Multiple assessments of personality and problem-solving performance in captive Asian elephants (Elephas maximus) and African savanna elephants (Loxodonta africana)

Article *in* Journal of Comparative Psychology · June 2021

DOI: 10.1037/com0000281

2 authors:

Lisa P. Barrett
Oklahoma City Zoo

Sarah Benson-Amram
University of Wyoming

Journal of Comparative Psychology

Multiple Assessments of Personality and Problem-Solving Performance in Captive Asian Elephants (Elephas maximus) and African Savanna Elephants (Loxodonta africana)

Lisa P. Barrett and Sarah Benson-Amram

Online First Publication, June 24, 2021. http://dx.doi.org/10.1037/com0000281

AMERICAN PSYCHOLOGICAL ASSOCIATION

Journal of Comparative Psychology

ISSN: 0735-7036

https://doi.org/10.1037/com0000281

Multiple Assessments of Personality and Problem-Solving Performance in Captive Asian Elephants (*Elephas maximus*) and African Savanna Elephants (*Loxodonta africana*)

Lisa P. Barrett and Sarah Benson-Amram
Department of Zoology and Physiology, University of Wyoming
Program in Ecology, University of Wyoming

Animal personality has been shown to predict many behavioral responses across taxa, but the relationship between personality and performance on cognitive tasks remains unclear. To address this gap, we investigated whether personality predicted problem-solving performance and learning in captive Asian and African savanna elephants. We leveraged 3 novel problem-solving tasks to assess success rate, latency to touch the apparatus, exploratory diversity (the number of different behaviors exhibited toward the task), work time (the proportion of time working on the tasks), and latency to solve. To measure multiple different personality traits, such as boldness, activity, aggressiveness, curiosity, and sociability, across contexts, we carried out novel object presentations, behavioral coding through observations, and trait rating through surveys with zookeepers. We found evidence of personality through behavioral observations and surveys, but not through novel object testing. Aggressiveness and activity were important predictors of problem solving, but this was task-dependent, and the traits we measured did not significantly predict learning. Elephants solved 2 out of 3 tasks faster over time, but they did not vary their latency to touch, exploratory diversity, or work time. We discuss our results in terms of task difficulty and previous work on personality in elephants. Results from this study lay the foundation for future work connecting individual variation in personality to cognitive performance in elephants. In addition, for zoo-housed animals, individual differences research could inform enrichment and welfare decisions as well as conservation strategies.

Keywords: individual differences, cognition, innovation, learning, trap-tube task

Supplemental materials: https://doi.org/10.1037/com0000281.supp

Individuals within many species exhibit personality or behavioral differences that are consistent across time or context (Réale et al., 2007). For example, some individuals are bolder and more exploratory than others across diverse situations (Bell, 2007; Sih et al., 2004). Not only has this variation in personality been linked to differences in life history strategies (Réale et al., 2010; Wolf et al., 2007), but it may equip some individuals to fare better in human-altered environments (reviewed in Barrett et al., 2019). Moreover, a population containing a

Lisa P. Barrett https://orcid.org/0000-0001-6072-3479
Sarah Benson-Amram https://orcid.org/0000-0003-0147-7559
Sarah Benson-Amram is now at Department of Forest and Conservation Sciences, Department of Zoology, and Biodiversity Research Centre, University of British Columbia.

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant DGE-1747504 to Lisa P. Barrett. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed (San Diego Zoo IACUC Protocol 15-014, National Zoological Park IACUC 15-25, and Oklahoma City Zoo IACUC 2015-013). We are very grateful for the assistance of incredible elephant keepers and zoo staff, especially Ann Alfama, Tony Barthel, Laura Bottaro, Debra Bastin, Robbie Clark, Rachel Emory, Debbie Flinkman, Marie Galloway, Jason Gue, Amy Hofmeister, Scott Morford, Nick Newby, Rebecca Snyder, and Kayleigh Sullivan. We appreciate immense guidance and support from Greg Vicino. Thank you to Karl Hanold for remarkable apparatus construction, and to research assistants Kelsea Anthony, Kendall Burnside, Haley Gordon, Jackelynn Gutierrez, Stephanie Hart, Jennifer Hayward, Leah Mucciarone, Frederic Reuter, and Rebecca Shoer for invaluable help conducting observations and behavioural coding. Thanks to the UW Animal Behaviour & Cognition Lab, Ellen Williams, and Sophie Wasserman for helpful feedback and discussion. We thank UW Biodiversity Institute, UW Zoology & Physiology Department, and UW Botany Department for supporting this work.

Lisa P. Barrett served as lead for conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, visualization, and writing−original draft, review, and editing. Sarah Benson-Amram served as lead for supervision and served in a supporting role for conceptualization, funding acquisition, methodology, project administration, and writing–original draft, review, and editing.

Correspondence concerning this article should be addressed to Lisa P. Barrett, who is now at Oklahoma City Zoo, 2000 Remington Way, Oklahoma City, OK 73111, United States. Email: lisapbarrett.lpb@gmail.com

wider variety of behavioral types (in which some individuals exhibit different responses than other individuals) may be more likely to cope with environmental change than a population composed of individuals with all similar behavioral types (Dingemanse & Wolf, 2013).

Personality is related to many aspects of an animal's behavioral ecology (reviewed in Wolf & Weissing, 2012), including mating success (Sih et al., 2014), invasion success (Fogarty & Sih, 2011), and dispersal tendency (Cote et al., 2010). There has been burgeoning interest within the field of animal behavior to examine the effects of personality on other facets of behavior, including cognition (reviewed in Carere & Locurto, 2011; Dougherty & Guillette, 2018; Griffin et al., 2015). For instance, researchers have found links between personality type and the following cognitive abilities: spatial learning (Carazo et al., 2014), behavioral flexibility (Brust et al., 2013), and social learning (Carter et al., 2014). Moreover, previous work has highlighted the presence of cognition syndromes, which link differences in personality and cognition and are driven by speed-accuracy trade-offs (Sih & Del Giudice, 2012). For example, "slower" individuals (those that are usually less exploratory) tend to continually gather and use information. Individuals with "fast" personality types, on the other hand, learn about or habituate to risky stimuli more quickly and readily form routines (Sih & Del Giudice, 2012). Boldness is one key personality trait that has been studied with regard to cognition because boldness is hypothesized to predict whether an animal will investigate a novel resource item and innovate (Greenberg, 2003). In this way, an individual's personality type could predict its ability to solve a novel problem in the environment, such as the many challenges animals face as a result of human population growth (Barrett et al., 2019). Despite interest in personality and cognition, studies comparing performance of behavioral types on cognitive tasks have produced discrepant results about which personality types are better equipped to innovate and learn. For instance, several studies have found that animals that are bolder perform better in tasks of innovation (Reader, 2003; Seferta et al., 2001; Webster & Lefebvre, 2001) and learning (Guillette et al., 2009; Range et al., 2006), whereas other work shows that animals at either of the extreme ends of the bold–shy continuum tend to have poorer learning performance (Arnold et al., 2007). A recent meta-analysis found that equal numbers of studies found a positive relationship between boldness and learning as studies that found a negative relationship between boldness and learning (Dougherty & Guillette, 2018; Wilson et al., 2019). Boldness has also been defined using different contexts (e.g., latency to approach a novel object, time spent near a novel object, approach of object despite risk of predation, etc.) in different studies. Thus, the relationship between boldness and cognition remains unclear. Moreover, a critical gap in our understanding remains about whether *multiple* dimensions of personality predict *multiple* cognitive abilities (Boogert et al., 2018; Griffin et al., 2015). It is also critical to study boldness and cognition in threatened species, particularly given potential implications for individual-based conservation strategies (Greggor et al., 2014). For instance, human–wildlife conflict mitigators could tailor intervention efforts to personality types of "problem" individuals that consistently innovate ways of overcoming deterrents. To address these gaps in a threatened species, we used several different puzzle-box tasks and multiple forms of personality assessment to assess individual variation and capacity to innovate a solution to problem-solving tasks in elephants.

Elephants provide an intriguing study system for tests of personality and cognition, as they are social (Bates et al., 2008), possess large brains (reviewed in Hart et al., 2008), and are considered highly intelligent (Roth & Dicke, 2005). In the wild, farmland may represent a novel threat for elephants, in which some elephants overcome barriers (e.g., navigate around or through electric fences or habituate to deterrents) to access novel food sources (Barrett et al., 2019; Goodyear & Schulte, 2015; Mutinda et al., 2014). It is possible that some elephants are better at innovating and learning to surmount barriers in complex environments characterized by human-induced changes to the landscape including deterrents (e.g., fences, auditory deterrents), novel food resources, and the threat of killings by humans (Mumby & Plotnik, 2018). We therefore focused on testing innovation and learning abilities of elephants through the use of novel problem-solving tasks (Roth & Dicke, 2005). Furthermore, personality research could determine which type of individual is more likely to succeed in problem solving. Although some studies have focused on elucidating elephant personality through genetics, hormones, and trait rating (also known as zookeeper or field-researcher surveys; Freeman et al., 2010; Grand et al., 2012; Horback et al., 2013; Lee & Moss, 2012; Seltmann et al., 2018; 2019; Webb et al., 2020; Williams et al., 2019; Yasui et al., 2013); no study has yet examined whether personality relates to problem-solving performance or learning in elephants. In particular, previous work has examined how personality traits relate to social interactions among elephants (Bonaparte-Saller & Mench, 2018; Horback et al., 2013; Williams et al., 2019) or the reliability of using trait ratings to measure personality (Freeman et al., 2010; Posta et al., 2013), with implications for captive animal welfare and management. Personality traits found in elephants include curiosity (Horback et al., 2013), dominance (Freeman et al., 2010), sociability (Grand et al., 2012; Horback et al., 2013), aggression (Grand et al., 2012; Seltmann et al., 2018), activity (Williams et al., 2019), and fearfulness (Williams et al., 2019). Furthermore, confidence, neophobia, and risk-taking have been suggested to be important traits in terms of which elephants approach and invade farmland (Mumby & Plotnik, 2018). Elephants spend between 40% and 75% of their day foraging on grass and browse (which is unevenly distributed in space) sometimes moving over long distances (Sukumar, 2003), so we would also expect traits like activity to be ecologically important. Moreover, differences in boldness and dominance, for example, could be related to mate acquisition and reproductive success, especially for males (Seltmann et al., 2019). Thus far, empirical cognitive work with elephants has shown that they are capable of problem solving and learning. For example, Asian elephants can access out-of-reach food by blowing (Mizuno et al., 2016) or adding water (Barrett & Benson-Amram, 2020) and solve puzzle boxes via stimulus enhancement, a form of social learning (Greco et al., 2013). Asian elephants have also been shown to use tools to reach food via insightful problem solving (Foerder et al., 2011), discriminate quantities of food by smell (Plotnik et al., 2019), and learn to cooperate with a conspecific to access food (Plotnik et al., 2011).

Focusing on Asian and African savanna elephants across three zoos, we asked the following questions: (a) Is there individual variation among elephants that is repeatable (akin to personality)? (b) Do personality traits relate across different methods of assessment? and (c) How does personality in elephants relate to problem-solving and (d) learning ability? The rationale for examining captive populations is to overcome limitations inherent in wild studies, such as habituating elephants to apparatuses, locating individuals for testing, and obtaining access to background information about individual elephants (though we recognize that captive studies are not completely free of these limitations). We also took advantage of the fact that the keepers were familiar with their animals by having them provide an assessment of elephant personality. Third, by focusing on captive elephants, this study provides the necessary foundation for extending personality and cognition research to wild populations and other threatened species in the future. Prior to the present study, novel object testing, behavioral coding, and trait rating have not been used simultaneously, so this work provides important comparisons among methods that will inform future studies of animal personality. Lastly, if we want results of zoo studies to be comparable to wild studies, we need to determine how trait ratings compare to other personality assessment methods that can be used with wild populations. Although this study took place in zoos, we used methods that can be implemented in the wild to measure elephant personality, such as behavioral coding and novel object testing. We also compared results from observations and novel object tests to those of trait ratings to determine reliability of the different assessment methods. By assessing the relationship between innovation and personality and by implementing multiple methods of assessment of personality and problem-solving performance, our study lays the foundation for future studies on elephant personality and cognition.

We had a number of specific predictions based on the personality traits we measured. We expected to find evidence of consistent reactions to novel objects, scored behaviors in enclosures, and rated traits according to zookeepers within individuals (i.e., individuals will be consistently active, aggressive, bold, and sociable) based on previous findings of personality in Asian and African savanna elephants (Freeman et al., 2010; Horback et al., 2013; Lee & Moss, 2012; Seltmann et al., 2018; Webb et al., 2020; Williams et al., 2019; Yasui et al., 2013). Although other studies have used observations of behavior of elephants to relate sociable interactions to personality traits determined by trait ratings (e.g., Asian and African savanna elephants, Williams et al., 2019); few have tested the consistency of behavioral coding (or the behaviors observed) over time (but see Horback et al., 2013 with African savanna elephants), so we contribute to this method of using repeated observations as a measure of personality in elephants. We expected that individuals would exhibit temporal consistency in their behaviors (such as walking, grooming, and interacting with conspecifics; Horback et al., 2013). We predicted, in addition to consistent personality differences, that corresponding measures would be related across assessment methods (Highfill et al., 2010). Previous work with elephants has found correlations between specific personality rated traits produced by trait rating and coded behaviors (for example, Dominance, Discipline, and Solicitous rated traits and approach behaviors: Freeman et al., 2010 with African savanna elephants; Playful rated trait and Playful/Curious behaviors: Horback et al., 2013; Sociable rated trait with positive behavior interactions: Williams et al., 2019). We sought to extend this work by addressing a wider variety of both rated traits and coded behaviors. We expected individuals that were bolder toward novel objects would also be bolder according to trait ratings (Powell & Svoke, 2008) and observed behaviors.

Next, we investigated whether individual personality predicted problem-solving success, as measured by latency to solve and success rate. We predicted that individuals that are bolder (i.e., quicker to approach novel objects) would solve each puzzle-box task faster (on average), and have a greater success rate on each task, than shyer individuals. We expected that elephants that are rated as more active, curious, intelligent, playful, and attentive, but less anxious, shy, fearful, and quitting (i.e., quick to lose interest) would have shorter average latencies to solve and higher success rates. We also expected elephants rated as more sociable, dominant, and less solitary might have shorter average latencies to solve and higher success rates. Lastly, we predicted that elephants coded as being more active, aggressive, investigative, and sociable would have shorter average latencies to solve and higher success rates. We expected self-comforting behaviors, such as grooming, rubbing, and scratching, to be positively correlated with average latency to solve and negatively correlated with success rate because elephants that spend more time engaging in self-comforting behaviors may spend less time focused on a problem-solving task.

Finally, if there is evidence of learning on the tasks (i.e., decrease in latency across trials), we expected that individual measures (i.e., boldness, aggression, sociability, and activity) would be related to learning, with the same predicted relationships as those for average latency to solve and success rate. We also expected that successful individuals would demonstrate evidence of learning by reducing their latency to touch the apparatus over time (Benson-Amram & Holekamp, 2012) and employing a smaller variety of behaviors directed toward the task across trials. Likewise, successful individuals that learn the task should solve the task faster as they gain experience with it and would therefore spend less time interacting with the task (i.e., work time; Chow et al., 2016).

Method

Subjects

Subjects were 18 elephants (15 Asian elephants and three African savanna elephants), including three males and 15 females, that ranged in age from 2.5 to 69 years (Table 1). Elephants were housed at Smithsonian's National Zoo (NZP; NZP-IACUC Protocol 15–25), the San Diego Zoo (SDZ; IACUC Protocol 15-014), and the Oklahoma City Zoo (OKC; ACUC Protocol 2015-013). The study took place from June to August, 2016 (SDZ), June 20 to July 27, 2017 (NZP), and July 30 to August 30, 2017 (OKC). Asian elephants were the main focus of the study, but because SDZ had a mixed herd, we also tested African elephants on some portions of the study (Table 1). For novel object tests and problem-solving tasks, subjects were tested alone in an indoor enclosure, separated visually (but not acoustically or olfactorily) from keepers and other elephants.

Personality Assessments

Zookeeper Trait Rating

Prior to any experimental testing (Figure 1), zookeepers who had worked with elephants for at least 6 months were asked to

Table 1
Subject Information

Location	Name	Species	Sex	Age	Personality assessments: Trait rating (*n* = 18)	Personality assessments: Behavioral coding (*n* = 15)	Personality assessments: Novel object presentation (*n* = 15)	Problem-solving tasks: Boxed Ball (*n* = 12)	Problem-solving tasks: Rod Ball (*n* = 11)	Problem-solving tasks: Trap Tube (*n* = 11)
OKC	Achara	Asian	F	2	■	■	■	■	■	■
	Asha	Asian	F	21	■	■	■	■	■	■
	Bamboo	Asian	F	51	■	■	■	■	■	■
	Chandra	Asian	F	20	■	■	■	■	■	■
	Kandula	Asian	M	15	■	■	■	■	■	■
	Rex	Asian	M	48	■	■	■	■	■	■
NZP	Ambika	Asian	F	69	■	■	■			
	Bozie	Asian	F	42	■	■	■			
	Kamala	Asian	F	42	■	■	■			■
	Maharani	Asian	F	26	■	■	■			■
	Shanthi	Asian	F	41	■	■	■			■
	Swarna	Asian	F	42	■	■	■			■
SDZ	Devi	Asian	F	39	■	■	■	■	■	
	Mary	Asian	F	52	■	■	■	■	■	
	Mila	African savanna	F	43	■			■	■	
	Ranchipur	Asian	M	50	■	■	■	■		
	Shaba	African savanna	F	36	■			■	■	
	Tembo	African savanna	F	45	■			■	■	

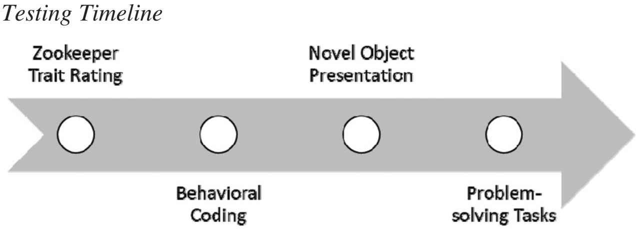
Note. OKC = Oklahoma City Zoo; NZP = Smithsonian's National Zoo; SDZ = San Diego Zoo. Gray shading indicates tests in which elephants participated.

anonymously rate each elephant (*n* = 18) at their institution on 20 personality traits (Table 2). The study conducted received ethical approval from the University of Wyoming review board under institutional review board Protocol 20160415LB01165. Traits included a brief description, and ratings were based on a Likert scale (used with Asian and African savanna elephants, Horback et al., 2013; Yasui et al., 2013) ranging from 1 (*strongly disagree/never applies*) to 5 (*strongly agree/always applies*). Zookeepers were instructed not to share their responses with others. For each trait, we averaged scores from the keepers at each elephant's respective institution. At OKC and at NZP, six keepers rated each elephant. At SDZ, seven keepers rated each elephant.

Behavioral Coding

We observed behaviors of Asian elephants (*n* = 15) for 15-min focal sampling periods (approximately 169 total hr of observations, or 11.25 hr per elephant). We aimed to observe each elephant for at least 40 sampling periods over at least 21 days. Observation periods took place in the morning (between 08:00 and 12:00) or the afternoon (between 12:00 and 16:00) while elephants interacted freely in their enclosures to capture natural "baseline" behavior. We identified elephants for observation by their unique physical characteristics (e.g., ear shape, hair, tusks, relative size, trunk scar). Video-recorded observations were coded (for frequency of behaviors) by a single research assistant (i.e., all observations by the same coder) using an a priori ethogram based on elephant ethograms in the literature (Table S1 in the online supplemental materials; Asher et al., 2015; de Silva, 2010; Freeman et al., 2010; Posta et al., 2013). The coder was carefully trained and met a reliability criterion of 90% with Lisa P. Barrett before coding began.

Figure 1
Testing Timeline



Novel Object Presentation

We observed Asian elephants' (n = 15) responses to three unbaited, novel objects to measure levels of boldness (i.e., response to a novel object). Novel objects included mylar balloons (placed outside of an indoor enclosure; Video 1 in the online supplemental materials), a burned log (placed inside of an indoor enclosure; Video 2 in the online supplemental materials), and a cardboard box filled with hyena or lion (depending on which species was available at the zoo) urine-soaked hay (placed outside of an indoor enclosure; Video 3 in the online supplemental materials). During the novel object presentation tests, elephants were tested alone for 20 min, after which they were shifted out of the enclosure. The following variables were extracted: latency to face the object and the proportion of time spent interacting with the object. We recorded latency to face instead of latency to approach the object because latency to face gave us a clearer measure of when the elephant saw/started paying attention to the object. In most trials, an elephant had to physically approach the object while the keeper was stationing the elephant (before the official start of a trial), so this would not give us an accurate measure of the elephant's boldness toward the object.

Table 2
Personality Traits and Their Descriptions on Zookeeper Trait Rating

N	Adjective	Description
1	Active/ Energetic	Spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.
2	Affectionate/ Friendly	Seems to have a warm attachment or closeness with other elephants or with keepers. This may entail frequent touching or spending time next to others.
3	Aggressive	Causes harm or potential harm to other elephants (i.e., bites). Causes or threatens harm to people and elephants it does not like.
4	Anxious	Hesitant, indecisive, tentative, jittery.
5	Attentive	Seems to attend/listen closely to everything keepers say or do.
6	Curious	Readily explores new situations or objects. Manipulates enrichment, investigates areas of enclosure.
7	Defiant	Assertive or contentious in a way inconsistent with the usual dominance order, or disobedient to keepers.
8	Dominant	Behaves only as it pleases and becomes aggressive when interrupted.
9	Excitable	Quick to become highly aroused by situations.
10	Fearful	Subject reacts excessively to real or imagined threats by exhibiting behaviors such as vocalizing, charging, running away, or other signs of anxiety or distress.
11	Intelligent	Appears to act or play in a novel or creative way. Quick to discover how new toys work.
12	Irritable/Moody	Is inconsistent and wildly/varying in its moods and behaviors.
13	Mischievous	Engages in activities or behavior with the goal of provoking negative reactions from other elephants or keepers.
14	Playful	Is eager to engage in lively, vigorous, or sportive bowing, wrestling, or other play behaviors with or without other elephants or enrichment items.
15	Predictable	Behavior is consistent and steady over extended periods of time. Does little that is unexpected or rarely deviates from its usual behavioral routine.
16	Protective	Shows concern for other elephants and often intervenes to prevent harm or consoles elephants in distress.
17	Quitting	Easy to attract elephant's attention but quickly becomes uninterested with regard to keeper interactions.
18	Sociable	Seeks social contacts with other elephants, keepers, or other people.
19	Solitary	Prefers to spend considerable time alone and seems to avoid contact with other elephants.
20	Timid/Shy	Lacks confidence, is easily alarmed, and is hesitant to venture into new social or nonsocial situations.

Problem-Solving Tasks

We presented three novel puzzle-box foraging apparatuses to test cognitive ability (specifically, the capacity to innovate a solution to a novel problem and learning ability) in elephants by themselves: The Boxed Ball (Video 4 in the online supplemental materials), the Rod Ball (Video 5 in the online supplemental materials), and the Trap Tube (Video 6 in the online supplemental materials; Figure 2; for details on the tasks please see Document 1 in the online supplemental materials). Elephants were shifted into a testing enclosure by keepers who called their name and stationed them with positive reinforcement. Elephants were all familiar with retrieving food out of enrichment devices, but none had been exposed to the tasks used here prior to the study. Trials took place in the mornings (between 06:00 and 09:00) without any food deprivation and lasted until the elephant solved or up to 20 min, with the exception of Trap Tube trials: Here, elephants were given up to 10 min to solve the task, with three trials with the trap on the left side and then three trials with the trap on the right side (order of trap side presentation was counterbalanced among elephants) for a total of six trials (note that at NZP, Maharani received only five trials (two trials with the trap on the right side and three trials with the trap on the left side), and Swarna and Kamala received nine trials (six trials with the trap on the right side and three trials with the trap on the left side)). A successful trial resulted in the elephant retrieving a food reward. At the conclusion of each trial, a keeper would station an elephant and shift them out of the testing enclosure. All individuals received the same reward on a task, but some tasks provided Timothy pellets and one task (the Trap Tube) provided an apple. All problem-solving trials were video-recorded for coding purposes. The Boxed Ball ($n = 12$ [nine Asian elephants and three African elephants], Table 1) could be solved by rotating a counterweighted ball inside of a stainless-steel box to expose a hole in the ball that contained a food reward. The apparatus was chained to a mesh wall. Elephants received three trials on this task, except for the NZP elephants that received one trial (due to time limitations), and Ranchipur at SDZ that received two trials (due to musth-related changes in behavior). To solve the Rod Ball ($n = 11$ [eight Asian elephants and three African elephants], Table 1), elephants had to pull a hollow rod out of a ball to expose a hole in the ball, and then hold the apparatus by the rod to allow the food reward to fall out of the ball. The apparatus was not attached to any mesh walls. The rod could not be completely removed from the ball because of a stopper screw that would catch on the inside of the ball. We gave each elephant three trials on the Rod Ball, except for the NZP elephants that received one trial. After testing at SDZ, we realized the Boxed Ball and Rod Ball were solved very quickly, so we implemented the Trap Tube task at our final two institutions (NZP and OKC; Table 1). The Trap Tube (adapted from Visalberghi & Limongelli, 1994; $n = 12$ Asian elephants, Table 1) was solved by blowing or sucking an apple out of a clear Plexiglas tube and simultaneously avoiding a "trap" on one side. If an elephant blew or sucked from the incorrect end of the tube, the apple would fall into the trap and the trial would end. This task was originally used to assess causal understanding (Visalberghi & Limongelli, 1994), but here we used the task to assess the capacity to innovate. The order of the initial side elephants received on this task was randomized. Elephants could not reach their trunks inside of the tube. The apparatus was bolted to a mesh wall at elephant head height. Elephants received five to nine trials on this task.

For each trial, we measured the elephant's latency (in seconds) to touch the apparatus, latency to solve the task, exploratory diversity (the count of different behaviors, such as push, pull, suck, kick, shake, and smell, exhibited toward the task; Benson-Amram & Holekamp, 2012), and proportion of time spent working on the task (i.e., proportion of time spent using behaviors directed toward the apparatus until solved, such as push, pull, suck, kick, shake, and smell). We also measured each elephant's success rate (how

Figure 2
Puzzle-box Tasks

Note. A: Boxed Ball, B: Rod Ball, and C: Trap Tube (correct solution would involve blowing from the left or sucking from the right). See the online article for the color version of this figure.

many trials were solved out of the total trials received) on each task. A task was deemed solved when a reward was retrieved.

Statistical Analysis

To address our first question about whether elephants exhibit consistent personality traits, as measured through rating, coding, and novel object tests, we first examined interrater reliability of ratings across the keepers at each zoo by calculating intraclass correlation coefficients (ICC) using the "psych" package in R (Revelle, 2019). We removed adjectives that were not reliable across keepers (removed adjectives with ICC $<$ .60 average agreement among keepers at each institution [Cicchetti, 1994]) from further analysis and then we conducted principal components analysis (PCA), using the "psych" package in R (Revelle, 2019) to collapse remaining variables. We retained factors with eigenvalues greater than 1. To determine if behaviors exhibited by elephants in outside enclosures/yards at the zoos (i.e., counts of behaviors) were consistent over time, we first filtered our data by excluding observations that were less than 2 hr apart. This exclusion criterion allowed us to maintain independence of observation events. Next, we randomly chose 32 trials for each elephant and calculated the proportion of total variation attributed to variation within individuals versus variation between individuals across the 32 trials (also known as ICC) using the "rptR" package in R (Stoffel et al., 2017). To test whether individuals exhibited consistent boldness responses on the three novel object tests, we also calculated repeatability using the "rptR" package, using criteria of R $>$ .20 and $p < .05$. To answer our second question and determine validity of the personality assessments, we used Spearman rank correlation to correlate repeatable measures across methods (and calculated a Bonferroni correction for multiple comparisons).

After measuring consistency of personality traits, we addressed our third question about predictors of problem-solving performance, using generalized linear models with Akaike Information Criterion (AIC) model selection. Our response measures were average latency to solve and success rate for each task. Latencies were rounded to the nearest whole number, and we considered them as count measures for analyses. For each model, predictors included repeatable personality traits from the three methods of assessment. We did not include factors such as sex and age because of our small sample size. We used location as a fixed effect to account for any potential differences among institutions.

To address our fourth question about learning on each problem-solving task, we used generalized linear mixed-effects models with trial as a fixed effect, ID as a random effect, and latency to solve, exploratory diversity, latency to touch, and work time (proportion of time working on the task) as the responses and evaluated significance of trial with p values ($p < .05$). To test whether individual differences predicted learning, we used Poisson generalized linear models containing repeatable personality traits (one in each model) and location as fixed effects and latency to solve in the second trial minus latency to solve in the first trial as the response. For the Trap Tube, which switched sides, we used beta regression (for proportion data) with repeatable personality traits (one in each model) and location as fixed effects and proportion of trials solved in the second period of testing (after the tube flipped) minus proportion of trials solved in the first period of testing (before the tube flipped). Zeros and ones were converted to .0001 and .999, respectively. Although our sample represented a varied population of elephants in terms of age, species, and sex, we could not include these as predictors due to our small sample size. Elephants that received fewer than three trials or that never solved a given task were excluded from analyses of learning, and elephants' unsuccessful trials received a maximum latency. African Savanna elephants were included in analyses of learning on the Boxed Ball and Rod Ball only (i.e., not analyses of personality

Table 3
Principle Component Analysis of Repeatable Rated Traits

Personality adjective	Component 1	Component 2	Component 3	Component 4
Active		−.71		
Affectionate	.95			
Aggressive			.84	
Anxious		.87		
Curious	.61	−.63		
Defiant			.90	
Excitable	.69			.62
Mischievous				−.88
Protective	.76		.45	
Sociable	.98			
Solitary	−.92			
Shy		.84		

Note. Loadings > .40 are shown.

and problem solving, personality and learning, or Trap Tube analyses). AICc values were calculated using the "MuMIn" package in R (Barton, 2018). Analyses were conducted in R (R Development Core Team, 2014) Version 3.6.2. We evaluated the residuals of our models graphically to determine that the models fit the data well.

Results

Personality

Zookeeper Trait Rating

Twelve rated traits (Active, Affectionate, Aggressive, Anxious, Curious, Defiant, Excitable, Mischievous, Protective, Sociable, Solitary, and Shy) were significantly repeatable (ICC > .60) across keepers at each institution (and provided evidence of personality differences; Table S2 in the online supplemental materials). Our PCA of these repeatable traits revealed four principal components (Table 3). We found that the first principal component explained 35.30% of the variance.

Behavioral Coding

Five behaviors from our observations were significantly repeatable: Aggress, Body Touch, Investigate, Rub/Scratch, and Walk (Table S3 in the online supplemental materials). The five repeatable behaviors were retained to be used as predictors in problem-solving and learning models. We tested various intertrial intervals and found similar results (Table S8 in the online supplemental materials).

Novel Object Presentation

Neither latency to face the novel objects nor the proportion of time spent interacting with the objects were repeatable across the three objects (Table S4 in the online supplemental materials). Therefore, we excluded these responses from further analysis.

Trait Ratings and Behavioral Coding

Our second research question examined whether repeatable personality traits were related across assessments used in this study. Spearman rank correlations indicated as follows: Curious ratings were positively related to Walk behaviors (r = .60, n = 15, p = .02); Sociable ratings were positively correlated with Aggressive behaviors (r = .52, n = 15, p = .05); Defiant ratings were positively correlated with Investigate behaviors (r = .55, n = 15, p = .03); Protective ratings were positively correlated with Investigate behaviors (r = .64, n = 15, p = .01) and Rub behaviors (r = .57, n = 15, p = .03); and Mischievous ratings were positively correlated with Rub behaviors (r = .57, n = 15, p = .03). When we corrected for multiple comparisons with a Bonferroni correction (i.e., p < .0008), however, these relationships were no longer significant (Table S5 in the online supplemental materials).

Problem-Solving Tasks

On the Boxed Ball, 14 out of the 18 participants solved 100% of the trials they received. Only three elephants never solved the task. Of the successful trials, elephants took a median of 77 (512) s (median [IQR]) to solve in their very first trial (n = 15). On the Rod Ball, all 16 participants solved 100% of the trials they received. Elephants solved the Rod Ball in 65.5 (219.25) s (median [IQR]) in their first trial (n = 16). The 11 Trap Tube participants solved, on average, 48% of the trials they received. Successful elephants solved the Trap Tube in 41.5 (57) s (median [IQR]) in their first trial (n = 4). A few elephants employed an unexpected method of solution to the Trap Tube (besides blowing the apple from the correct end of the tube). These elephants blew the apple over the trap and out of the tube, such that they could solve by blowing from the "incorrect" end of the tube. We categorized the blow-over method as successful because it resulted in the elephant accessing the apple reward.

We addressed our third research question about which personality traits best predicted performance (i.e., latency to solve and success rate) on our three problem-solving tasks (Table S6 in the online supplemental materials). First, for the Boxed Ball, average latency to solve was best predicted by PC3—out of all of the repeatable personality measures from both coded behaviors and rated traits, as well as location. Elephants with a higher PC3 score (i.e., more aggressive, defiant, and protective) tended to solve the Boxed Ball faster, on average (R^2 = .78; Table S7 in the online supplemental materials). When predicting success rate on the Boxed Ball, PC3 was included in our top model, but it did not significantly predict success (R^2 = .43; Table S7 in the online supplemental materials). There was an effect of location. Please refer to Table S6 in the online supplemental materials to see all models that ranked closely in ΔAICc.

Second, we modeled latency to solve the Rod Ball (Table S6 in the online supplemental materials). For latency to solve, our top personality model included Walk behaviors. Elephants that walked more tended to take longer to solve the Rod Ball, on average, and there was an effect of location (R^2 = .56; Table S7 in the online supplemental materials). There was no variation in—and thus we did not model—success rate on the Rod Ball.

Third, we tested predictors of latency to solve and success rate on the Trap Tube (Table S6 in the online supplemental materials). On the Trap Tube, latency to solve was best predicted by Walk behaviors, where elephants that were more active, on average, were faster at solving the Trap Tube (R^2 = .27; Table S7 in the online supplemental materials). There was also an effect of location. For success rate on the Trap Tube, PC3 was the top predictor, where a higher PC3 score resulted in a higher success

Table 4
Summary Tables for Learning Models

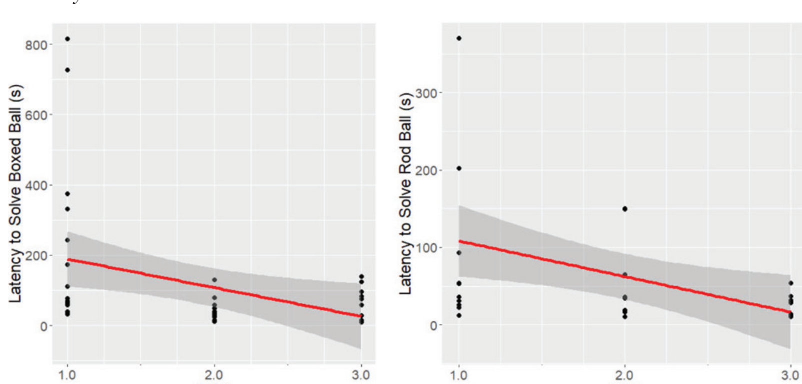
Model	Type (distribution)	*df*	R^2	AICc	ΔAICc	Akaike weight
Boxed ball learning ~ Personality measures + Location						
Difference in latency ~ Investigate + Location*	GLM (Gaussian)	4	.46	126.8	0	.28
Difference in latency ~ Aggress + Location	GLM (Gaussian)	4	.46	126.9	.10	.26
Difference in latency ~ Walk + Location	GLM (Gaussian)	4	.46	126.9	.10	.26
Difference in latency ~ Rub + Location	GLM (Gaussian)	4	.33	128.9	2.02	.10
Difference in latency ~ Body touch + Location	GLM (Gaussian)	4	.32	128.9	2.09	.10
Difference in latency ~ PC 2 + Location	GLM (Gaussian)	4	.20	161.5	34.70	0
Difference in latency ~ PC 1 + Location	GLM (Gaussian)	4	.10	162.9	36.09	0
Difference in latency ~ PC 3 + Location	GLM (Gaussian)	4	.03	163.8	36.92	0
Difference in latency ~ PC 4 + Location	GLM (Gaussian)	4	.00,006	164.2	37.34	0
Rod ball learning ~ Personality measures + Location						
Difference in latency ~ Walk + Location*	GLM (Gaussian)	4	.45	119.9	0	.32
Difference in latency ~ Investigate + Location	GLM (Gaussian)	4	.38	120.9	.98	.20
Difference in latency ~ Body touch + Location	GLM (Gaussian)	4	.37	120.9	1.05	.19
Difference in latency ~ Aggress + Location	GLM (Gaussian)	4	.33	121.4	1.49	.15
Difference in latency ~ Rub + Location	GLM (Gaussian)	4	.33	121.4	1.52	.15
Difference in latency ~ PC 3 + Location	GLM (Gaussian)	4	.25	151.9	32.05	0
Difference in latency ~ PC 4 + Location	GLM (Gaussian)	4	.17	153.0	33.07	0
Difference in latency ~ PC 1 + Location	GLM (Gaussian)	4	.11	153.7	33.83	0
Difference in latency ~ PC 2 + Location	GLM (Gaussian)	4	.10	153.8	33.95	0

Note. AIC = Akaike information criterion; GLM = generalized linear models. Top models are indicated by an asterisk (*).

rate, and there was an effect of location (Table S7 in the online supplemental materials).

Finally, to address our fourth research question, we determined whether there was evidence of learning on the tasks across trials (Table 4). On average, elephants solved the Boxed Ball (n = 11, $p < .001$) and the Rod Ball (n = 11, $p < .001$) faster over time (Figure 3). Trial Period (i.e., first three trials vs. second three trials) did not predict proportion of trials solved of the Trap Tube task (n = 10, Beta: p = .45). We next assessed which personality and problem-solving measures influenced learning on the Boxed Ball and Rod Ball (measured by subtracting latency to solve on the first trial from latency to solve on the second trial). For learning on the Boxed Ball, Investigate and Location were included in our top model, but they did not significantly predict learning (R^2 = .46; Figure 4; Table S7 in the online supplemental materials). For learning on the Rod Ball, Walk and Location were included in our top model, but they did not significantly predict learning (R^2 = .45; Figure 4; Table S7 in the online supplemental materials). We also examined the change of problem-solving measures, latency to touch, exploratory diversity, and work time, over time. We found that latency to touch did not change over time for solvers on the Boxed Ball (n = 10, p = .11) or Rod Ball (n = 10, p = .08) but increased across trials on the Trap Tube (n = 10, $p < .001$). Exploratory diversity did not change over time for solvers on the Boxed Ball (n = 10, p = .21), the Rod Ball (n = 10, p = .12), or the Trap Tube (n = 10, p = .39). The proportion of time spent working on the task did not vary across trials for solvers on the Boxed Ball (n = 10, p = .20) or the Rod Ball (n = 10, p = .44), or across trial Period on the Trap Tube (n = 10, p = .56), likely because trials ended right after an elephant solved, which meant that total trial length decreased over time for successful individuals.

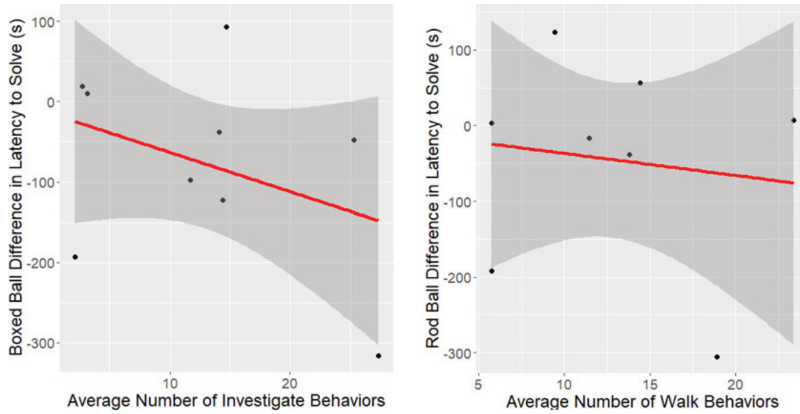
Figure 3
Latency to Solve Across Three Trials on the Boxed Ball and Rod Ball



Note. See the online article for the color version of this figure.

Figure 4

Personality and Learning on the Boxed Ball and Rod Ball



Note. *Y* axis shows latency to solve on trial two minus latency to solve on trial one, so lower values on the *y* axis indicate faster learning. See the online article for the color version of this figure.

Discussion

Overall, we found evidence of personality in captive elephants using methods that can be applied with wild elephants. We also uncovered task-dependent effects of personality on innovation and learning, so if personality influences elephant cognition, it may be a complex relationship where multiple personality traits play a role, or cognition may determine the behaviors we identified as personality traits. Alternatively, it is possible that other factors (e.g., physiological, neurological, herd composition, etc.) are related to both personality and cognition. In general, walk (from behavioral coding) and aggressive/defiant (from trait rating) were important for innovation, and investigate and walk (from behavioral coding) were important for learning, but the direction of the relationships was not consistent across the tasks used here, suggesting that the tasks measured slightly different aspects of innovation.

We found evidence of personality in captive Asian elephants through two methods of assessment, behavioral coding and zookeeper trait ratings, thereby validating and expanding on other studies of elephant personality (Freeman et al., 2010; Horback et al., 2013). The behaviors Walk, Aggress, Body Touch, Rub, and Walk were repeatable. In previous studies of elephant personality, Walk behaviors have been measured to assess traits such as Active and Curious (Seltmann et al., 2018); Aggress behaviors have been measured to measure the trait Aggressive (Seltmann et al., 2018); Body Touch behaviors have been used to describe traits like Affectionate and Sociable (Seltmann et al., 2018); and Rub behaviors have been related to grooming-related behavior and could indicate comfort-seeking (Asher et al., 2015; Posta et al., 2013).

Across the repeatable rated traits, we found four components of personality in our population. Our first component (PC1) included more Sociable, Affectionate, Protective, Excitable, Curious, and less Solitary traits; our second component (PC2) included more Anxious, more Shy, less Active, and less Curious traits; our third component (PC3) included more Defiant, Aggressive, and Protective traits; and our fourth component (PC4) included more Excitable, less Mischievous traits (Table 3). Other studies of elephant personality have measured a variety of personality traits and uncovered three (Attentiveness, Sociability, and Aggressiveness: Seltmann et al., 2018, 2019), four (Leadership, Playful, Gentle, and Constancy: Lee & Moss, 2012; Effective, Fearful, Sociable, and Aggressive: Grand et al., 2012), or five dimensions (Dominance, Neuroticism, Agreeableness, Curiosity, and Impulsiveness: Yasui et al., 2013). Given the variation in personality traits measured (and thus their findings) across these studies, we attempted to choose traits on which most previous studies overlapped. It is important to standardize which traits are assessed so that we can compare personality across species and between captive and wild elephants. Alternatively, however, captive and wild elephants may exhibit different personality traits due to differential environmental pressures, so it is crucial to choose valid traits for assessment depending on the study population (Seltmann et al., 2018). Nevertheless, some of the methods used here can be applied to elucidate wild elephant personality. Researchers and managers could apply the ethogram used here for behavioral scoring, for instance, to reveal personality differences among individual elephants. Such methods would highlight the traits relevant in wild elephants. Future work could then look into what the effects of personality differences are for survival (and cause of mortality, such as conflict with humans) and reproduction, as well as how traits differ between captive and wild settings. After more work on personality in elephants, managers could, for example, screen orphaned elephants to identify "problem" individuals in the group before releasing the rest of the group back into the wild.

Although the correlations we found between coded traits (from behavioral coding) and rated traits (from keeper surveys) were no longer significant after a Bonferroni correction, perhaps with a larger sample size, stronger relationships would emerge. In fact, since it is possible that a Bonferroni correction is too conservative (i.e., inflates type II error; e.g., Armstrong, 2014; Chandler, 1995), we interpret some results below but note they should be interpreted with caution. The positive (nonsignificant) correlation we found between Walk and Curious, for example, suggests that we were measuring similar traits—notably activity and/or exploration—across these methods. In our ethogram, Walk behaviors included Approaches (Table S1 in the online supplemental materials). Approach behaviors have been found to be related to traits such as Playful and Curious in another study of elephant personality (African elephants: Horback et al., 2013); which could explain the relationship between Walk and Curious in the present study. Contrary to our predictions, coded behavior traits and rated traits were not significantly correlated, so perhaps keepers consider their human-elephant interactions more than elephant-elephant interactions when assigning individual elephant personality (e.g., Kis et al., 2012; Mullan & Main, 2007; but see Bonaparte-Saller & Mench, 2018). It is also possible that keeper personality and experience influenced their rating of the elephants' personalities, as has been proposed in semicaptive elephant personality studies where mahouts score their elephant's personality (Seltmann et al., 2018). We also recommend that future studies use matching definitions between rated traits and scored behaviors as much as possible for ease of comparison. It would be interesting for future studies to investigate whether enclosure size, schedule predictability, training time, or other factors are related to consistency of rated traits. For instance, keepers may be "closer" with one animal due to training routines and this could influence ICC of rated traits. Institutions with fewer animals may have more time for training and may, in a sense, be more familiar with their animals than institutions with less time for training. This could influence ICC compared among institutions.

We did not find evidence of consistent boldness responses during novel object tests. Although we carefully chose objects that were sufficiently different from one another to avoid habituation, it is possible that the novel objects were different enough that they each elicited slightly different types of responses/traits, such as neophilia, exploration, and/or response to a predation threat. We also cannot rule out the possibility that the objects were not truly novel. It is possible that the elephants had been exposed to balloons or burned logs in their past. It is also likely that elephants can smell the lions/hyena in the zoo. This is a challenge of working with a long-lived species, which has already been exposed to many human-made objects through enrichment and life in close proximity to people (e.g., logging camps, circuses, etc.). Nevertheless, with guidance from keepers, we deemed the proximity of the objects (and the concentration of the urine scent) to the elephants be sufficiently novel. A recent study of semicaptive Asian elephants showed that several measures of novel and known object interactions (e.g., object pick up and holding time) were repeatable across objects, including a novel water bottle, a novel green plastic disk, and pieces of timber as known objects (Webb et al., 2020). Given the differing measures and objects used between the two studies, it is difficult to make strong conclusions about why novel object interactions (measured as latency to face and time spent interacting) were not repeatable in the present study. In the Webb et al., (2020) study, however, elephants were instructed to pick up the objects by their mahout, which could have been related to repeatability. Although novel object testing is a common test for object neophobia with other species (Powell & Svoke, 2008), more trials with different objects are required to determine if novel object testing is a reliable method of measuring personality in zoo elephants.

To test our third question about personality and problem solving, we presented elephants with three puzzle-box tasks. The elephants were capable of solving all three tasks, but the Trap Tube had a much lower average success rate than the Boxed Ball or the Rod Ball. Some elephants innovated another solution to the Trap Tube by blowing hard enough that the apple went over the trap and out the opposite end of the tube. With so few trials, we cannot determine whether elephants understood cause and effect, as was originally intended with the Trap Tube (Visalberghi & Limongelli, 1994), but future work could address this now that we know elephants can solve the task in multiple ways. In general, our results show that the Boxed Ball and Rod Ball tasks were very easy for most elephants to solve and that we likely require more difficult tasks or a larger sample size for relationships between personality and problem solving to emerge. The lack of variation among elephants in their latencies to solve (and success rates on Boxed Ball and Rod Ball) also highlights important considerations for enrichment for zoo animals. Despite these tasks being relatively easy for the elephants (or in the case of Trap Tube, relatively difficult), they continued to interact with the tasks for multiple trials to retrieve food reward. This confirms anecdotal observations that elephants are very food motivated and suggests that puzzle-box enrichment maintained interest for these elephants. However, we presented the tasks for only one to three trials, so further testing is required to conclude whether the tasks maintain continual interest over longer periods of time. Nevertheless puzzle-box tasks like those used here can be used as appropriate challenges for zoo elephants and provide cognitively stimulating opportunities for them to work for their food (Meehan & Mench, 2007).

We found that, out of the personality traits we measured, some traits played a bigger role than others in explaining problem-solving performance in zoo elephants. For average latency to solve on the Boxed Ball, more aggressive/defiant/protective elephants were faster solvers, which was in line with our expectations. Contrary to our predictions, elephants that were less active (i.e., exhibited fewer walk behaviors during observations), tended to solve the Rod Ball fastest on average. Perhaps elephants that were more active were faster explorers and therefore were less accurate in problem solving (Sih & Del Giudice, 2012). Similar to the Boxed Ball, more active elephants solved the Trap Tube faster, which could have to do with the energy required to blow and move back and forth between both ends of the apparatus for this task. On the Trap Tube, more aggressive/defiant elephants (i.e., with higher PC3 scores) had higher success rates. We note that several of our success rate models, however, were ranked closely in terms of AICc, so it seems that multiple traits tended to be equally important in solving. Nevertheless, we found that personality was important for problem solving in a task-dependent manner for zoo elephants.

In addition to testing whether elephants could innovate a solution on the novel foraging tasks, we asked whether elephants solved the tasks faster over time. We found that elephants learned to solve the tasks faster over time (i.e., latency to solve decreased over trials; although this result was not significant for the Trap Tube). Surprisingly, however, latency to touch, exploratory diversity, and work time did not decrease over time (in fact, latency to touch increased over time on the Trap Tube), contrary to our expectations for learning. In other words, it seems that the elephants were no more or less engaged over time (but rather maintained interest, at least across one to three trials) even though they were solving faster over time. Given their interest in the tasks and decreases in latency to solve over time, the elephants could have been taking time approaching, investigating, and interacting with the tasks and not solving as quickly as possible (akin to play behavior), while still solving faster over time for the Boxed Ball and Rod Ball. Learning (i.e., the difference in latencies to solve on trial one and trial two) was not significantly influenced by personality traits, although Walk and Investigate measured from behavioral coding were included in our top models and deserve further investigation in future work. Although all of our tasks were designed to measure innovation, the tasks required different behaviors to solve and some tasks (e.g., Rod Ball) were easier than others (Trap Tube), which could explain why elephants did not perform consistently across all three tasks, though we did not measure repeatability of innovation here. Thus, it is likely that certain traits improved solving speed or number of trials solved, depending on the task (e.g., Activity for the Trap Tube). Order of presentation of the tasks could also play a role. For example, investigation was important for learning on the first task the elephants received, where it could be more important to investigate a novel item to solve compared to later trials when elephants were used to receiving tasks. At the same time, however, two personality traits, Aggressive/Defiant and Active, were important across the different tasks. Finally, we controlled for potential effects of location (i.e., zoo institution) in our problem-solving and learning models, but because it was not something we explicitly tested for here, it would be an interesting follow-up for future studies. Location effects could be due to a variety of reasons, such as the previous history of the elephants at different institutions, enrichment programs at the zoos, enclosure size, enclosure location relative to other species, and herd stability.

Beyond contributing to our knowledge about enrichment and welfare in captive settings, this study has potential implications for wild elephants (Bechert et al., 2019). Elephants are threatened in part due to conflict with humans, which culminates when elephants exploit farmland by learning how to overcome barriers and deterrents intended to prevent crop raiding (Barrett et al., 2019; Mumby & Plotnik, 2018). We used novel problem-solving tasks as a proxy for how wild elephants acquire food in novel ways, which may share cognitive similarities to crop-raiding behavior. Our work with captive elephants lays the foundation for future work with wild elephants. By expanding on our present research and measuring problem solving and learning in wild elephants, conservationists could better understand and predict the behavior of "problem individuals" that tend to habituate to deterrents more quickly or frequently come in to contact with humans. Unfortunately, Asian elephants are in decline in the wild and also fare poorly in zoo settings, and an inability to cope with environmental change may underlie this fate (Mason et al., 2013). Moreover, investigations of animal personality and cognition can reveal individual differences in responses to environmental change, such as conversion of habitat for agricultural use (Barrett et al., 2019; Mumby & Plotnik, 2018). In wild or semiwild elephant populations, personality can inform management and conservation decisions, such as identification of candidates for translocation and for pairing mahouts and elephants based on personality types (Seltmann et al., 2018). This work can also be applied with captive elephants across Asia to assess which individuals would be successful candidates to be released into the wild, as has been done with captive-bred swift foxes (Bremner-Harrison et al., 2004) and lobsters (Carere et al., 2015).

Despite the importance of this study for captive and wild elephants, we acknowledge some weaknesses of our study. In particular, we recognize that our small sample size limited our modeling ability. Similarly, although we sought to investigate a comprehensive list of personality traits in elephants (e.g., 20 rated traits [12 retained for PCA] for 18 elephants), PCA is thought to be more powerful when there is a larger sample size, particularly for a study with a large number of traits. Now that we have highlighted some potential key traits, future work can examine these more closely and in a greater number of animals. It is possible that there is an effect of age on personality or cognition that we were not able to capture in this study. Although we had a wide age range of subjects in this study, our sample size was not sufficient to investigate statistically the effect of age on personality or cognitive performance. Likewise, it is possible that some personality characteristics are more prevalent in elephants at different age classes. Given our small sample size, we could then mistakenly attribute some of our findings to personality differences that are instead solely due to age effects. Studies with larger sample sizes of individuals across all age classes would help disambiguate the role of age versus personality in cognitive performance. We are also aware that we may not have provided enough trials to give sufficient opportunity for learning on the Trap Tube, where elephants received three trials with the apparatus facing one direction and three trials with the apparatus facing the opposite direction. We also reemphasize that our work showed it is possible that cognition and personality are related, but it is possible that cognition underlies the personality traits we measured or that other factors were related to personality and cognition in our study. For example, motivation could have played a role in mediating associations between personality and cognition. If, for instance, more food-motivated animals walked more in their outdoor enclosures and solved the trap tube faster, we would not be able to disentangle effects of motivation from the effects of personality on cognition. Furthermore, due to the ceiling effects for performance on the problem-solving tasks, we may have been limited in our ability to detect associations with personality. Nevertheless, results from this study inform the literature by expanding on methods used for assessing personality and by making connections between personality on innovation and learning in threatened species. For future work, we advocate the importance of continuing to use multiple different forms of personality assessment (Ellis, 2020). Future research could then help elucidate which methods are fastest and most accurate to incorporate personality and cognition into routing management decisions across taxa in both zoo and wild settings.

References

Armstrong, R. A. (2014). When to use the Bonferroni correction. *Ophthalmic and Physiological Optics*, *34*(5), 502–508. https://doi.org/10.1111/opo.12131

Arnold, K. E., Ramsay, S. L., Donaldson, C., & Adam, A. (2007). Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1625), 2563–2569. https://doi.org/10.1098/rspb.2007.0687

Asher, L., Williams, E., & Yon, L. (2015). *Developing behavioural indicators, as part of a wider set of indicators, to assess the welfare of elephants in U.K. zoos*. Department for Environment, Food & Rural Affairs.

Barrett, L. P., & Benson-Amram, S. (2020). Can Asian elephants use water as a tool in the floating object task? *Animal Behavior and Cognition*, *7*(3), 310–326. https://doi.org/10.26451/abc.07.03.04.2020

Barrett, L. P., Stanton, L. A., & Benson-Amram, S. (2019). The cognition of 'nuisance' species. *Animal Behaviour*, *147*, 167–177. https://doi.org/10.1016/j.anbehav.2018.05.005

Barton, K. (2018). *MuMIn: Multi-Model Inference (1.42.1.)*. R Foundation for Statistical Computing.

Bates, L. A., Sayialel, K. N., Njiraini, N. W., Poole, J. H., Moss, C. J., & Byrne, R. W. (2008). African elephants have expectations about the locations of out-of-sight family members. *Biology Letters*, *4*(1), 34–36. https://doi.org/10.1098/rsbl.2007.0529

Bechert, U. S., Brown, J. L., Dierenfeld, E. S., Ling, P. D., Molter, C. M., & Schulte, B. A. (2019). Zoo elephant research: Contributions to conservation of captive and free-ranging species. *International Zoo Yearbook*, *53*(1), 89–115. https://doi.org/10.1111/izy.12211

Bell, A. M. (2007). Evolutionary biology: Animal personalities. *Nature*, *447*(7144), 539–540. https://doi.org/10.1038/447539a

Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087–4095. https://doi.org/10.1098/rspb.2012.1450

Bonaparte-Saller, M., & Mench, J. A. (2018). Assessing the dyadic social relationships of female African (*Loxodonta Africana*) and Asian (*Elephas maximus*) zoo elephants using proximity, tactile contact, and keeper surveys. *Applied Animal Behaviour Science*, *199*, 45–51. https://doi.org/10.1016/j.applanim.2017.10.011

Boogert, N. J., Madden, J. R., Morand-Ferron, J., & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, *373*(1756), Article 20170280. https://doi.org/10.1098/rstb.2017.0280

Bremner-Harrison, S., Prodohl, P. A., & Elwood, R. W. (2004). Behavioural trait assessment as a release criterion: Boldness predicts early death in a reintroduction programme of captive-bred swift fox (Vulpes velox). *Animal Conservation*, *7*(3), 313–320. https://doi.org/10.1017/S1367943004001490

Brust, V., Wuerz, Y., & Kruger, O. (2013). Behavioural flexibility and personality in zebra finches. *Ethology*, *119*, 559–569. https://doi.org/10.1111/eth.12095

Carazo, P., Noble, D., Chandrasoma, D., & Whiting, M. (2014). Sex and boldness explain individual differences in spatial learning in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), 1–9. https://doi.org/10.1098/rspb.2013.3275

Carere, C. & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology*, *57*(4), 491–498. https://doi.org/10.1093/czoolo/57.4.491

Carere, C., Nascetti, G., Carlini, A., Santucci, D., & Alleva, E. (2015). Actions for restocking of the European lobster (*Homarus gammarus*): A case study on the relevance of behaviour and welfare assessment of cultured juveniles. *Rend. Fis. Acc. Lincei*, *26*, 59–64. https://doi.org/10.1007/s12210-014-0361-6

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *PeerJ*, *2*, e283, https://doi.org/10.7717/peerj.283

Chandler, C. R. (1995). Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour*, *49*(2), 524–527. https://doi.org/10.1006/anbe.1995.0069

Chow, P. K. Y., Lea, S. E. G., & Leaver, L. A. (2016). How practice makes perfect: The role of persistence, flexibility and learning in problem-solving efficiency. *Animal Behaviour*, *112*, 273–283. https://doi.org/10.1016/j.anbehav.2015.11.014

Cicchetti, D. V. (1994). Guidelines, criteria, and rules of thumb for evaluating normed and standardized assessment instruments for psychology. *Psychological Assessment*, *6*(4), 284–290. https://doi.org/10.1037/1040-3590.6.4.284

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biolofical Sciences*, *365*, 4065–4076. https://doi.org/10.1098/rstb.2010.0176

de Silva, S. (2010). Acoustic communication in the Asian elephant, Elephas maximus maximus. *Behaviour*, *147*(7), 825–852. https://doi.org/10.1163/000579510X495762

Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: causes and consequences. *Animal Behaviour*, *85*(5), 1031–1039. https://doi.org/10.1016/j.anbehav.2012.12.032

Dougherty, L. R., & Guillette, L. M. (2018). Linking personality and cognition: A meta-analysis. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *373*(1756), Article 20170282. https://doi.org/10.1098/rstb.2017.0282

Ellis, C. F. (2020). *Exploring domestic rabbit (Oryctolagus cuniculus) personality utilising beahviour coding, behaviour testing, and a novel beahviour rating tool*. University of Northampton.

Foerder, P., Galloway, M., Barthel, T., Moore, D. E., III,., & Reiss, D. (2011). Insightful problem solving in an Asian elephant. *PLoS ONE*, *6*(8), e23251. https://doi.org/10.1371/journal.pone.0023251

Fogarty, S., Cote, J., & Sih, A. (2011). Social personality polymorphism and the spread of invasive species: A model. *The American Naturalist*, *177*(3), 273–287. https://doi.org/10.1086/658174

Freeman, E. W., Schulte, B. A., & Brown, J. L. (2010). Using behavioral observations and keeper questionnaires to assess social relationships among captive female African elephants. *Zoo Biology*, *29*(2), 140–153. https://doi.org/10.1002/zoo.20249

Goodyear, S. E., & Schulte, B. A. (2015). Habituation to auditory stimuli by captive African elephants (Loxodonta africana). *Animal Behavior and Cognition*, *2*(4), 292–312. https://doi.org/10.12966/abc.11.01.2015

Grand, A. P., Kuhar, C. W., Leighty, K. A., Bettinger, T. L., & Laudenslager, M. L. (2012). Using personality ratings and cortisol to characterize individual differences in African elephants (Loxodonta Africana). *Applied Animal Behaviour Science*, *142*(1–2), 69–75. https://doi.org/10.1016/j.applanim.2012.09.002

Greco, B. J., Brown, T. K., Andrews, J. R. M., Swaisgood, R. R., & Caine, N. G. (2013). Social learning in captive African elephants (Loxodonta africana africana). *Animal Cognition*, *16*(3), 459–469. https://doi.org/10.1007/s10071-012-0586-7

Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds: Why study ecological innovation? In S. M. Reader & K. N. Laland (Eds.), *Animal innovation* (pp. 175–196). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198526223.003.0008

Greggor, A. L., Clayton, N. S., Phalan, B., & Thornton, A. (2014). Comparative cognition for conservationists. *Trends in Ecology & Evolution*, *29*(9), 489–495. https://doi.org/10.1016/j.tree.2014.06.004

Griffin, A. S., Guillette, L. M., & Healy, S. D. (2015). Cognition and personality: An analysis of an emerging field. *Trends in Ecology and Evolution*, *30*(4), 207–214. https://doi.org/10.1016/j.tree.2015.01.012

Guillette, L. M., Reddon, A. R., Hurd, P. L., & Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, Poecile atricapillus. *Behavioural Processes*, *82*(3), 265–270. https://doi.org/10.1016/j.beproc.2009.07.005

Hart, B. L., Hart, L. A., & Pinter-Wollman, N. (2008). Large brains and cognition: Where do elephants fit in? *Neuroscience and Biobehavioral Reviews*, *32*(1), 86–98. https://doi.org/10.1016/j.neubiorev.2007.05.012

Highfill, L., Hanbury, D., Kristiansen, R., Kuczaj, S., & Watson, S. (2010). Rating vs. coding in animal personality research. *Zoo Biology*, *29*(4), 509–516. https://doi.org/10.1002/zoo.20279

Horback, K. M., Miller, L. J., & Kuczaj, S. A., II (2013). Personality assessment in African elephants (Loxodonta africana): Comparing the temporal stability of ethological coding versus trait rating. *Applied Animal Behaviour Science*, *149*(1–4), 55–62. https://doi.org/10.1016/j.applanim.2013.09.009

Kis, A., Turcsán, B., Miklósi, Á., & Gácsi, M. (2012). The effect of the owner's personality on the behaviour of owner-dog dyads. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems*, *13*(3), 373–385. https://doi.org/10.1075/is.13.3.03kis

Lee, P. C., & Moss, C. J. (2012). Wild female African elephants (Loxodonta africana) exhibit personality traits of leadership and social integration. *Journal of Comparative Psychology*, *126*(3), 224–232. https://doi.org/10.1037/a0026566

Mason, G., Burn, C. C., Dallaire, J. A., Kroshko, J., McDonald Kinkaid, H., & Jeschke, J. M. (2013). Plastic animals in cages: Behavioural flexibility and responses to captivity. *Animal Behaviour*, *85*(5), 1113–1126. https://doi.org/10.1016/j.anbehav.2013.02.002

Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, *102*(3–4), 246–261. https://doi.org/10.1016/j.applanim.2006.05.031

Mizuno, K., Irie, N., Hiraiwa-Hasegawa, M., & Kutsukake, N. (2016). Asian elephants acquire inaccessible food by blowing. *Animal Cognition*, *19*(1), 215–222. https://doi.org/10.1007/s10071-015-0929-2

Mullan, S. M., & Main, D. C. J. (2007). Behaviour and personality of pet rabbits and their interactions with their owners. *The Veterinary Record*, *160*(15), 516–520. https://doi.org/10.1136/vr.160.15.516

Mumby, H. S., & Plotnik, J. M. (2018). Taking the elephants' perspective: Remembering elephant behavior, cognition and ecology in human-elephant conflict mitigation. *Frontiers in Ecology and Evolution*, *6*, Article 122. https://doi.org/10.3389/fevo.2018.00122

Mutinda, M., Chenge, G., Gakuya, F., Otiende, M., Omondi, P., Kasiki, S., Soriguer, R. C., & Alasaad, S. (2014). Detusking fence-breaker elephants as an approach in human-elephant conflict mitigation. *PLoS ONE*, *9*(3), e91749. https://doi.org/10.1371/journal.pone.0091749

Plotnik, J. M., Brubaker, D. L., Dale, R., Tiller, L. N., Mumby, H. S., & Clayton, N. S. (2019). Elephants have a nose for quantity. *Proceedings of the National Academy of Sciences, USA, USA of the United States of America*, *116*(25), 12566–12571. https://doi.org/10.1073/pnas.1818284116

Plotnik, J. M., Lair, R., Suphachoksahakun, W., & de Waal, F. B. M. (2011). Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences, USA, USA of the United States of America*, *108*(12), 5116–5121. https://doi.org/10.1073/pnas.1101765108

Posta, B., Huber, R., & Moore, D. E., III (2013). The effects of housing on zoo elephant behavior: A quantitative case study of diurnal and seasonal variation. *International Journal of Comparative Psychology*, *26*(1), 37–52.

Powell, D. M., & Svoke, J. T. (2008). Novel environmental enrichment may provide a tool for rapid assessment of animal personality: A case study with giant pandas (Ailuropoda melanoleuca). *Journal of Applied Animal Welfare Science*, *11*(4), 301–318. https://doi.org/10.1080/10888700802329673

Range, F., Bugnyar, T., Schlogl, C., & Kotrschal, K. (2006). Individual and sex differences in learning abilities of ravens. *Behavioural Processes*, *73*(1), 100–106. https://doi.org/10.1016/j.beproc.2006.04.002

R Development Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reader, S. M. (2003). Innovation and social learning: individual variation and brain evolution. *Animal Biology*, *53*(2), 147–158.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society*, *82*(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Revelle, W. (2019). psych: Procedures for psychological, psychometric, and personality research (R Package version 1.9.12). https://cran.r-project.org/package=psych

Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences*, *9*(5), 250–257. https://doi.org/10.1016/j.tics.2005.03.005

Seferta, A., Guay, P.-J., Marzinotto, E., & Lefebvre, L. (2001). Learning differences between feral pigeons and Zenaida doves: The role of neophobia and human proximity. *Ethology*, *107*, 281–293. https://doi.org/10.1046/j.1439-0310.2001.00658.x

Seltmann, M. W., Helle, S., Adams, M. J., Mar, K. U., & Lahdenperä, M. (2018). Evaluating the personality structure of semi-captive Asian elephants living in their natural habitat. *Royal Society Open Science*, *5*(2), Article 172026. https://doi.org/10.1098/rsos.172026

Seltmann, M. W., Helle, S., Htut, W., & Lahdenperä, M. (2019). Males have more aggressive and less sociable personalities than females in semi-captive Asian elephants. *Scientific Reports*, *9*(1), Article 2668. https://doi.org/10.1038/s41598-019-39915-7

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, *19*(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, *367*(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Sih, A., Ehlman, S., & Halpin, R. (2014). On connecting behavioral responses to HIREC to ecological outcomes: A comment on Wong and Candolin. *Behavioral Ecology*, *26*(3), 676–677. https://doi.org/10.1093/beheco/aru229

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *8*(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Sukumar, R. (2003). *The living elephants: Evolutionary ecology, behavior, and conservation*. Oxford University Press.

Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *108*(1), 15–22. https://doi.org/10.1037/0735-7036.108.1.15

Webb, J. L., Crawley, J. A. H., Seltmann, M. W., Liehrmann, O., Hemmings, N., Nyein, U. K., Aung, H. H., Htut, W., Lummaa, V., & Lahdenperä, M. (2020). Evaluating the reliability of non-specialist observers in the behavioural assessment of semi-captive Asian elephant welfare. *Animals*, *10*(1), Article 167. https://doi.org/10.3390/ani10010167

Webster, S. J. & Lefebvre, L. (2001). Problem solving and neopohbia in a columbiform-passeriform assemblage in Barbados. *Animal Behaviour*, *62*(1), 23–32. https://doi.org/10.1006/anbe.2000.1725

Williams, E., Carter, A., Hall, C., & Bremner-Harrison, S. (2019). Exploring the relationship between personality and social interactions in zoo-housed elephants: Incorporation of keeper expertise. *Applied Animal Behaviour Science*, *221*, Article 104876. https://doi.org/10.1016/j.applanim.2019.104876

Wilson, V., Guenther, A., Øverli, Ø., Seltmann, M. W., & Altschul, D. (2019). Future directions for personality research: Contributing new insights to the understanding of animal behavior. *Animals*, *9*(5), 240 https://doi.org/10.3390/ani9050240

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*(7144), 581–584. https://doi.org/10.1038/nature05835

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology and Evolution*, *27*(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Yasui, S., Konno, A., Tanaka, M., Idani, G., Ludwig, A., Lieckfeldt, D., & Inoue-Murayama, M. (2013). Personality assessment and its association with genetic factors in captive Asian and African elephants. *Zoo Biology*, *32*(1), 70–78. https://doi.org/10.1002/zoo.21045

Received July 22, 2020
Revision received March 10, 2021
Accepted March 13, 2021 ■