Animal Behaviour 205 (2023) 227–239

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Innovating to solve a novel puzzle: wild Asian elephants vary in their ability to problem solve

Sarah L. Jacobson [a, b, *], Juthapathra Dechanupong [c], Wantida Horpiencharoen [c], Marnoch Yindee [d], Joshua M. Plotnik [a, b, *]

[a] Department of Psychology, Hunter College, City University of New York, NY, U.S.A.
[b] Department of Psychology, The Graduate Center, City University of New York, NY, U.S.A.
[c] Golden Triangle Asian Elephant Foundation, Chiang Rai, Thailand
[d] Akkhraratchakumari Veterinary College, Walailak University, Nakhon Si Thammarat, Thailand

ARTICLE INFO

Article history:
Received 21 April 2023
Initial acceptance 7 June 2023
Final acceptance 10 July 2023
Available online 23 September 2023
MS. number: A23-00198R

Keywords:
Asian elephant
exploratory diversity
field experiment
innovation
multi-access box
neophilia
persistence
wild cognition

An animal's capacity for innovation or solving novel problems likely has important implications for how quickly they can adapt to environmental change. Asian elephants, *Elephas maximus*, living in zoos have previously demonstrated a capacity to innovate, but problem solving has never been studied experimentally in a wild elephant population. We installed puzzle boxes with multiple possible solutions inside a protected area in western Thailand to determine individual variation in innovation, as well as other behavioural traits associated with elephants' problem solving, including persistence, exploratory diversity and neophilia. We recorded 77 elephants approaching the puzzle box, with 44 interacting with the box in their first exposure. Individuals varied widely in their success opening the doors of the puzzle box. Such success was influenced by persistence and exploratory diversity in both the first interaction as well as across multiple interactions. However, when considering each individual's overall innovation scores, which represented how many different doors elephants were able to open across all of their interactions with the puzzle box, only greater persistence and interaction number were associated with reaching a higher innovation score. We observed that elephants who interacted with the box multiple times learned to open a door of any type more quickly as their interactions increased, but we did not see evidence of learning to open specific door types over time. Overall, this study about how innovation and its associated behaviours vary in wild elephants not only informs our understanding of how a capacity for problem solving is expressed, but also how well elephants may be able to adapt to, overcome or avoid increasingly frequent interactions with humans within their natural habitat.

Whether it is sulphur-crested cockatoos, *Cacatua galerita*, breaking into trash cans (Klump et al., 2022) or Japanese macaques, *Macaca fuscata*, washing the sand off potatoes (Kawai, 1965), many animals innovate to improve their access to or processing of resources. Innovation is the ability to invent new behaviours or use pre-existing behaviours in a novel context (Kummer & Goodall, 1985; Reader & Laland, 2003). This ability can be beneficial to survival, as it allows animals to adapt to novel or changing environments (Lefebvre et al., 2004). Innovation may provide significant fitness benefits for animals, as such a demonstration of cognitive flexibility allows them to exploit new resources or to establish themselves in new environments (e.g. Sol et al., 2005), particularly when navigating the challenges of human-altered ecosystems (Barrett et al., 2018).

While rates of innovation observed in the wild have been compared across species (e.g. Lefebvre et al., 1997; Reader & Laland, 2002), an experimental approach provides an opportunity to investigate intraspecific variability in innovative problem solving. In such experiments, researchers typically introduce novel problems for animals to solve, requiring them to extract food from an artificial foraging device. This work has been conducted with both captive (e.g. Auersperg et al., 2011; Young et al., 2019) and wild animals (e.g. Benson-Amram & Holekamp, 2012; Williams et al., 2021). Research with avian species has demonstrated that experimental measures of innovation are representative of a species' tendency to innovate in a natural setting, as the bird species that were more successful in a problem-solving task also were observed anecdotally to innovate more in the wild outside of experimental settings (Webster & Lefebvre, 2001).

* Corresponding authors.
E-mail addresses: sjacobson1112@gmail.com (S. L. Jacobson), Joshua.Plotnik@gmail.com (J. M. Plotnik).

https://doi.org/10.1016/j.anbehav.2023.08.019
0003-3472/

A methodology that has been used frequently to investigate innovation and behaviours related to it involves assessing an individual's ability to repeatedly innovate using a multi-access device, a method first developed to compare problem solving between kea, *Nestor notabilis*, and New Caledonian crows, *Corvus moneduloides*, by Auersperg et al. (2011). This paradigm involves the presentation of an extractive foraging device that has multiple potential solutions; innovation is measured by assessing the individual's ability to discover one or more of these solutions. Many species have been tested on their ability to repeatedly innovate using variations of this methodology (e.g. North American raccoons, *Procyon lotor*: Daniels et al., 2019; spotted hyaenas, *Crocuta crocuta*: Johnson-Ulrich et al., 2018; yellow-bellied marmots, *Marmota flaviventer*: Williams et al., 2021; chimango caracara, *Daptrius chimango*: Biondi et al., 2022; African lions, *Panthera leo*, snow leopards, *Panthera uncia*: O'Connor et al., 2022).

Researchers have shown that innovation varies between species (e.g. Auersperg et al., 2011; Griffin & Diquelou, 2015; Manrique et al., 2013) and between individuals within a species (e.g. Benson-Amram & Holekamp, 2012; Daniels et al., 2019; Day et al., 2003; Griffin et al., 2014; Johnson-Ulrich et al., 2018; Williams et al., 2021) that are tested with the same novel problem. Within a species, the sex and age of an individual may affect innovation, although the direction of this effect appears to vary between species (reviewed in Griffin & Guez, 2014). A recent meta-analysis of innovation studies suggested that older individuals and the sex with the greater body mass within a species are more innovative, but it also revealed that interindividual differences may be more important than demographic factors (Amici et al., 2019). Some behavioural traits that have been identified as relevant to innovation are an individual's responses to novelty, persistence and diversity of motor actions. These traits relate to the acquisition, processing and storage of information occurring at a cognitive level, all of which may result in an individual's ability to innovate. Some of these traits have exhibited a more consistent relationship with innovation than others across studies while some observed differences appear to be based on methodology or species (reviewed in Amici et al., 2019; Griffin & Guez, 2014). Attraction to novelty (neophilia) or fear of novelty (neophobia) affects an individual's likelihood of initially engaging with a novel problem. Several studies have demonstrated that individuals that are more attracted to and less fearful of novelty are more likely to innovate (Benson-Amram & Holekamp, 2012; Johnson-Ulrich et al., 2018; Massen et al., 2013). However, there seems to be wide variation in the quality of this relationship, likely due to differences in terminology and methodology used to evaluate responses to novelty across studies (Griffin & Guez, 2014). Persistence, or the time an animal spends engaged with a task, has been consistently associated with successful problem solving and innovation such that higher persistence increases the likelihood of discovering solutions (e.g. Griffin et al., 2014; Jacobson et al., 2022; Johnson-Ulrich et al., 2018; O'Connor et al., 2022; Petelle et al., 2022; but also see Amici et al., 2019). Another influential trait may involve the number of different motor actions an animal uses when interacting with a task (i.e. exploratory diversity; e.g. Benson-Amram & Holekamp, 2012). An increase in the number of diverse actions an individual uses in initial interactions with a task also increases the potential that one or a combination of those actions could result in innovations (Daniels et al., 2019; Johnson-Ulrich et al., 2018; Massen et al., 2013; Williams et al., 2021). Across multiple exposures, however, exploratory diversity is expected to decrease as animals learn the solution to the problem (Benson-Amram & Holekamp, 2012; Daniels et al., 2019).

In the current study, we sought to investigate variability in innovation in Asian elephants, *Elephas maximus*, a large-brained, socially complex mammal known for their capacity for problem solving (Byrne et al., 2009; Jacobson et al., 2022). Elephants are a good model for innovative problem solving for several reasons. First, greater innovative ability has been associated with larger relative brain size in primates and birds (Lefebvre et al., 2004; Reader & Laland, 2002; Sol et al., 2005). Second, elephants have a complex, fission–fusion social structure that requires flexibility in behaviour to navigate their physical and social environments (de Silva et al., 2011; Nandini et al., 2017). While elephant foraging behaviour may not inherently require innovation due to elephants' generalist diet and little need for extraction of food resources in their natural environment, elephants may possess a domain-general cognitive toolkit similar to that which has been proposed for corvids that innovate when using tools in captivity that they do not use in the wild (Bird & Emery, 2009). This cognitive flexibility could permit elephants to express innovation when foraging as needed. Specifically, the increase in availability of high-calorie food grown in agricultural fields that have encroached upon natural Asian elephant habitat has led some elephants to forage in areas where innovation is suddenly needed (Mumby & Plotnik, 2018; Plotnik & Jacobson, 2022). For instance, African savannah, *Loxodonta africana*, and Asian elephants have been observed innovating to circumvent the human-created barriers, such as fences, protecting agricultural areas in the wild (Mutinda et al., 2014; Natarajan et al., 2021; Thouless & Sakwa, 1995). In addition, both species have demonstrated the capacity for innovation in several experimental studies carried out in zoos. Barrett and Benson-Amram (2021) found that Asian and African elephants were able to solve novel foraging problems and that aggression and locomotion were traits associated with success, although this relationship seemed to differ across tasks. In a study assessing social learning, African elephants also successfully solved novel problems, and these successes did not appear to be due to social imitation (Greco et al., 2013). One Asian elephant has demonstrated insightful problem solving, innovating a way to access food without trial-and-error learning (Foerder et al., 2011). In our own work, we found variability in innovation between zoo-housed Asian elephants tested using a three-solution multi-access puzzle box (Jacobson et al., 2022). Higher persistence when interacting with the box was a significant predictor of success for these individuals. Interestingly, lower exploratory diversity was associated with success (Jacobson et al., 2022), whereas studies of other species have found that greater exploratory diversity predicts success (e.g. Daniels et al., 2019; Johnson-Ulrich et al., 2018). Neophilia, measured as latency to contact the puzzle box for each individual's first exposure, did not seem to vary between individuals and was not related to innovation in this population (Jacobson et al., 2022). This study provided initial insights into innovation in Asian elephants but was limited by a relatively small sample size and the constraints of captivity.

We adapted the methodology in Jacobson et al. (2022) to investigate innovation in a wild population of Asian elephants in Thailand. To our knowledge, this is the first experimental approach to studying cognition in wild Asian elephants. Studying cognitive abilities in wild elephants allows us to determine how these abilities vary in natural ecological conditions and independent of the limitations of captivity. Understanding variation in innovation is particularly important given the prevalence of human–elephant conflict due to elephant foraging in human-dominated agricultural areas in Asia (Shaffer et al., 2019). The ability to innovate may influence where these wild elephants choose to live and forage within their fragmented habitats as it could allow individuals to navigate human barriers to access high-calorie resources (Mumby & Plotnik, 2018). Asian elephants are an endangered species threatened by human development and habitat fragmentation, with approximately 50 000 remaining across Asia (Menon & Tiwari, 2019). While innovation may help some individual elephants survive in anthropogenic environments, these innovations may also lead to negative interactions with people that are sometimes lethal (Fernando et al., 2008; Shaffer et al., 2019). However, the prevalence of this foraging strategy throughout Southeast Asia (Sukumar, 2006) suggests that there is a net benefit relative to the risk. The factors that might influence variation in innovative ability between individuals are unknown. Investigating these factors can inform our understanding of wild elephant behavioural flexibility and its potential impact on conservation management or human–elephant conflict mitigation.

We aimed to determine whether the relationships between behavioural traits and innovation that we observed in zoo-housed elephants would exist in wild elephants that had not experienced the novel extractive foraging devices frequently used in zoos. Multi-access puzzle boxes were installed on trees in the protected Salakpra Wildlife Sanctuary in Thailand, home to more than 200 wild elephants, and interactions were recorded without humans present. We expected that the likelihood of an elephant's initial interaction with the puzzle box would vary based on its sex and age class and whether it was in a group. We hypothesized that males would be more likely to interact in their first exposure than females, since males are likely more exploratory as the dispersing sex and less risk-averse because they are unlikely to be accompanied by calves (McKay, 1973; Srinivasaiah et al., 2019). We also hypothesized that subadults would be more likely to interact than adults as younger animals tend to be more exploratory in novel contexts (e.g. Benson-Amram & Holekamp, 2012; Sherratt & Morand-Ferron, 2018; Thornton & Sampson, 2012). We hypothesized that group size (1 or more) would affect interaction potential with the box, but we did not have an a priori prediction about the direction of the effect. Either lone individuals would be more likely to interact with the puzzle box than individuals approaching with a group because they are more likely to also be males (McKay, 1973), or individuals in a group could be more likely to interact because fear of novelty can be reduced in the presence of conspecifics (e.g. tufted capuchins, *Cebus apella*: Visalberghi & Addessi, 2000; grey wolves, *Canis lupus*, and domestic dogs, *Canis familiaris*: Moretti et al., 2015). We hypothesized that there would be individual variability in innovation similar to the results we found for zoo-housed elephants (Jacobson et al., 2022). We also hypothesized that, as in zoo-housed elephants and in many other species (Griffin & Guez, 2014), higher persistence towards the box would be associated with greater innovation. Lastly, we hypothesized that higher neophilia and higher exploratory diversity would be associated with greater innovation, although these results were not supported with zoo-housed Asian elephants (Jacobson et al., 2022). This relationship has been observed with many other species (e.g. Daniels et al., 2019; Johnson-Ulrich et al., 2018; Massen et al., 2013), and we predicted that we would observe this association with the larger sample size in this study. For elephants who interacted with the puzzle box multiple times, we hypothesized that individuals' latencies to open box doors would decrease over time, demonstrating the elephants' capacity for learning.

METHODS

Study Site

All data were collected in the Salakpra Wildlife Sanctuary in Kanchanaburi, Thailand (henceforth, 'Salakpra'). Salakpra is part of the Western Forest Complex, a priority area for elephant conservation and a biodiversity hotspot in western Thailand (Williams et al., 2020). The sanctuary is a protected area approximately 860 km^2 and is not open to public tourism. The landscape is composed of mixed deciduous forest, dry dipterocarp forest and disturbed areas (Chaiyarat et al., 2015). There are estimated to be more than 200 elephants living within Salakpra (Salakpra Wildlife Sanctuary Annual Report, Thai Department of National Parks Wildlife and Plant Conservation; Chaiyarat et al., 2015). Salakpra is surrounded by human development including villages and agricultural fields consisting of multiple crops, including cassava, sugar cane, corn and pumpkin. Human–elephant conflict is frequent in these areas, with 96% of local farmers reporting crop raiding at least once a month and 54% reporting raiding daily (van de Water & Matteson, 2018).

Ethical Note

The subjects in this study were wild elephants and therefore could choose to participate in the research or not without any human intervention. We minimized any disturbance to the animals by using remote-activated camera traps to record video during the day, with a built-in infrared light to record video at night. The research protocol was approved by the Hunter College, City University of New York Institutional Animal Care and Use Committee (JP-Elephant Behavior 5/21) and permission was granted to collect data in Salakpra Wildlife Sanctuary by the National Research Council of Thailand (Plotnik 1/62) on behalf of the Thai Department of National Parks, Wildlife and Plant Conservation.

Puzzle Box Procedure

We installed two custom-made, multi-access puzzle boxes of the same design as those previously provided to captive Asian elephants to test innovation (Jacobson et al., 2022) at a watering hole inside Salakpra. Each box consisted of three separate compartments, each measuring 46 × 25 × 29 cm and made of 4 mm thick steel (Fig. 1). All compartments had 1.5 cm diameter holes drilled into the door and side of the box to provide olfactory access to the food rewards inside. Each compartment had a different solution door (20 × 20 cm) that could either be opened by pulling a chain so that the door opened towards the elephant, pushing the door so it swung open into the box, or sliding the door open to the right to access food inside. The pull and push doors were secured shut against gravity with magnets. We designed these solutions to incorporate typical foraging behaviours of elephants such as pulling down branches, stripping bark and pushing with the trunk or body. The compartments of each of the two boxes were stacked together in two different pseudoranomized orders throughout testing (Fig. 1).

The two boxes were installed from October 2019 to April 2020 approximately 30 m apart in order to maximize interactions by elephants at each visit. We attached each compartment to a tree using metal brackets such that the bottom of the stacked compartments was between 128 cm and 164 cm high depending on the morphology of the tree. Three Browning Spec Ops Advantage camera traps were also installed at each box to provide three views, one from the left and right sides and another from above the box. The cameras recorded 20 s of high-resolution video when motion-activated from up to 25 m away and were set with a fast trigger speed (0.4 s) to minimize gaps between videos. The cameras used infrared light at night to capture clear night-vision video. Each compartment was baited with a piece of jackfruit measuring approximately 12 × 10 cm. Jackfruit was chosen as the food reward because of its olfactory salience and thus the likelihood that it would attract elephants to the puzzle box. The research team, consisting of students, Thai staff or park rangers, visited the boxes one to two times per day and checked to (1) see whether jackfruit

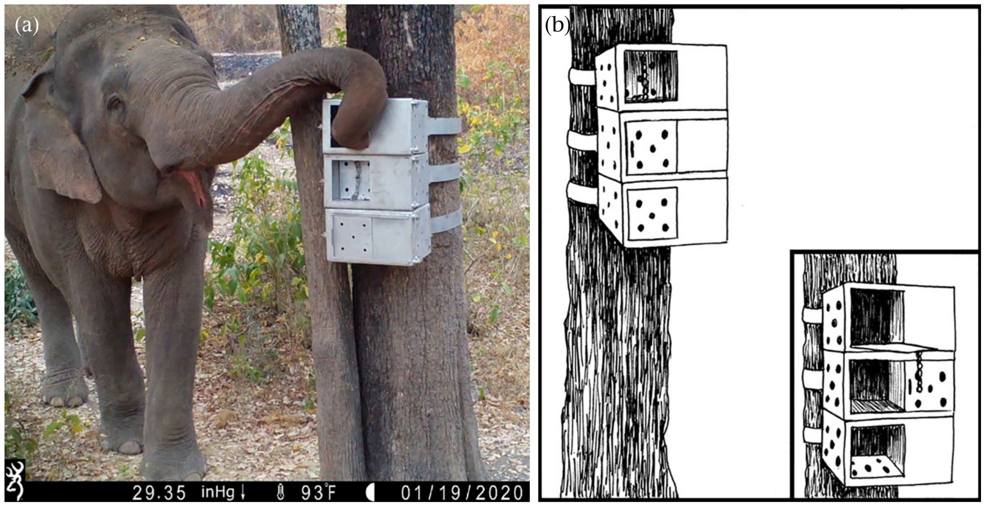

Figure 1. (a) Camera trap video screenshot (cropped) of a male elephant interacting with one of the puzzle boxes. The configuration of this puzzle box had a push door at the top, a pull door in the middle and a slide door on the bottom. (b) Diagram of the three-door configuration of the other puzzle box with doors closed (on the left) and open (insert, on right), with the pull door on top, the slide door in the middle and the push door on the bottom. Diagram drawing by Anne Jacobson.

was eaten, (2) reset the box if doors were open or compartments shifted and (3) replace jackfruit if it was rotten. We replaced SD cards and checked batteries approximately every 10 days.

We individually identified elephants in each video; in order to be identified, elephants had to be observed entering a measured, 5 m perimeter around the box and orienting towards it (i.e. their head was facing the box and/or their trunk was reaching towards it). This allowed us to exclude individuals that may not have perceived the box at all. The first author identified individuals using morphological characteristics following an identification protocol similar to one we developed previously for this population (Montero-de la Torre et al., 2023). Three other students familiar with our database reviewed identities in a random 20% of all observations and reached 100% agreement. We included only data for adults and subadults that entered the 5 m perimeter due to the difficulty of reliably identifying younger elephants (Montero-de la Torre et al., 2023).

The first author coded videos using an ethogram that was similar to one we developed previously for a study with zoo-housed elephants (Jacobson et al., 2022). That ethogram included details of the possible motor actions and body parts used by the elephants in their interactions with the box (Appendix, Table A1). We calculated each elephant's exploratory diversity score (EDS, the number of unique behaviours or unique motor actions while interacting with the box) using these coded behaviours and following the definition in Table 1. We also recorded an elephant's neophilia (i.e. their latency to touch the box after approaching within 5 m of it), duration of interaction with the box and exit from the 5 m perimeter. The 5 m perimeter was estimated using reference videos that included a rope of known length. A measure of an elephant's persistence during an observation was calculated as the proportion of time spent interacting with the puzzle box over the total time spent within 5 m of it. We determined that a door was solved if it was opened wide enough so that an elephant's trunk could fit inside, and the latency to solve was recorded following the definition in Table 1. Success and innovation score were recorded as the number and types of doors solved, respectively (Table 1). We determined that an observation began when an elephant entered within 5 m of the box and ended when all doors were opened or the elephant left the 5 m radius. However, if an elephant approached the box multiple times within 12 h without another elephant interacting with the box and before we could reset it, then we combined the observations and considered them as a single visit. If multiple elephants were present at a puzzle box, we recorded the identity of any elephant within the 5 m radius camera view when a door was solved to account for the potential of previous exposure affecting subsequent success by the observer. We also recorded the duration that an elephant's interactions with the puzzle box were out of view, such as when they were blocking the camera view and we could not see their trunk. The puzzle box was out of view for 2% of all interactions.

Analysis

To assess inter-rater reliability of the measures outlined in Table 1, the first author coded all observations in which an elephant interacted with the box while another observer independently coded 20.69% of the same observations. We selected these

Table 1
Behavioural measures calculated from coded videos

Measure	Definition	Based on
Innovation score	Maximum number of types of doors opened	Across all visits
Success	Proportion of doors opened over available doors	Each visit
Solving latency	Duration of interaction prior to door solved. If the door was the second or third door solved, then the interaction duration included only the interaction after the previous door solve	Each visit
Neophilia	Latency to contact after first step within a 5 m perimeter. If contact never occurred, then a maximum value was assigned (corresponding to the lowest degree of neophilia)	First visit only
Exploratory diversity score (EDS)	Number of unique motor actions based on different body parts used to interact with the box	Each visit
Persistence	Proportion of time interacting with the box out of the total time observed within 5 m. Interaction began with an elephant's first touch to the puzzle box	Each visit

observations pseudorandomly in order to cover all motor actions observed as well as to provide a relatively equal number of day and night videos. Using an intraclass correlation (ICC) analysis, we found excellent agreement between coders for latencies (ICC(1) = 0.996, $F_{51,52} = 500$, $P < 0.001$), durations (ICC (1) = 0.99, $F_{71,72} = 132$, $P < 0.001$) and EDS (ICC(1) = 0.94, $F_{23,24} = 30.8$, $P < 0.001$). The two coders had 100% agreement for the number and type of doors opened in those observations.

We did not include data on elephant behaviours when interacting with the puzzle box after all doors were already open, either after the subject had themselves opened doors or if an elephant interacted after all doors were opened previously by another individual. We did not include these behaviours because they would not be directed towards the goal of retrieving food; in these situations, the elephants could not be rewarded since all the food had already been retrieved by others or by themselves. However, we did consider data on whether an individual interacted with the box or not and their latency to do so during their very first exposure to the apparatus even if all doors were already open.

First visit

To address which variables may be associated with an elephant's decision to first interact with the box, we initially considered each elephant's first visit to the box location ($N = 77$ elephants). We created a logistic regression model using whether an individual interacted with the box (1) or approached within 5 m of the box but did not interact (0) as the outcome variable. Age class, sex and whether the subject was in a group or not when approaching were included as variables in the model.

First interaction

We then focused on instances when doors were available during the elephants' first interactions with the puzzle box ($N = 44$ elephants; we labelled this data set as 'first interaction'). In some of these first interactions ($N = 12$), one or two doors had previously been opened by other elephants. These interactions were still included in the data set because the elephants had the opportunity to open at least one door. We also included the factor of 'completely unopened box' (i.e. whether all doors were available or not) in the analysis to account for potential effects of limited door availability on the elephants' behaviour. Three logistic regression models were fitted to assess the association of each behavioural trait with success, i.e. the proportion of available doors successfully opened. For this analysis, opening three out of three available doors was equivalent to opening one out of one available door in order to treat elephants similarly if they opened all the doors available to them in a given observation. Each model had one behavioural trait (neophilia, EDS, persistence) as well as sex, age class and whether the box was completely unopened as fixed effects.

Multiple interactions

We then considered observations of elephants that interacted with the box more than once to see whether the relationship between behavioural traits and success was consistent across experience (we labelled this data set as 'multiple interactions'). We removed one individual who was included in the first interaction data set from this and later analyses because she had observed another individual solve a door before solving it herself in the subsequent interaction. Since she was the only elephant with experience observing a door solve who went on to subsequently solve a door later, we decided to exclude her data rather than account for this unusual factor/experience in the analysis. We limited this data set to a maximum of seven interactions with an unopened box (all doors closed) for each subject ($N_{\text{elephants}} = 20$, $N_{\text{interactions}} = 90$ across all elephants), so some individuals could have had more than seven interactions included if some of those interactions occurred with a box with already-solved doors. All interactions where at least one door was available were included in this analysis through the seventh interaction with a completely unopened box. This limit led to the exclusion of additional interactions with the box for only four individuals in this data set. To determine the relative association of behavioural traits with success across all interactions, we created a logistic regression model with the outcome variable as the proportion of doors successfully opened over the total available in each interaction (e.g. 1/3, 2/2, 0/1, etc.). Elephant identification was included as a random effect, with sex, age class, interaction number and whether the box was completely unopened as fixed effects. We ran all analyses in R studio (R core team, 2022). All logistic regression models were fitted using the 'lme4' package (Bates et al., 2015) and model assumptions and residuals were evaluated using the 'performance' package (Lüdecke et al., 2021) and 'DHARMa' package (Hartig, 2022).

Learning

Learning was assessed using the 'multiple interactions' data set. First, we evaluated learning using the solving latency for the first door of each observation (no matter the door type) in subsequent trials. We used a Cox's proportional hazards mixed model to analyse these data because it is a method to analyse outcomes measured as time to the occurrence of an event, originally developed to look at survival in medical or epidemiological studies. In these data sets, the event may not have occurred for all subjects within the observation period, creating 'right-censored' latencies, which should be treated differently than latencies for events that did occur (Austin, 2017; Jahn-Eimermacher et al., 2011). In our study, the event was the opening of a door, and some individuals did not solve a door in each interaction. We assigned interactions that did not result in a door being opened a maximum value of 250 s and ensured that this value only represented failure. The Cox's proportional hazards model allows for those instances of failures to be specified in the model (e.g. Biondi et al., 2022; Greenberg et al., 2017; Jahn-Eimermacher et al., 2011). We included a random effect of elephant identification in the model, as well as the interaction number, sex and age class as fixed effects. We used 'cox.zph' in the 'survival' package (Therneau, 2023) to evaluate the validity of the model's assumption of proportionality. We also assessed learning using the solving latency for each door type (push, pull, slide) across interactions to determine whether particular solution types were learned. The data set analysed for each door type contained only interactions from elephants that had more than one opportunity to solve that door type and only the interactions when that door type was available. Therefore, we analysed push-door solution learning from a data set of 65 interactions for 15 elephants, pull-door learning from 84 interactions for 20 elephants and slide-door learning from 75 interactions for 18 elephants. A Cox's proportional hazards mixed model was created for the solving latency of each door type (push, pull, slide), with a random effect of elephant identification and the fixed effects of interaction number, sex and age class included. We also assessed whether EDS was associated with interaction number in the multiple interactions data set, as decreases in exploratory diversity over time can also indicate learning (Benson-Amram & Holekamp, 2012). For this analysis, we used a Poisson regression model with EDS as the outcome variable and interaction number included as a fixed effect with elephant identification as a random effect.

Overall innovation

Lastly, we wanted to assess how the behavioural traits and other variables may be associated with the overall level of innovation that an elephant achieves across all of its interactions with the box, scored as the number of types of doors they were able to open (0, 1, 2 or 3). This allowed us to determine whether individuals were able to open all types of doors across multiple visits, even if some types were not available in each visit, which could happen if other elephants had already solved the doors before we could reset them, or if they solved one type in one visit and another type on a follow-up visit. Similar to the 'multiple interactions' data set, we capped the number of interactions at seven interactions with an unopened box for each elephant, but elephants that only interacted once with the puzzle box were also included in this data set. We used only data from elephants that had an opportunity to open all types of doors at least once across their interactions with the box ($N_{\text{elephants}} = 35$, $N_{\text{interactions}} = 94$) so as not to bias against elephants that could never achieve an innovation score of 3. We first used a Poisson regression model to assess the relationship between the fixed factors of age and sex with each individual's overall innovation score across all of their interactions. Next, to consider how innovation score may have changed across interactions due to the behaviours occurring in each interaction, we considered innovation scores to be cumulative in each sequential interaction such that once an elephant had opened one type of door, their score would be a 1 on subsequent interactions even if they did not open that door type in the next interaction. The score would remain a 1 until a second door type was opened, then would remain a 2 until a third door type was opened, for a maximum score of 3. Interactions following the maximum innovation score were not included in the analysis because we were interested only in the behaviours that resulted in initially reaching that innovation score, not how their behaviours changed with potential learning. To analyse these data, we used a cumulative mixed link model in the 'ordinal' package (Christenson, 2022) because innovation score was considered an ordinal variable. The cumulative innovation score at the time of each interaction was the outcome variable in this model. Elephant identification was included as a random effect with persistence, EDS and interaction number as fixed effects. We also conducted a likelihood ratio test to determine whether the mixed model with the inclusion of elephant identity fit the data better than the cumulative link model with the same fixed effects but without the random effect.

RESULTS

Out of the 77 elephants who entered the 5 m perimeter of the puzzle box, 30 interacted with the box on their first exposure and 44 interacted with it at least once across all of their experiences with the box. Of the 44 elephants who interacted with the box, 11 elephants solved one door type, eight elephants solved two door types and five elephants solved all three door types across all of their interactions (Supplementary Video S1). When looking at the frequency of different door types solved, of the 76 successful door opens when all doors were available in a box, 67% ($N = 51$) were push doors, 14% ($N = 11$) were pull doors and 18% ($N = 14$) were slide doors. Interactions with the box occurred when doors were already open in 27% ($N = 31$) of all 114 elephant interactions. The push door was already open for 25% ($N = 29$), the pull door was already open for 10% ($N = 11$) and the slide door was already open for 13% ($N = 15$) of all interactions.

First Visit and Interaction

Sex, age class or being in a group were not significantly associated with the likelihood that an elephant interacted with the puzzle box on its first exposure (Appendix, Table A2). When assessing first interactions and whether individual traits may influence success, we found that neophilia, sex, age class and whether the box was completely unopened were not predictive of success (Appendix, Table A3). EDS was significantly associated with success (estimate ± SE = 0.66 ± 0.17, $P < 0.001$) such that as EDS increased by 1, there was a 93% increase in the odds of success. Age class, sex and whether the box was completely unopened were not significantly associated with success (Table 2). Persistence, or the proportion of an observation's duration that an elephant was interacting with the puzzle box, was significantly associated with success (estimate ± SE = 0.62 ± 0.15, $P < 0.001$) such that as persistence increased by 0.10, there was an 86% increase in the odds of success. Age class, sex and whether the box was unopened were not significantly associated with success in this model either (Table 2).

Multiple Interactions

For elephants that interacted with the puzzle box multiple times, we first assessed the relative influence of EDS and persistence on success across the elephants' individual interactions. Both EDS and persistence were significantly associated with success (estimate ± SE: EDS: 0.17 ± 0.07, $P = 0.02$; persistence: 0.29 ± 0.10, $P < 0.001$), while sex, age class, interaction number and whether the box was completely unopened were not. As EDS increased by 1, there was a 19% increase in the odds of success and as persistence increased by 0.1, there was a 34% increase in the odds of success (Table 3).

Learning

Using the 'multiple interaction' data set and assessing the latency to solve the first door of the box in each interaction, the Cox proportional hazards model demonstrated that interaction number was significantly associated with solving latency (estimate ± SE = 0.12 ± 0.06, $P = 0.04$). This indicated that as interaction number increased, the hazard of a door being solved increased by 13% (Table 4); in other words, the latency to solve decreased as interaction number increased. Sex and age class were not significantly associated with solving latency (Table 4). However, when assessing solving latencies for each door type considering only interactions where that door type was available, there was no significant association between interaction number and solving latency for push, pull or slide solutions. Sex and age class also were not associated with solving latency in any of these models (Appendix, Table A4). Due to model convergence issues when including all variables for the slide door solving latencies, only sex and interaction number were included in the slide door model. We found that EDS was not associated with interaction number in the multiple interaction data set (Appendix, Table A5).

Overall Innovation

Overall innovation scores across all interactions were associated with age class (estimate ± SE = −1.24 ± 0.53, $P = 0.02$), such that subadults were less likely than adults to innovate (Appendix, Table A6). Cumulative innovation scores for each elephant's interactions who had access to all door types at least once were associated with persistence (estimate ± SE = 0.49 ± 0.16, $P = 0.002$) and interaction number (estimate ± SE = 0.52 ± 0.17, $P = 0.002$). Persistence and interaction number coefficients indicated that greater persistence and greater interaction numbers increased the probability of an elephant reaching a higher innovation score. The odds ratios indicated that an elephant was 1.64 times more likely to achieve a greater innovation score as persistence increased by 0.1 and was 1.69 times more likely to achieve a

Table 2
Parameter estimates of binomial logistic regression models for success in elephants' first interactions with the puzzle box

Model	Fixed effect	Estimate	SE	Odds ratio	Odds ratio 95% CIs	*z*	*P*
EDS[a]	**Intercept**	**−4.64**	**1.34**	**0.01**	**0.00, 0.10**	**−3.45**	**<0.001**
	EDS	**0.66**	**0.17**	**1.93**	**1.42, 2.75**	**3.94**	**<0.001**
	Sex (male)	0.33	0.74	1.39	0.34, 6.66	0.45	0.65
	Age class (subadult)	0.12	0.72	1.13	0.26, 4.59	0.17	0.87
	Unopened box (yes)	1.46	1.01	4.30	0.75, 45.77	1.44	0.15
Persistence[b]	**Intercept**	**−6.13**	**1.68**	**0.00**	**0.00, 0.04**	**−3.64**	**<0.001**
	Persistence[c]	**0.62**	**0.15**	**1.86**	**1.42, 2.59**	**4.10**	**<0.001**
	Sex (male)	0.93	0.85	2.54	0.51, 15.04	1.10	0.27
	Age class (subadult)	0.55	0.83	1.73	0.33, 9.39	0.66	0.51
	Unopened box (yes)	1.40	0.89	4.05	0.82, 31.13	1.57	0.12

CIs: confidence intervals; EDS: exploratory diversity score. Significant results are shown in bold ($P < 0.05$).
[a] $N = 44$, $df = 39$, McFadden's $R^2 = 0.21$.
[b] $N = 44$, $df = 39$, McFadden's $R^2 = 0.24$. Reference category: sex = female; age class = adult; unopened box = no.
[c] Persistence proportions were scaled so that a unit change in persistence = 0.10.

Table 3
Parameter estimates for the binomial logistic regression mixed model[a] for elephants that interacted with the puzzle box multiple times

Fixed effect	Estimate	SE	Odds ratio	Odds ratio 95% CIs	*z*	*P*
Intercept	**−4.30**	**1.28**	**0.01**	**0.00, 0.17**	**−3.36**	**<0.001**
EDS	**0.17**	**0.07**	**1.19**	**1.03, 1.38**	**2.35**	**0.02**
Persistence[b]	**0.29**	**0.10**	**1.34**	**1.10, 1.63**	**2.93**	**<0.001**
Sex (male)	0.77	0.91	2.16	0.37, 12.73	0.85	0.40
Age class (subadult)	0.78	1.19	2.19	0.21, 22.53	0.66	0.51
Interaction number	−0.05	0.07	0.95	0.82, 1.10	−0.72	0.47
Unopened box (yes)	0.86	0.60	2.35	0.72, 7.66	1.42	0.15

CIs: confidence intervals; EDS: exploratory diversity score. Significant results are shown in bold ($P < 0.05$).
[a] $N = 90$, $df = 82$, conditional $R^2 = 0.24$, marginal $R^2 = 0.20$. Reference category: sex = female; age class = adult; unopened box = no.
[b] Persistence proportions were scaled so that a unit change in persistence = 0.10.

Table 4
Parameter estimates for the Cox's proportional hazards model[a] of solving latency for first door solved, while accounting for individual differences across elephants' interactions

Fixed effect	Estimate	SE	Hazard ratio	Hazard ratio 95% CIs	*z*	*P*
Interaction number	**0.12**	**0.06**	**1.13**	**1.01, 1.27**	**2.05**	**0.04**
Sex (male)	0.49	0.73	1.63	0.39, 6.82	0.67	0.50
Age class (subadult)	−0.38	0.92	0.68	0.11, 4.11	−0.42	0.68

CIs: confidence intervals. Significant results are shown in bold ($P < 0.05$).
[a] The hazard ratio shows the proportional change in response to a unit change in interaction number or a change from the reference category (sex = female; age class = adult). $N = 90$.

greater innovation score as interaction number increased. The innovation score was not associated with EDS (Table 5). A likelihood ratio test between the cumulative link mixed model including elephant identity and a model without identity as a random factor demonstrated that the mixed model was significantly different ($\chi^2_1 = 18.89$, $P < 0.001$), indicating that there was significant variation in innovation score due to elephant identity (Fig. 2).

DISCUSSION

There was considerable individual variation in behaviour when elephants interacted with the puzzle box in this wild cognition experiment. This variation was exhibited in whether elephants interacted with the puzzle box at all, how many doors they were able to open on their first visit and how successful they were across multiple interactions with the puzzle box. For the elephants that interacted with the box at least once, there was wide variation in how many types of doors they were able to open across their interactions with the box. Most of these elephants opened a minimum of one door type, but only five individuals managed to open all three door types. This confirmed our expectation that there would be variability in innovation across the population and was also supported by the significant contribution of individual identity to variance in our model of innovation score. While this study is not directly comparable to our previous investigation in U.S. zoos (Jacobson et al., 2022), it is not surprising that a greater percentage

Table 5
Parameter estimates for a cumulative link mixed model[a] assessing cumulative innovation scores for elephants across multiple interactions

Fixed effect	Estimate	SE	Odds ratio	Odds ratio 95% CIs	*z*	*P*
EDS	0.22	0.14	1.25	0.96, 1.64	1.63	0.10
Persistence[b]	**0.49**	**0.16**	**1.64**	**1.19, 2.26**	**3.14**	**0.002**
Interaction number	**0.52**	**0.17**	**1.69**	**1.21, 2.37**	**3.06**	**0.002**

CIs: confidence intervals; EDS: exploratory diversity score. Significant results are shown in bold ($P < 0.05$).
[a] $N = 101$.
[b] Persistence proportions were scaled so that a unit change in persistence = 0.10.

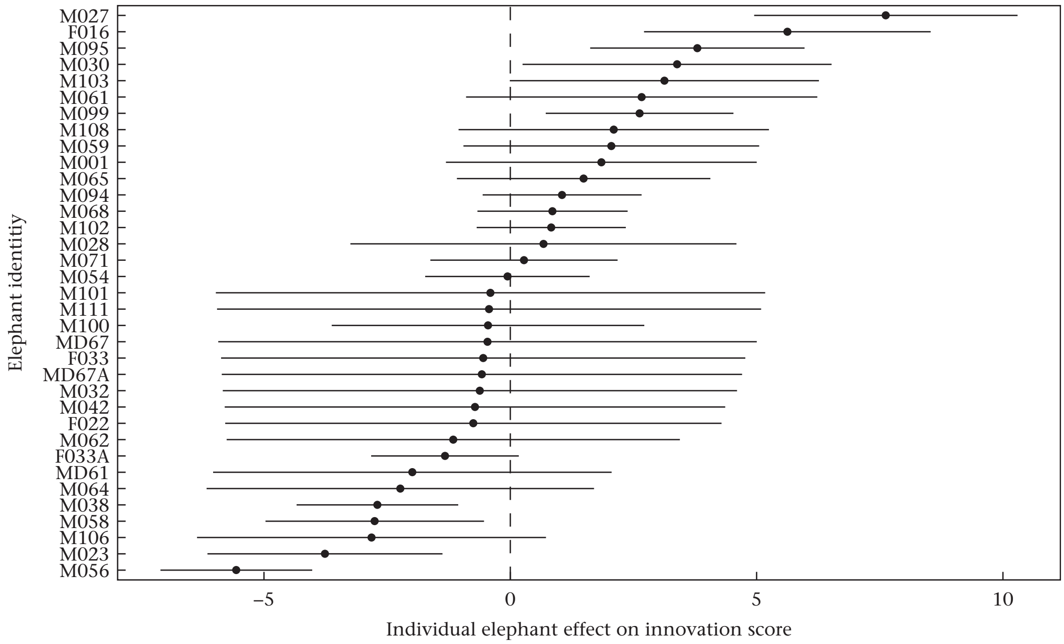

Figure 2. The conditional effect of elephant identity on innovation score and 95% confidence intervals of conditional variance compared to an average elephant in this sample. The dashed vertical line at 0 represents the average elephant in this sample.

of elephants tested in zoos (62%) compared to those tested in the wild (11%) were able to open all three doors given the dramatic differences in environment and experience. Zoo-housed elephants are often provided with enrichment devices that require extractive foraging (Greco et al., 2016), so were likely to have had experience 'problem solving' for food, whereas wild elephants graze and browse and rarely, if ever, have to extract food from or around obstacles. It is also likely that zoo-housed elephants have more motivation to work to get food rewards from the puzzle box because there are fewer competing motivations; in the wild, elephants have other significant priorities such as engaging in social group dynamics and obtaining natural food sources. The wild environment also presents more unpredictable risks or distractions than captivity, which could make wild individuals less likely to engage with a novel object in their environment or discourage them from consistently engaging with the box, a requirement for solving all the doors.

Not all behavioural traits we measured were associated with the wild elephants' performance. Persistence and exploratory diversity were associated with greater success in the elephants' first interactions with the puzzle box and across multiple interactions. However, when considering the cumulative innovation scores representing how many different doors elephants were able to open, only greater persistence and interaction number were associated with reaching a higher innovation score. We observed that elephants who interacted with the box multiple times learned to open a door of any type more quickly as their interactions increased, but we did not see evidence of learning to open specific door types over time.

First Visit

Over half of the individuals who came within 5 m of the box interacted with it the first time they saw it. Surprisingly, none of the variables that we predicted would influence the likelihood of interacting with this novel object in their environment were associated with the likelihood of interaction in the first visit. We had hypothesized that females would be less likely to interact with the box than males due to the potential risk that a novel object presents to accompanying calves. We also predicted that subadults would be more likely to interact with the box than adults due to greater exploration in younger individuals observed in other species (e.g. hyaenas: Benson-Amram & Holekamp, 2012; meerkats, *Suricata suricatta*: Thornton & Sampson, 2012). However, it appears that individual differences in interest in the puzzle box or the elephants' potential perception of it as a threat, which may be related to personality traits, drove the likelihood of interacting with the puzzle box rather than sex or age. While we had predicted that whether an elephant was with a group would affect the likelihood of them interacting with the puzzle box, this factor also did not have an influence.

First Interaction

To assess factors that may have influenced the individual variation in doors successfully solved, we further investigated how the behavioural traits of neophilia, EDS and persistence affected individuals' success in their first interaction with the box. We chose to first assess success only in the first interaction so that we could evaluate elephants with comparable experience and include the most elephants (since many individuals only interacted with the box a single time). Contrary to our prediction, neophilia towards the box was not associated with success in this task. This aligns with our results for captive elephants (Jacobson et al., 2022) and provides support for the idea that attraction to novelty may not have a strong influence on innovation (reviewed in Griffin & Guez, 2014). While attraction to the novel puzzle box was measured as neophilia in this study, it would be interesting to see whether measuring an individual's degree of neophilia as a repeatable trait (i.e. testing for it in multiple contexts, both with and without food) would be associated with the elephant's innovative abilities. It is possible that the elephants' responses to novelty are impacted by the presence of food, as in the puzzle box, and thus removing food and providing more than one measure of neophilia with multiple novel objects could yield different results.

Persistence was associated with success in the first interaction, supporting our hypothesis and providing results similar to those we found for zoo-housed elephants (Jacobson et al., 2022). Many studies with other species have also found that the more an individual interacts with a puzzle box, the more likely they are to find one or more solutions (e.g. Griffin et al., 2014; Johnson-Ulrich et al., 2018; O'Connor et al., 2022; Petelle et al., 2022). As we hypothesized, greater EDS was also associated with greater success, a result that has been shown in other species as well (e.g. raccoons: Daniels et al., 2019; hyaenas: Johnson-Ulrich et al., 2018; chimpanzees, *Pan troglodytes*: Massen et al., 2013; marmots: Williams et al., 2021). This result supports the idea that the more actions an individual attempts when interacting with a puzzle, the more likely they are to perform a combination of actions that result in an innovation. Interestingly, this association between EDS and success was in the opposite direction of that demonstrated in our zoo study, where we observed that lower EDS was associated with success for elephants. However, the study with zoo-housed elephants followed a different protocol than the current study with a wild population. The zoo-housed elephants were provided with two phases; the first provided three push-door compartments, while the second was identical to the current study and provided all three door types. The initial experience solving one type of solution may have shaped the exploratory actions that zoo-housed elephants used in the second phase to innovate. Specifically, this experience could have influenced the elephants' use of fewer actions in the second phase because they were already ‘primed’ to use actions that had been successful in opening push doors (Jacobson et al., 2022).

Multiple Interactions

For the 20 elephants that interacted with the puzzle box more than once, we wanted to assess the relative influence of persistence and EDS on their success across trials. We found that both were significantly associated with greater success even when accounting for the influence of the other and for the fixed effects of age class, sex and interaction number. Age class and sex were not significantly associated with success, which was not surprising since neither variable affected success during the elephants' first interactions. We were surprised that interaction number did not affect success, because we predicted that the more experience that elephants had interacting with the puzzle box, the more successful they would be in innovating to solve more door types. This may have been confounded, however, by the fact that elephants did not always have the opportunity to open all door types in each interaction, and the actions learned for one door may not apply to the actions needed to open another.

Elephants likely learned that rewards could be retrieved from the box over multiple interactions, as results showed that latency to solve the first door in each interaction decreased as the number of interactions increased. However, this analysis did not consider whether the first door opened was the same door type in each interaction. When we focused the analysis on instances of solving only the same type of door in subsequent interactions, we did not see a significant association between interaction number and the latency to solve any of the door types. Therefore, it appears that while elephants may have been able to access food more quickly with more experience with the puzzle box, they may not have learned particular solutions over time in this study. It is possible that this is due to the features of our apparatus; with multiple solutions and rewards available simultaneously, elephants may not focus on specific solutions as they interact with the puzzle box. The solving latency measure we used to assess learning only accounted for time interacting with the box after solving the previous door, unless the door in question was the first solved, in order to separate out interactions focused on other solution types. However, this latency may still include other interactions by elephants such as reaching into empty compartments that are not related to solving unopened doors. Therefore, latencies may not be the best way to measure learning with this type of apparatus. We also looked at EDS as a potential assessment of learning, as exploratory diversity is expected to decrease over time as solutions are learned (Benson-Amram & Holekamp, 2012). However, we did not find an association between interaction number and EDS across the elephants' multiple interactions with the puzzle box. This also supports the possibility that elephants were learning more generally about how to interact with the box but not necessarily learning specific actions.

Overall Innovation

For overall innovation scores across all interactions, we found that subadult elephants innovated less than adults; these results are in line with those of other studies showing that older individuals tend to be more innovative (Amici et al., 2019). Our analysis of cumulative innovation scores across elephants' interactions demonstrated the continued importance of persistence in leading to higher scores. Persistence was also apparent in another sense, as persistently visiting the puzzle box and getting more experience interacting with it (i.e. greater interaction numbers) led to higher innovation scores. Interestingly, EDS was not associated with innovation score as we had expected based on its association with success for elephants' first interactions and for multiple interactions with the puzzle box. Given the potential for elephants to interact with a box with some doors already solved in this wild setting, our measure of success across multiple interactions may reflect individuals solving the same type of door multiple times when other doors were not available. This could mean that while using more types of actions helped elephants continue to solve door types they had already solved, it did not contribute to their ability to innovate new solutions. Potentially, the higher success associated with higher EDS in elephants' first interactions demonstrates that this behavioural trait is important for an initial innovation but may not influence elephants' abilities to repeatedly innovate beyond the first success in subsequent experiences. In addition, the design of our puzzle box makes disentangling the relationship between EDS, learning and repeated innovations challenging. If the EDS decreases for a particular solution to a door once that door is solved, then this may impact the overall EDS for that elephant's interaction.

Unlike most studies investigating innovation that have used a multi-access box with multiple solutions available to reach one reward (e.g. Daniels et al., 2019; Johnson-Ulrich et al., 2018), our puzzle box had multiple solutions that were each rewarded and available simultaneously, allowing us to opportunistically collect the most data possible in a single visit by an elephant. We were also unable to intentionally change the availability of doors based on an individual's previous success to encourage further innovation since we could not guarantee that the same elephant would visit on any given day. These methodological differences may have influenced elephants in our population to be less motivated to focus on previously unsolved door types when rewards could be retrieved from other doors. This focus may have also changed the diversity of actions that an elephant performed when interacting with the box such that they were not attempting as many different actions as animals may exhibit when the only option to retrieve food is a previously unsolved door (as in Daniels et al., 2019; Johnson-Ulrich et al., 2018). Therefore, our apparatus design and protocol, which were tied to the constraints of testing elephants in the wild, may explain why EDS was not significantly associated with innovation score in this analysis, contrary to the positive relationship observed in other studies with the standard apparatus design (e.g. Daniels et al., 2019; Johnson-Ulrich et al., 2018; Williams et al., 2021).

While we believe it is important to test cognition in Asian elephants in the wild, we recognize that our lack of control in some aspects of this study also could have influenced the results. Individuals did not always have equal experience with the puzzle box, as some may have encountered it freshly baited and others when conspecifics had already opened doors. We attempted to create measures that accounted for this variability and we analysed different subsets of these data for this reason, but those variable experiences could still have impacted our results. In addition, many elephants appeared to be motivated by the food reward, even though it is a small part of their daily food intake, but there were likely many other competing motivations in the wild. For example, vocalizations by a nearby group of elephants or the sexual state of either the subject or surrounding elephants may have influenced whether an individual consistently interacted with or even visited the puzzle box. Unlike in the zoo study, elephants were completely free to engage with other individuals at any time. We were also unfortunately not able to control for olfactory cues from other elephants on the surface of the box due to the difficulty of removing any trace of elephant scent in the field. In any case, solved doors could not be 're-solved' by elephants arriving later (but prior to any rebaiting by the experimenters), and thus we do not suspect that odour cues from other elephants had a significant impact on late-arriving elephants' tendencies to solve other doors. It is possible that elephants that initially encountered an already-solved box were less likely to interact with it in subsequent visits due to their initial unrewarded experience, however, we believe that the presence of the food reward would override this possibility.

Information about variation in innovative ability and associated traits in Asian elephants is important not only for comparisons of innovation across species, but also for the development of novel conservation strategies. Innovation is a cognitive ability that can allow an individual to adapt quickly to novel environments (Lefebvre et al., 2004). In rapidly changing anthropogenic landscapes, behavioural flexibility is an adaptive strategy for navigating human-dominated landscapes and obtaining alternative food sources (Barrett et al., 2018). While learning to forage on agricultural crops may be beneficial for elephants' survival and reproduction, it also leads to increased negative interactions between farmers and wildlife. This conflict can result in injuries or death for both people and elephants and negatively affects people's livelihoods (Fernando et al., 2008). This consequently leads to a drop in people's support for conservation efforts (Barua et al., 2013; Shaffer et al., 2019). We aim to expand our puzzle box study to other locations inside and on the periphery of Salakpra to compare innovation in individuals that spend time in both human-dominated and protected landscapes. This comparison will contribute to one of our long-term applied research goals of identifying characteristics that relate to an elephant's likelihood of foraging in crops and overcoming the barriers erected to keep them out. It is possible that innovation will vary based on the level of risk each location exhibits and that elephants with particular personality or cognitive profiles will be more likely to engage in human–elephant conflict (Plotnik & Jacobson, 2022). This would have important implications for both our understanding of how innovative abilities impact wildlife decision making in anthropogenic landscapes, as well as for the development of conservation strategies that take wildlife behaviour, cognition and personality at the individual rather than the population level into consideration. Conducting cognitive studies in a wild environment is challenging. However, it provides the best opportunity for both maximizing ecological validity when investigating a species' behavioural and cognitive flexibility and for demonstrating the importance of the field of animal cognition to wildlife conservation.

Author Contributions

Sarah L. Jacobson conceived and designed the study, collected data, coded videos and analysed the data, prepared figures and/or tables, authored or reviewed drafts of the article and approved the final draft. Juthapathra Dechanupong designed the study, collected data, authored or reviewed drafts of the article and approved the final draft. Wantida Horpiencharoen designed the study, collected data, authored or reviewed drafts of the article and approved the final draft. Marnoch Yindee administered the study, authored or reviewed drafts of the article and approved the final draft. Joshua M. Plotnik conceived and designed the study, administered the study, authored or reviewed drafts of the article and approved the final draft.

Data Availability

Data and R scripts used for this study are available in the figshare repository https://doi.org/10.6084/m9.figshare.22662526.

Declaration of Interest

J.M.P. is founder of Think Elephants International, Inc., an elephant conservation charity. Otherwise, the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgments

We thank two anonymous referees for their helpful suggestions in revising this manuscript. We thank Parntep Ratanakorn for his facilitation of our collaborations during this study. We also thank the National Research Council of Thailand, the Thai Department of National Parks, Wildlife and Plant Conservation and the Salakpra Wildlife Sanctuary (particularly the sanctuary chief, Paitoon Intarabut, and his staff) for allowing us to conduct this research. We are appreciative of Alexander Godfrey's assistance with the puzzle box design and discussions with the Oklahoma City Zoo staff regarding the initial design of the apparatus used in an earlier study in captivity. Thank you to our field team in Thailand (Weerach Charerntantanakul, Pornpimol Kubsanit and Prawit Innoy) for collecting all the videos from the field and maintaining the camera traps and to the park rangers and local community members in Kanchanaburi, Thailand that provided invaluable assistance and support during this study. Thank you to Melissa Schmitt for guidance on the analyses performed in this study and to Sabana Gonzalez for her assistance with coding for interrater reliability. Lastly, many thanks to Miranda Trapani, Robbie Ball and Matthew Rudolph for their assistance confirming the identities of elephants in this study. This work was funded by the U.S. Fish and Wildlife Service's Asian Elephant Conservation Fund (Grants F18AP00456; F19AP00052; F22AP00035), Elephant Family (Grant THA-175), the Golden Triangle Asian Elephant Foundation and the Research Foundation of the City University of New York on behalf of Hunter College. This material is based upon work supported by a U.S. National Science Foundation Graduate Research Fellowship under Grant No. (DGE-1646736) awarded to S.L.J.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2023.08.019.

References

Amici, F., Widdig, A., Lehmann, J., & Majolo, B. (2019). A meta-analysis of interindividual differences in innovation. *Animal Behaviour, 155*, 257–268. https://doi.org/10.1016/j.anbehav.2019.07.008

Auersperg, A. M. I., von Bayern, A. M. P., Gajdon, G. K., Huber, L., & Kacelnik, A. (2011). Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PLoS One, 6*(6), Article e20231. https://doi.org/10.1371/journal.pone.0020231

Austin, P. C. (2017). A tutorial on multilevel survival analysis: Methods, models and applications. *International Statistical Review, 85*(2), 185–203. https://doi.org/10.1111/insr.12214

Barrett, L. P., & Benson-Amram, S. (2021). Multiple assessments of personality and problem-solving performance in captive Asian elephants (*Elephas maximus*) and African savanna elephants (*Loxodonta africana*). *Journal of Comparative Psychology, 135*(3), 406–419. https://doi.org/10.1037/com0000281

Barrett, L. P., Stanton, L. A., & Benson-Amram, S. (2018). The cognition of 'nuisance' species. *Animal Behaviour, 147*, 167–177. https://doi.org/10.1016/j.anbehav.2018.05.005

Barua, M., Bhagwat, S. A., & Jadhav, S. (2013). The hidden dimensions of human–wildlife conflict: Health impacts, opportunity and transaction costs. *Biological Conservation, 157*, 309–316. https://doi.org/10.1016/j.biocon.2012.07.014

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

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

Biondi, L. M., Fuentes, G., & Susana, M. (2022). Behavioural factors underlying innovative problem-solving differences in an avian predator from two contrasting habitats. *Animal Cognition, 25*(3), 529–543. https://doi.org/10.1007/s10071-021-01569-2

Bird, C. D., & Emery, N. J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences of the United States of America, 106*(25), 10370–10375. https://doi.org/10.1073/pnas.0901008106

Byrne, R. W., Bates, L. A., & Moss, C. J. (2009). Elephant cognition in primate perspective. *Comparative Cognition & Behavior Reviews, 4*, 65–79. https://doi.org/10.3819/ccbr.2009.40009

Chaiyarat, R., Youngpoy, N., & Prempree, P. (2015). Wild Asian elephant *Elephas maximus* population in Salakpra Wildlife Sanctuary, Thailand. *Endangered Species Research, 29*(2), 95–102. https://doi.org/10.3354/esr00706

Christensen, R. H. B. (2022). *ordinal: Regression models for ordinal data* (R package Version 2022.11-16). https://CRAN.R-project.org/package=ordinal.

Daniels, S. E., Fanelli, R. E., Gilbert, A., & Benson-Amram, S. (2019). Behavioral flexibility of a generalist carnivore. *Animal Cognition, 22*, 387–396. https://doi.org/10.1007/s10071-019-01252-7

Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. (2003). Neophilia, innovation and social learning: A study of intergeneric differences in callitrichid monkeys. *Animal Behaviour, 65*(3), 559–571. https://doi.org/10.1006/anbe.2003.2074

Fernando, P., Kumar, M. A., Williams, A. C., Wikramanayake, E., Aziz, T., & Singh, S. M. (2008). *Review of human–elephant conflict mitigation measures practiced in South Asia*. Gland, Switzerland: WWF.

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

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

Greco, B. J., Meehan, C. L., Miller, L. J., Shepherdson, D. J., Morfeld, K. A., Andrews, J., Baker, A. M., Carlstead, K., & Mench, J. A. (2016). Elephant management in North American zoos: Environmental enrichment, feeding, exercise, and training. *PLoS One, 11*(7), Article e0152490. https://doi.org/10.1371/journal.pone.0152490

Greenberg, J. R., & Holekamp, K. E. (2017). Human disturbance affects personality development in a wild carnivore. *Animal Behaviour, 132*, 303–312. https://doi.org/10.1016/j.anbehav.2017.08.023

Griffin, A. S., & Diquelou, M. C. (2015). Innovative problem solving in birds: A cross-species comparison of two highly successful passerines. *Animal Behaviour, 100*, 84–94. https://doi.org/10.1016/j.anbehav.2014.11.012

Griffin, A. S., Diquelou, M., & Perea, M. (2014). Innovative problem solving in birds: A key role of motor diversity. *Animal Behaviour, 92*, 221–227. https://doi.org/10.1016/j.anbehav.2014.04.009

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes, 109*, 121–134. https://doi.org/10.1016/j.beproc.2014.08.027

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models* (R package version 0.4.6). https://CRAN.R-project.org/package=DHARMa.

Jacobson, S. L., Puitiza, A., Snyder, R. J., Sheppard, A., & Plotnik, J. M. (2022). Persistence is key: Investigating innovative problem solving by Asian elephants using a novel multi-access box. *Animal Cognition, 25*, 657–669. https://doi.org/10.1007/s10071-021-01576-3

Jahn-Eimermacher, A., Lasarzik, I., & Raber, J. (2011). Statistical analysis of latency outcomes in behavioral experiments. *Behavioural Brain Research, 221*(1), 271–275. https://doi.org/10.1016/j.bbr.2011.03.007

Johnson-Ulrich, L., Johnson-Ulrich, Z., & Holekamp, K. (2018). Proactive behavior, but not inhibitory control, predicts repeated innovation by spotted hyenas tested with a multi-access box. *Animal Cognition, 21*(3), 379–392. https://doi.org/10.1007/s10071-018-1174-2

Kawai, M. (1965). Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates, 6*, 1–30.

Klump, B. C., Major, R. E., Farine, D. R., Martin, J. M., & Aplin, L. M. (2022). Is bin-opening in cockatoos leading to an innovation arms race with humans? *Current Biology, 32*(17), R910–R911. https://doi.org/10.1016/j.cub.2022.08.008

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences, 308*(1135), 203–214.

Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution, 63*(4), 233–246. https://doi.org/10.1159/000076784

Lefebvre, L., Whittle, P., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour, 53*, 549–560.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software, 6*(60), Article 3139. https://doi.org/10.21105/joss.03139

Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour, 85*(1), 195–202. https://doi.org/10.1016/j.anbehav.2012.10.026

Massen, J. J. M., Antonides, A., Arnold, A. M. K., & Bionda, T. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology, 75*(9), 947–958. https://doi.org/10.1002/ajp.22159

McKay, G. M. (1973). *Behavior and ecology of the Asiatic elephant in southeastern Ceylon. Smithsonian Contributions to Zoology, No. 125*. Smithsonian Institution Press.

Menon, V., & Tiwari, S. K. (2019). Population status of Asian elephants *Elephas maximus* and key threats. *International Zoo Yearbook, 53*(1), 17–30. https://doi.org/10.1111/izy.12247

Montero- De La Torre, S., Jacobson, S. L., Yindee, M., & Plotnik, J. M. (2023). Day and night camera trap video is effective for identifying wild Asian elephants. *PeerJ, 11*, Article e15130. https://doi.org/10.7717/peerj.15130

Moretti, L., Hentrup, M., Kotrschal, K., & Range, F. (2015). The influence of relationships on neophobia and exploration in wolves and dogs. *Animal Behaviour, 107*, 159–173. https://doi.org/10.1016/j.anbehav.2015.06.008

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), Article e91749. https://doi.org/10.1371/journal.pone.0091749

Nandini, S., Keerthipriya, P., & Vidya, T. N. C. (2017). Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. *Animal Behaviour, 134*, 135–145. https://doi.org/10.1016/j.anbehav.2017.10.012

Natarajan, L., Kumar, A., Qureshi, Q., Desai, A. A., & Pandav, B. (2021). Evaluation of wall-barriers to manage human conflict with Asian elephants in India. *Wildlife Society Bulletin, 45*(2), 215–220. https://doi.org/10.1002/wsb.1195

O'Connor, V. L., Thomas, P., Chodorow, M., & Borrego, N. (2022). Exploring innovative problem-solving in African lions (*Panthera leo*) and snow leopards (*Panthera uncia*). *Behavioural Processes, 199*, Article 104648. https://doi.org/10.1016/j.beproc.2022.104648

Petelle, M. B., Jacobs, P. J., & le Roux, A. (2022). Innovative problem-solving in a small, wild canid. *Animal Cognition, 26*, 405–413. https://doi.org/10.1007/s10071-022-01678-6

Plotnik, J. M., & Jacobson, S. L. (2022). A 'thinking animal' in conflict: Studying wild elephant cognition in the shadow of anthropogenic change. *Current Opinion in Behavioral Sciences, 46*, Article 101148. https://doi.org/10.1016/j.cobeha.2022.101148

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America, 99*(7), 4436–4441. https://doi.org/10.1073/pnas.062041299

Reader, S. M., & Laland, K. N. (2003). Animal innovation: An introduction. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 3–36). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198526223.003.0001.

Shaffer, L. J., Khadka, K. K., Van Den Hoek, J., & Naithani, K. J. (2019). Human–elephant conflict: A review of current management strategies and future directions. *Frontiers in Ecology and Evolution, 6*, Article 235. https://www.frontiersin.org/articles/10.3389/fevo.2018.00235.

Sherratt, T. N., & Morand-Ferron, J. (2018). The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Animal Behaviour, 138*, 59–67. https://doi.org/10.1016/j.anbehav.2018.01.025

de Silva, S., Ranjeewa, A. D., & Kryazhimskiy, S. (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology, 11*(1), Article 17. https://doi.org/10.1186/1472-6785-11-17

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America, 102*(15), 5460–5465. https://doi.org/10.1073/pnas.0408145102

Srinivasaiah, N., Kumar, V., Vaidyanathan, S., Sukumar, R., & Sinha, A. (2019). All-male groups in Asian elephants: A novel, adaptive social strategy in increasingly

anthropogenic landscapes of southern India. *Scientific Reports, 9*(1), Article 8678. https://doi.org/10.1038/s41598-019-45130-1
Sukumar, R. (2006). A brief review of the status, distribution and biology of wild Asian elephants *Elephas maximus*. *International Zoo Yearbook, 40*(1), 1–8. https://doi.org/10.1111/j.1748-1090.2006.00001.x
Therneau, T. (2023). *A package for survival analysis in R* (R package Version 3.5-0). https://CRAN.R-project.org/package=survival.
Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour, 83*(6), 1459–1468. https://doi.org/10.1016/j.anbehav.2012.03.018
Thouless, C. R., & Sakwa, J. (1995). Shocking elephants: Fences and crop raiders in Laikipia District, Kenya. *Biological Conservation, 72*(1), 99–107. https://doi.org/10.1016/0006-3207(94)00071-W
Visalberghi, E., & Addessi, E. (2000). Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Animal Behaviour, 60*(1), 69–76. https://doi.org/10.1006/anbe.2000.1425
van de Water, A., & Matteson, K. (2018). Human–elephant conflict in western Thailand: Socio-economic drivers and potential mitigation strategies. *PLoS One, 13*(6), Article e0194736. https://doi.org/10.1371/journal.pone.0194736
Webster, S. J., & Lefebvre, L. (2001). Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour, 61*, 23–32. https://doi.org/10.1006/anbe.2000.1725
Williams, C., Tiwari, S. K., Goswami, V. R., De Silva, S., Kumar, A., Baskaran, N., Yoganand, K., & Menon, V. (2020). *Elephas maximus. The IUCN red list of threatened species* (Version 2020: e.T7140A45818198). https://www.iucnredlist.org/species/7140/45818198 [Retrieved December 2021].
Williams, D. M., Wu, C., & Blumstein, D. T. (2021). Social position indirectly influences the traits yellow-bellied marmots use to solve problems. *Animal Cognition, 24*, 829–842. https://doi.org/10.1007/s10071-020-01464-2
Young, J. K., Touzot, L., & Brummer, S. P. (2019). Persistence and conspecific observations improve problem-solving abilities of coyotes. *PLoS One, 14*(7), Article e0218778. https://doi.org/10.1371/journal.pone.0218778

Appendix

Table A1
Ethogram of the possible behaviours and body parts used by the elephants in their interactions with the box

Behaviour	Possible body part used	Definition
Pushing	(1) Trunk middle, (2) trunk base, (3) head, (4) body, (5) foot	Touching with visible pressure on box surface, typically accompanied by a swift approach and/or a noisy impact
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 or the height of the box; continuous, repetitive back-and-forth pressure on the box
Investigation	Not specified	Using trunk tip to investigate surface of the box using a variety of pressure
Blowing	Not specified	Releasing air audibly from the trunk when interacting with box
Grasping	Not specified	Using trunk to curl around or using trunk tip to grip an extended feature of the box
Reaching	Not specified	Extending trunk over the top of the box to the other side and can include trunk pressure down onto the surface of the box and pulling towards the elephant
Mouthing	Not specified	Using open mouth or tongue to apply pressure on the surface of the box
Pulling	Not specified	Elephant moves trunk inwards towards itself and/or downward while grasping chain
Interaction with the box	Not specified	Time from when individual first contacts the box until contact stops for at least 5 s

Table A2
Parameter estimates for the binary logistic regression model[a] of elephants interacting with the puzzle box when first exposed to the box

Fixed effect	Estimate	SE	Odds ratio	Odds ratio 95% CIs	*z*	*P*
Intercept	−1.17	0.76	0.31	0.06, 1.30	−1.53	0.13
Sex (male)	0.72	0.78	2.06	0.47, 11.16	0.93	0.35
Age class (subadult)	0.23	0.51	1.26	0.46, 3.42	0.46	0.65
Group (yes)	0.49	0.78	1.63	0.37, 8.72	0.62	0.53

CIs: confidence intervals.
[a] $N = 77$, $df = 76$, McFadden's $R^2 = 0.01$. Reference category: sex = female; age class = adult; group = not in a group.

Table A3
Parameter estimates for the binomial logistic regression model[a] of success for elephants' first interactions with the puzzle box

Fixed effect	Estimate	SE	Odds ratio	Odds ratio 95% CIs	*z*	*P*
Intercept	**−1.86**	**0.89**	**0.16**	**0.02, 0.76**	**−2.10**	**0.04**
Neophilia	0.005	0.01	1.00	0.99, 1.02	0.66	0.51
Sex (male)	0.16	0.66	1.17	0.34, 4.72	0.24	0.81
Age class (subadult)	−1.04	0.60	0.35	0.09, 1.07	−1.72	0.09
Unopened box (yes)	0.61	0.83	1.84	0.42,13.02	0.73	0.46

CIs: confidence intervals. Significant results are shown in bold ($P < 0.05$).
[a] $N = 44$, $df = 39$, McFadden's $R^2 = 0.05$. Reference category: sex = female; age class = adult; unopened box = no.

Table A4
Parameter estimates for Cox's proportional hazards models[a] of solving latency for push doors ($N_{solves} = 65$, $N_{elephant} = 15$), pull doors ($N_{solves} = 84$, $N_{elephant} = 20$) and slide doors ($N_{solves} = 75$, $N_{elephant} = 18$)

Model	Fixed effect	Estimate	SE	Hazard ratio	Hazard ratio 95% CIs	*z*	*P*
Push door solving latency	Interaction number	0.09	0.06	1.09	0.97, 1.23	1.41	0.16
	Sex (male)	−0.70	0.74	0.50	0.12, 2.12	−0.94	0.35
	Age class (subadult)	−1.47	1.23	0.23	0.02, 2.53	−1.20	0.23
Pull door solving latency	Interaction number	−0.27	0.21	0.76	0.51, 1.14	−1.32	0.19
	Sex (male)	−0.24	1.31	0.79	0.06, 10.19	−0.18	0.85
	Age class (subadult)	0.86	1.58	2.35	0.11, 52.21	0.54	0.59
Slide door solving latency	Interaction number	−0.10	0.14	0.90	0.68, 1.19	−0.73	0.47
	Sex (male)	0.79	1.19	2.20	0.21, 22.85	0.66	0.51

CIs: confidence intervals.
[a] The hazard ratio shows the proportional change in response to a unit change in interaction number or a change from the reference category (sex = female; age class = adult).

Table A5
Parameter estimates for Poisson regression model[a] of elephants' exploratory diversity scores across multiple interactions

Fixed effect	Estimate	SE	Odds ratio	Odds ratio 95% CIs	*z*	*P*
Intercept	**1.13**	**0.12**	**3.10**	**2.45, 3.94**	**9.35**	**<0.001**
Interaction number	0.02	0.03	1.02	0.96, 1.07	0.58	0.56

CIs: confidence intervals. Significant results are shown in bold ($P < 0.05$).
[a] $N = 90$.

Table A6
Parameter estimates for Poisson regression model[a] of overall innovation score for each elephant

Fixed effect	Estimate	SE	Odds ratio	Odds ratio 95% CIs	*z*	*P*
Intercept	0.03	0.51	1.04	0.31, 2.48	0.07	0.95
Sex (male)	0.40	0.53	1.49	0.59, 5.01	0.75	0.45
Age class (subadult)	**−1.24**	**0.53**	**0.29**	**0.09, 0.73**	**−2.34**	**0.02**

CIs: confidence intervals. Significant results are shown in bold ($P < 0.05$).
[a] $N = 35$. Reference category: sex = female; age class = adult.