hitting, blowing, and mouthing; hitting with backside of finger; resting trunk over box while using trunk tip	Trunk tip/middle and body pushing; swinging trunk middle opened slide	N/A	Failed to open pull door; shortest latency to solve first door in a session

These findings provide greater insight into the problem-solving abilities, innovative capacity, and overall behavioral flexibility of Asian elephants. Since persistence and exploratory motor diversity were related to problem-solving in zoo-housed elephants, these may also be important traits when considering future cognitive testing in both captive and wild Asian elephants. These findings also support the need to study individual variation within species, as there were clear behavioral and morphological differences in this study that affected performance. Specifically, for populations under human care, it may be possible to cater to the individual when considering enrichment items and social access. Similarly, human-wild elephant conflict mitigation programs can benefit from individual behavioral profiles and understanding the social relationships between wild elephants (Srinivasaiah, Anand, Vaidyanathan, & Sinha, 2012; Mumby & Plotnik, 2018).

This study also has implications for convergent cognitive evolution research. We used a common paradigm for this study; thus, results are comparable with other species tested with foraging puzzle boxes, particularly those with multiple solutions. Our findings support the idea that expressions of cognition in elephants may be similar to those in great apes and corvids (Seed, Emery, & Clayton, 2009; Van Horik, Clayton, & Emery, 2012; Roth, 2015). Complex cognitive capacities like innovation may be found in distantly related species who share other traits such as large brains and complex sociality (Van Horik et al., 2012). Behavioral flexibility–which we saw in this study played a role in innovation–can also play a role in fluid social dynamics and navigating human-altered spaces. Asian elephants, for example, can form groups with different matrilines in response to habitat fragmentation (Vidya, Varma, Dang, Van Thanh, & Sukumar, 2007) or alter their home ranges and movement patterns to avoid human encroachment (Alfred et al., 2012). Like humans, elephants show great adaptability, social

dynamics, and complex cognition, which gives us cause to reevaluate the evolution of cognitive abilities across evolutionarily distant species and further explore cognition in other nonhuman animals with similar traits.

This study lays a foundation for future cognitive studies in Asian elephants, both under human care and in the wild. These findings provide greater insight into the problem-solving abilities, innovative capacity, and overall behavioral flexibility of Asian elephants. Since persistence and neophilic behavior were related to problem-solving and innovation in zoo-housed elephants, these may also be important traits when considering innovation in wild elephants and its role in human-elephant conflict. These findings also support the need to study individual variation within species, as there are behavioral and morphological differences that can affect their well-being. With populations under human care, catering to the individual can positively influence overall welfare as well as social access. Future conservation research with wild Asian elephants should also continue to focus on individual variation as this can lead to models that predict behavior and thus, decrease human-elephant conflict.

Glossary

Term	Definition
Behavioral flexibility	The ability to alter behavior in response to changing environments and inhibit previously successful behavior[a]
Innovation	The ability to invent novel behaviors or use pre-existing ones in novel contexts[b]
Inhibitory control	The ability to resist performing previously learned behavior when it is inappropriate, such that the behavior will yield no reward[c]

[a]Coppens, de Boer, & Koolhaas, 2010
[b]Reader, Morand-Ferron, & Flynn, 2016
[c]MacLean et al., 2014

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