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How does object play shape tool use emergence? Integrating observations and field experiments in longtailed macaques

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It has long been suggested that object play facilitates the development and evolution of tool use, through enhanced perception of an object's properties and potential for manipulation. However, ecologically relevant support for this claim is scant. We examined whether a form of culturally maintained object play, named stone handling, characterized by high interindividual variation in its behavioural expression, promotes the acquisition and further expression of stone-tool use in a nonhuman primate species.

We conducted a series of field experiments in a free-ranging group of Balinese longtailed macaques, *Macaca fascicularis*, to test whether the stone-handling profiles of different individuals predicted their ability to solve a foraging task, whose solution required the functional and action-specific use of stones as tools. Frequentist network-based diffusion analysis, Bayesian multilevel regression modelling and descriptions of individuals' learning trajectories showed that the solutions to different foraging tasks required varying reliance on social and asocial learning strategies. Our results suggest that certain stone-handling profiles may increase an individual's likelihood of expressing stone-tool use. However, other trait- and state-dependent variables may also contribute to explaining individual differences in the development and expression of stone-tool use. The behavioural idiosyncrasies associated with stone handling in longtailed macaques may serve as an exaptive reservoir for the possible emergence of stone-tool use. To our knowledge, this is the first study to experimentally evaluate the role of stone-directed play in the acquisition of stone-tool use.

Tools and utilitarian artefacts permeate humans' lives. Hence, they have played a pivotal role in theories of human evolution and much attention has been given to how the ability to skilfully manipulate objects in an instrumental way emerges. It has long been suggested that the playful manipulation of objects facilitates the development and evolution of tool use (Bruner, 1972; Parker & Gibson, 1977). Indeed, children and juveniles (and to a lesser extent adults) of several species that habitually use tools spend a large amount of time playing with and exploring novel objects (e.g. children: Smith & Connolly, 1980; chimpanzees, *Pan troglodytes*: Ramsey & McGrew, 2005; capuchin monkeys, *Sapajus apella*: Jordan et al., 2022; longtailed macaques, *Macaca fascicularis*: Tan, 2017; New Caledonian crows, *Corvus moneduloides*: Lambert et al., 2017). The idea that play is a particularly potent experience for the development of tool use is at the core of the affordance learning theory (Gibson, 1979; Gibson, 1982). According to this view, which is rooted in the perception–action framework (Lockman, 2000), during pressure-free opportunities for object manipulation that are integral to object-directed play, an individual's visual and tactile experience with objects allows them to perceive the objects' potential for actions, including how to use these objects as tools (Lockman, 2000). Affordance learning theory has gained strong support in developmental psychology, a discipline in which experimental evidence from preschool children showed a facilitatory effect of object play in problem-solving tasks involving tools (e.g. Sylva et al., 1976), and in cognitive psychology, a

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field in which evidence from captive apes experimentally showed that the ability to combine objects (e.g. sticks and clamps) into tools improved after playful manipulation (e.g. Birch, 1945). However, the affordance learning theory remains loosely and inconsistently tested and empirical evidence connecting these two activities across animal taxa is scant (Smith, 2010).

In captive nonhuman animals, several experimental studies have suggested that exploratory, playful manipulation without the presentation of supplemental rewards promotes the acquisition of instrumental knowledge of objects (e.g. Birch, 1945; Jordan et al., 2020; Polizzi di Sorrentino et al., 2014). In an experimental study on four great ape species, Ebel and Call (2018) tested whether previous playful manipulation of an empty puzzle box facilitated its opening when baited with food, which required subjects to drop a stone inside a tube to release the reward (i.e. a tool use task). Of the 25 apes tested, the ones who first had the opportunity to playfully manipulate the empty apparatus were quicker to solve the puzzle box in the baited condition, compared to the ones that did not have this pretest exposure. Additionally, when considering the first trial in both conditions (i.e. whether the puzzle box was baited with food or not), individuals starting with the food-baited puzzle box took longer to drop a stone inside the tube than those who started with the nonbaited puzzle box; thus, intrinsically motivated object manipulation, such as object play, may provide meaningful information on the action–outcome affordances of a task. Even though these results provide some support for the affordance learning theory, they come with two main caveats.

First, the study by Ebel and Call (2018), like most other studies exploring the relationship between playful manipulation and acquisition of instrumental object-related knowledge, tested captive animals. It is noteworthy that in captive settings, animals outperform their wilder counterparts on cognitive tasks, including tool use tasks; this phenomenon is known as the ‘captivity bias’ (Haslam, 2013). For instance, species that have not been observed using tools (or do not do so extensively) in the wild are occasionally able to combine objects to solve foraging tasks in captive settings (Bandini & Tennie, 2020). Specifically, bonobos, *Pan paniscus*, and gorillas, *Gorilla gorilla*, which were tested by Ebel and Call (2018), are not proficient and habitual tool users in the wild (but see Samuni et al., 2022 for an example of tool use in three wild communities of bonobos); still, they were able to provide stone tool-assisted solutions to the puzzle box similarly to the chimpanzees and orang-utans, *Pongo abelii*, tested by Ebel and Call (2018). Second, although laboratory settings have high internal validity, by allowing for controlled conditions to individually test subjects and a detailed examination of their individual learning pathways, they do not replicate the environmental context in which animals acquire tool use in the wild. Indeed, evidence from field research emphasizes the complex interplay of asocial and social strategies in learning how to use tools (e.g. chimpanzees: Whiten et al., 2022; bearded capuchin monkeys, *Sapajus libidinosus*: Falótico, 2022; New Caledonian crows: Holzhaider et al., 2010). Whenever possible, an individual's social environment should be taken into consideration when inferring how animals acquire physical knowledge of their surroundings (Rowe & Healy, 2014). Thus, taken together, these limitations prompt researchers to question the ecological validity of conclusions coming from laboratory studies and to consider whether wild populations of nonhuman animals rely on similar perception–action processes when acquiring instrumental object manipulation.

To date, there are no reports on whether object-directed playful manipulation facilitates tool use in wild groups of nonhuman animals. However, evidence from innovative problem-solving experiments (involving tools or not) suggests that a higher behavioural flexibility (quantified as the number of different actions expressed during a task) is a key determinant of success (Griffin & Guez, 2014). In two neighbouring groups of wild hyaenas (*Crocuta crocuta*) living in Kenya, the likelihood of solving a novel food-retrieval task was predicted by the degree of behavioural flexibility expressed by individuals on an experimental apparatus (Benson-Amram & Holekamp, 2012). Animals who exhibited a greater diversity of exploratory behaviours in their first trial were significantly more successful than animals with lower exploration diversity (Benson-Amram & Holekamp, 2012). Although this experimental field study did not exclusively focus on tool-assisted problem solving, the positive relationship between behavioural flexibility and motor diversity, which are key underlying processes of object play behaviour, and the acquisition of novel solutions, which tool use may be an example of, suggest that previous playful manipulation may be important for an individual to discover the properties of objects that can be later used as tools. Thus, evaluating affordance learning theory in an ecologically relevant model is a promising and probably necessary step to understand how nonhuman animals acquire tool use.

Stone handling, a type of socially learned stone-directed play that is part of the cultural repertoire of several macaque species (Huffman & Hirata, 2003; Nahallage et al., 2016; Nahallage & Huffman, 2008), is an ideal behavioural candidate to test the ecological validity of affordance learning theory for several reasons. First, given that stone-handling behaviour lacks functional constraints typically observed in instrumental actions, the expression of specific stone-handling behavioural patterns is largely arbitrary (i.e. there is no wrong stone-directed action) and it is performed with stones of different sizes and textures, which afford for a large variety of actions to be expressed (Cenni, 2022; Cenni et al., 2021). As a result, stone handling is a versatile form of play, with a vast and complex, although seemingly functionless (but see below) behavioural repertoire of up to 45 stone-directed actions, including pounding a stone onto another stone, shifting a stone between hands and inserting/dropping stones into cavities (Leca et al., 2007a); such a large variety of stone-directed actions may constitute a pool of behavioural alternatives from which tool use can emerge (Cenni et al., 2020, 2022; Huffman & Quiatt, 1986; Leca et al., 2008a; Leca & Gunst, 2023; Pelletier et al., 2017). Second, stone-handling behaviour is performed on a daily basis by both males and females, across age classes (i.e. into adulthood, in contrast to most other animal taxa, in which object play is mainly expressed during immature life stages; Huffman, 1996; Leca et al., 2007b; Nahallage & Huffman, 2007; Pelletier et al., 2017), and it shows a high degree of interindividual variation, as monkeys of different age/sex classes display individual preference for certain stone-handling actions; that is, they have stone-handling profiles (Cenni, 2022). Third, in at least three instances, in the social, foraging and sexual domains, stone-handling behavioural patterns may have been co-opted into stone-tool use. In a group of Japanese macaques, *Macaca fuscata*, stone-throwing was integrated into agonistic displays in an apparent attempt to augment their effects (Leca, Nahallage, et al., 2008). In free-ranging Balinese longtailed macaques, *M. fascicularis*, stones are occasionally used as tools to collect and drink water (Cenni, Thierry, et al., 2023), and the repetitive tapping and rubbing of stones onto the genital area may be a form of self-directed tool-assisted masturbation (Cenni et al., 2020, 2022). Fourth, in longtailed macaques, some wild coastal populations living on the islands of Thailand customarily use tools to extract seafood from shells, despite not being reported to engage in stone-handling behaviour (Gumert et al., 2009, 2011; Muhammad et al., 2023). Therefore, (1) populations of longtailed macaques that do not habitually use stones as tools for extractive foraging have the cognitive and physical potential to do so and (2) testing the link between stone-handling activity and stone tool-assisted actions within the foraging domain has ecological relevance. Lastly, stone-handling behaviour is culturally maintained across macaque populations through direct social influences (i.e. response facilitation; Sciaky et al., 2022) and indirect social influences (i.e. stimulus/local enhancement; Leca et al., 2010a), underscoring the importance of considering an individual's social environment in the acquisition of object-assisted actions. Taken together, these characteristics suggest that stone-handling behaviour is amenable to the evaluation of affordance learning theory.

In this study, we conducted a series of field experiments to test whether individuals could solve food-baited puzzle boxes, namely a Dropping box and a Percussive box, whose solution required the functional action-specific use of stones as tools. First, we assessed whether individuals could solve the puzzle boxes and whether the action-specific use of stones was instrumental; that is, whether individuals used stones as ‘tools’ or as ‘toys’ when interacting with the experimental apparatus. In other words, we compared the performance of stone-assisted actions directed at the box during the experiments with those performed outside the experimental context to test for significant differences in their expression between the two settings. Second, we explored which individual attributes, both at the asocial and social levels, made individuals more likely to solve the Dropping box and the Percussive box. Third, we compiled a detailed description of the acquisition curves of individual solvers of different ages and sexes. Following a perception–action approach (Lockman, 2000), we expected covariation between an individual's stone-handling profile and the likelihood of that individual solving the foraging task. Specifically, an individual whose playful dropping actions were of longer duration (i.e. high Dropping stone-handling profile, see below) should be more likely to solve the Dropping box than an individual with a low Dropping stone-handling profile (Prediction 1). Similarly, an individual whose playful percussive actions were of longer duration (i.e. high Percussive stone-handling profile, see below) should be more likely to solve the Percussive box than individual with a low Percussive stone-handling profile (Prediction 2).

METHODS

Study Population and Site

We studied a population of free-ranging, urban-dwelling, habituated and provisioned Balinese longtailed macaques living within and around the Sacred Monkey Forest Sanctuary in Ubud, central Bali, Indonesia. The area is forested and surrounded by human settlements. At the time of the study, the population totalled approximately 1000 individuals and was composed of seven neighbouring groups with overlapping home ranges (Giraud et al., 2021). The monkeys were provisioned at least three times per day with fruits and vegetables by the temple staff.

Stone-handling Profiles

Spontaneous stone-handling activity in the Balinese longtailed macaques living in Ubud was defined as the (largely) noninstrumental manipulation of locally available stones, sometimes in combination with other objects, such as leaves, twigs or human artefacts, outside the context of the experimental trials. No stones were provided to the individuals to measure their spontaneous stone-handling activity. Observations were recorded from May to August 2018 and 2019, between 0800 and 1700 hours. Stone-handling activity was scored using the same stone-handling ethograms as in Pelletier et al. (2017), Cenni (2022) and Cenni et al. (2021). All the stone-handling sequences used in this study were videorecorded with a digital camera (Sony Full HD Handycam Camcorder). Stone-handling sequences were collected by C.C., J.B.A.C., J.B.L. and two field research assistants using ad libitum sampling methods (Altmann, 1974). During ad libitum sampling, the individual was filmed if performing stone-handling activity. Because the monkeys were highly habituated to humans, most video records were collected at close range (3–5 m), under good visibility conditions and without disturbing the animals. Whenever possible, the individuals were filmed from the front or side and about 2 m^2 in-frame.

For each individual, C.C. randomly selected and scored, on average, 27 min of cumulative stone-handling activity across multiple days. Whenever possible, we scored at least 30 min of cumulative stone-handling activity. We discarded individuals with less than 5 min of cumulative stone-handling activity from the analyses (i.e. 17 individuals out of 140 were discarded, for a total of 123 individuals). Only one individual that solved the box (i.e. Dropping box; see below) did not reach the 5 min of cumulative stone-handling activity and was excluded from the analysis. Nevertheless, the individuals that were excluded from the analyses were retained in the observation network (see below). Whenever possible, to ensure a more comprehensive representation of an individual's stone-handling activity, no more than 10 min of stone-handling activity per day were scored. To do so, stone-handling sequences longer than 10 min were randomly truncated with the use of a random time generator. However, if truncating stone-handling sequences resulted in less than 30 min of cumulative stone-handling activity, priority was given to scoring at least 30 min of cumulative stone-handling activity. Whenever possible, if the same individual participated in the field experiments in 2018 and 2019 (see below), two independent stone-handling profiles were scored, one for each year. However, if less than 30 min of stone-handling activity were available for each year, stone-handling sequences were taken from both years since stone-handling profiles did not differ significantly between 2018 and 2019 (Wilcoxon's signed rank test: Dropping stone-handling profile: $Z = 49.00$, $N = 18$, $P = 0.193$; Percussive stone-handling profile: $Z = 63.00$, $N = 18$, $P = 0.865$; Supplementary Material S1). After meeting all these selection criteria, we were able to score 123 stone-handling profiles out of 140 individuals that participated in the experimental trials (see below). C.C. used The Observer XT 15 (Noldus Information Technology, The Netherlands) and BORIS (Friard & Gamba, 2016) to score the videorecorded stone-handling sequences, with 1 s precision, and generate event-log files (i.e. a series of consecutive stone-handling behavioural patterns). For each individual interacting with each puzzle box (i.e. Dropping box and Percussive box, see below), we extracted its matching stone-handling profile (i.e. a Dropping stone-handling profile and a Percussive stone-handling profile). To assess reliability of video scoring of stone-handling profiles, we calculated an interscorer reliability test for C.C. and J.B.L. when transcribing the same samples of randomly selected video records, involving a total of 68 min of stone-handling activity across nine stone-handling sequences, with a total of 558 stone-handling behavioural patterns performed (Cohen's $\kappa = 0.97$; Martin & Bateson, 1993).

To determine Dropping stone-handling profiles and Percussive stone-handling profiles, we combined all stone-handling behavioural patterns that belonged to the macrocategories of Dropping and Percussive, respectively. Specifically, a Dropping stone-handling profile combined all the stone-handling behavioural patterns that required a monkey to hold one (or more) stone(s) with one or both hands and let it (them) fall, either by tossing, throwing, dropping or pushing the stone(s) through a cavity. As a result, a Dropping stone-handling profile comprised the following stone-handling behavioural patterns: Pick-and-Drop, Push-Through, Throw, Toss-and-Catch and Toss-Walk. As previously mentioned, longtailed macaques in Ubud habitually combine stones with other locally available objects. Specifically, these monkeys have often been observed combining stones with hollow objects, such as empty plastic bottles, water pipes and spigots (Bunselmeyer et al., 2022). As part of a Dropping stone-handling profile, we included stone-directed manipulation combining hollow objects, where an individual attempted to insert and retrieve one or more stones, often repeatedly. A Percussive stone-handling profile combined all the stone-handling behavioural patterns that required an individual to exert a vertical, forceful and percussive action onto a surface (including another stone). As a result, a Percussive stone-handling profile comprised the following stone-handling behavioural patterns: Flint, Pound, Pound-Drag and Slam. Video illustrations of stone-handling behavioural patterns included in Dropping stone-handling profiles and Percussive stone-handling profiles can be found in Supplementary Material S2.

Field Experiments to Induce Stone-tool Use

Food-baited boxes

To test whether the daily practice of stone-handling activity in Balinese longtailed macaques would covary with the probability of expressing experimentally induced stone-tool use, we designed two food-baited puzzle boxes whose food-release mechanisms required the use of one or more stones to be operated by means of actions that are structurally similar to those present in the stone-handling repertoire of this population. Specifically, we designed a Dropping box and a Percussive box.

The Dropping box consisted of a transparent box made of Lexan. The dimensions of this box were 20 × 20 × 40 cm in 2018 and 15 × 15 × 35 cm in 2019. Each box had an open chamber at the bottom and the open end of a tube attached to the top (Fig. 1a). Inside the box, a platform was held parallel to the top of the box by a Velcro strap (in 2019 the Velcro was replaced with a magnet). There was a food reward (e.g. pieces of fruit or raw egg) on the upper side of the platform, which could be released by inserting one (or several) stone(s) into the tube, provided the stone(s) was/were heavy enough to collapse the platform. The height of the box, together with an angular pipe attached internally to the tube, were meant to prevent smaller-armed individuals (e.g. juveniles, females) from reaching the food rewards by inserting their arms through the tube. Because macaques are mostly seated when performing spontaneous stone-handling activity (Leca et al., 2011), we provided two wooden logs, one on each side of the Dropping box, so that an individual could reach the top of the box with a stone while seated (Fig. 1a).

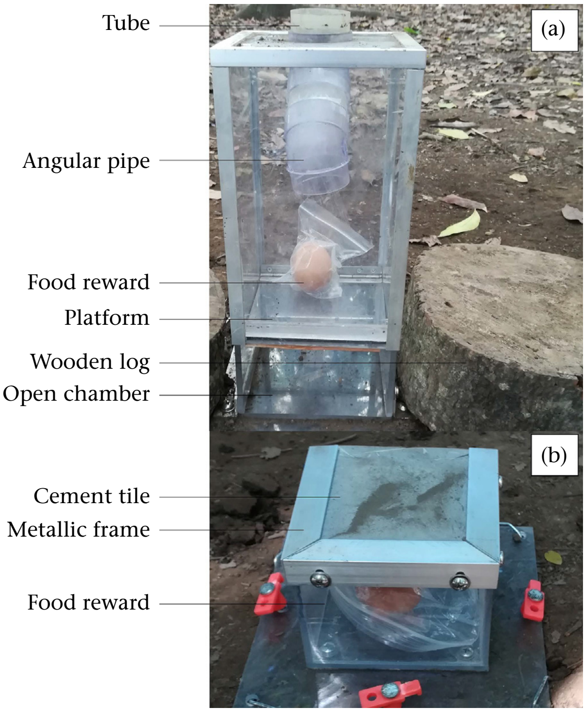

Figure 1. (a) Dropping box. (b) Percussive box.

The Percussive box consisted of a rectangular parallelepiped Lexan transparent box 15 × 15 × 10 cm with a metallic frame on its top through which a cement tile (15 × 15 × 1 cm) could be inserted to close the box (Fig. 1b). Each tile was custom-made in the field with a combination of one part cement and one part sand. Inside the box, there was a food reward (e.g. pieces of fruit or raw egg), which could be accessed by breaking the tile with the use of stone(s).

Each box was attached to an aluminium platform measuring 25 × 25 cm (in 2019, the aluminium was replaced with Lexan and the platform measured 20 × 20 cm) and anchored to the ground via long metallic pegs. When the box was not used for experimental tests, it remained in the experimental area, emptied of its food reward and covered by an opaque plastic bin anchored to the ground via long metallic pegs to prevent individuals from accessing the box between experimental sessions. In 2018, the experimental area was delimited by a mat locally made of banana leaves, similar to the ones habitually used in religious ceremonies at the Sacred Monkey Forest. The monkeys were familiar with the mat and there were no noticeable neophobic behaviours towards it. In 2019, we removed the mat, because, as interest towards the boxes increased, the monkeys appeared to be distracted by the mat, often tearing it apart. Thus, to delimit the experimental area, we swept the 1 m area around the box.

Stones

We provided 12 stones before the start of an experimental session to ensure that stones suitable to open the puzzle boxes would be readily available to the individuals interested in participating in the experiments. In 2018, these stones were placed within the experimental area, on the mat and, for the Dropping box, on the logs, making the stones highly visible. The 12 stones were randomly scattered inconspicuously 2 m from the experimental area (i.e. outside the swept area) to limit potential bias in 2019. Among the 12 stones, six were considered suitable and six were considered unsuitable. For the Dropping box, stone suitability was assessed by selecting stones that were easily inserted through the tube and heavy enough to collapse the platform, 10 times in a row, and thus solve the puzzle when tested by a human experimenter (C.C.). When testing stone suitability, C.C. released the stones without adding external force to her actions. For the Percussive box, we assessed stone suitability by selecting stones that could be grasped for pounding or slammed by a monkey and could potentially be heavy enough for a monkey to crack the tile (although we could not systematically assess this criterion). We preferentially selected stones from those previously manipulated in stone-handling sequences outside experimental sessions. In addition, we also chose suitable stones from those used to perform box-matching stone-handling patterns (i.e. a stone-handling pattern belonging to the Percussive category for the Percussive box and a stone-handling pattern belonging to the Dropping category for the Dropping box). If there were no stones available that had been previously used in stone-handling sequences outside field experimental sessions, we selected stones from the study area that met the suitability criteria (i.e. stones that were easily inserted through the tube and solved the Dropping box puzzle 10 times in a row, as well as graspable or suitable stones for slamming and heavy enough to crack open the lid of the Percussive box, when compared to similar stones previously used by monkeys).

Procedure

We conducted the experiments approximately daily (i.e. 142 out of 164 days; mean number = 3 sessions/day, mean duration = 1.5 h/day) between 0800 and 1700 hours, during two study periods, from June to August 2018 and from May to August 2019. Each box was tested one at a time over multiple days. Two experimenters were present during an experimental session, which was defined as the time window between the moment the opaque plastic bin covering a baited puzzle box was lifted by one of the experimenters, making it accessible to individuals, and the moment the food reward was released by an individual or the experimenter covered the box with the plastic bin after approximately 30–60 min.

Stones were placed before starting an experiment and they were taken away after the bin was put over the box. In 2019, stones were placed 1 min before the experiment started. The experimenter then left the area for 1 min and returned with another experimenter to begin the experiment. Once the plastic bin was lifted, two experimenters videorecorded an experimental session. One experimenter was responsible for continuously filming the experimental area, standing 3–5 m from the experimental area. The other experimenter moved 3–7 m from the experimental area and was responsible for recording the identity of the individuals and collecting behavioural data on all the individuals located within 5 m of the experimental area. Even if an individual released the food reward, we continuously filmed the experimental area until the opaque plastic bin was anchored and the box was covered.

Individual participation was recorded as trials within experimental sessions. An individual (experimental) trial was defined as the sum of all individual bouts, where bouts consisted of an individual touching the box and remaining within the experimental area for at least 5 s. That is, if an individual was within the experimental area but did not touch the box, it was not considered a bout for this individual. A bout ended when the individual exited the experimental area, or when the food reward was released by the individual itself or other monkeys in the experimental area. If the individual returned to the box, touched it and remained within the experimental area for at least 5 s, a new bout for this individual's trial started. For a trial to be considered successful, the individual had to open the puzzle box using stones. Any stone-directed action opening the box would qualify for a successful trial, and the last relevant stone-directed action before opening the box was considered the opening action. For example, if an individual pounded a stone on the cement tile making a hole, then swiftly scattered the stone to remove it from the tile, Pound was considered the last action. If the puzzle box was not opened, the trial was considered unsuccessful. If the puzzle box was opened by using only the mouth or the hands, but without using a stone, the trial was considered unsuccessful.

Participants

Across the study periods, 140 individually identified monkeys from a single group participated in the field experiments: 47 juvenile/subadult males (aged 2–6 years), 23 juvenile/subadult females (aged 2–4), 19 adult males (>6 years old) and 51 adult females (>4 years old; Table 1).

Data Analysis and Statistics

Stone-handling profiles and stone-directed actions performed at the Dropping box and Percussive box

To determine whether the action-specific use of stones was instrumental (i.e. whether individuals used stones as ‘tools’ or as ‘toys’ when interacting with the Percussive box and Dropping box), we considered only individuals that solved either box more than once. We extracted the duration of stone-assisted actions that matched the corresponding box type relative to the total duration of stone-assisted actions (encompassing both matching and nonmatching actions) observed during the field experiments (e.g. actions belonging to the macrocategory Percussive for the Percussive box; termed ‘relative duration’). We considered stone-assisted actions solely directed to the puzzle boxes, and we compared the relative duration of box-matching stone-assisted actions (e.g. percussive actions for the Percussive box) with an individual's box-matching stone-handling profile (e.g. Percussive stone-handling profile for the Percussive box), using a paired-sample *t* test (or a nonparametric Wilcoxon's signed-rank test, when assumptions for parametric statistical tests were violated). If the relative time spent performing box-matching stone-assisted actions aimed at the puzzle box significantly differed from the relative time spent performing such actions within a stone-handling context, we could conclude that actions directed at the puzzle boxes were not playful but rather utilitarian. To assess reliability of video scoring of stone-directed actions performed at the box, we calculated an interscorer reliability test for C.C. and J.B.L. when transcribing the same samples of randomly selected video records, involving a total of 167 min of videos across eight experimental sessions, with a total of 121 stone-handling behaviours performed (i.e. 6 min of stone-directed actions performed at the box; Cohen's $\kappa = 0.94$; Martin & Bateson, 1993).

Network-based diffusion analysis (NBDA)

To test whether individuals solving the Dropping box or Percussive box with stone-assisted actions relied on social or asocial information to acquire the solution to a given puzzle box, we used network-based diffusion analysis (NBDA; Franz & Nunn, 2009) using the package ‘NBDA’ (Hasenjager et al., 2020) in R 3.6.3 (R Core Team, 2013). NBDA is a powerful tool to investigate learning mechanisms in wild populations. First, although standard methods, such as the two-action and control design (Whiten & Mesoudi, 2008), are generally treated as the gold standard for distinguishing between social and asocial learning in the acquisition of behaviours, those techniques are difficult to implement in wild populations, whereas NBDA infers learning pathways in the spontaneous emergence of

Table 1
Number of participants and trials across experimental apparatuses and years

Box type	Year	Number of				Total number of trials
		Participants	Solvers	Successful trials	Unsuccessful trials	
PB	2018	65	1	17	209	226
PB	2019	103 (123)	11 (11)	62	357	419
DB	2018	78	7	33	186	219
DB	2019	91 (116)	12 (17)	88	318	406
	Total	140	21			

PB = Percussive box; DB = Dropping box. Cumulative number of individuals for PB or DB across study periods are given in parentheses.

behaviours when limited behaviour acquisition and production information is available (e.g. when a human experimenter does not have access to every expression of the behaviour, such as in an observational research design; Hasenjager et al., 2020). Second, NBDA quantifies the contribution of social and asocial influences in learning, using social networks to infer the transmission and spread of a behavioural innovation, while estimating the strength of social learning relative to asocial learning (Hasenjager et al., 2020; e.g. Garcia-Nisa et al., 2023). In our study, NBDA allowed us to test (1) the likelihood of solving a box via social and asocial contribution, (2) the percentage of first solution events attributable to asocial or social learning and (3) the contribution of individual level variables (ILVs; i.e. stone-handling profile, sex, age, dominance rank, whether an individual had already solved another puzzle box and exposure to the task, see below) to explain learning (via social and asocial components). We considered the contribution of ILVs on both social and asocial learning to uncover any possible correlation of ILVs with social influence effects (e.g. if social influence had a significant effect on learning and a social contribution of sex was significant for females, then social influence effects might explain the learning acquisition of females but not males).

For our social network, we used observation networks (sensu Hasenjager et al., 2020) obtained from all the individuals observing the last relevant stone-assisted actions followed by the opening of a box. Vision is the predominant sensory modality to gain social information in macaques (Macellini et al., 2012), and an observation network is the most direct means to evaluate and quantify social transmission (see Hasenjager et al., 2020). Due to the experimental nature of our study, we are confident that we recorded every instance in which individuals interacted with the puzzle boxes and could express the behavioural solution; hence, observation networks were the most effective way to capture social learning opportunities, as we recorded every individual observing the behavioural solution (see Hobaiter et al., 2014). As the witnessing history of an individual changed over the experimental phase, observation networks were dynamic and updated as new individuals solved the box (i.e. after each acquisition/new production of target behaviour; Hasenjager et al., 2020). Observation network dyads included one individual directly gazing at another individual opening the box with a stone-assisted action matching the opening mechanism of the box (i.e. a stone-handling behavioural pattern belonging to the Percussive category for the Percussive box and a stone-handling behavioural pattern belonging to the Dropping category for the Dropping box). Individuals could open a box with a stone-assisted action not matching the opening mechanism of the box (e.g. a stone-handling behavioural pattern belonging to the Dropping category for the Percussive box), and the trial was still considered successful. However, these instances, which represent a small proportion of the successful trials (12 out of 202 successful instances, i.e. 6%) were not counted within an observation network, because (1) observation networks tested whether direct observational social learning mechanisms explained the acquisition of the solution to a given puzzle box and (2) exposure to the task tested whether the ‘mere presence’ of individuals around the puzzle box (i.e. stimulus and local enhancement) could explain task acquisition.

Exposure to the task was defined as having access to the experimental area and was calculated by dividing the number of times an individual was present within 1 m of the box (i.e. within the experimental area) by its latency to solve the task, as any task exposure after this particular individual solved the box could not have influenced that individual's initial solving (Hobaiter et al., 2014; Nord, 2021). If an individual never solved the task, the number of times this individual was present was divided by the total duration of the experimental sessions. We included exposure to the task to control for the possibility that an individual spending more time in the experimental area would be more likely to solve the puzzle box regardless of whether or not this individual had observed the last relevant stone-assisted actions opening the box. A positive correlation between exposure to the task and social transmission would suggest a spurious effect of social transmission (see Hobaiter et al., 2014). We fitted the models using order of acquisition of diffusion analysis (OADA; Hasenjager et al., 2020), an NBDA variant that uses the order in which individuals acquire a target behaviour (here, puzzle box solution). The Dropping box and the Percussive box were each modelled as separate diffusions in order to test their different learning pathways (R code is available as Supplementary Material S3–S4). Since experimental sessions were conducted across two study periods, with a 9-month break in between, individuals that solved the box in 2018 were treated as demonstrators (although they were not ‘seeded’, that is, trained in the solution by a human experimenter, e.g. Hopper et al., 2007) in 2019. Due to the experimental nature of our study, we included the rate of performance for each individual, measured as transmission weight (i.e. an individual's number of successful trials divided by the difference in the duration of the experiment and the time when that individual first solved the puzzle box; Nord, 2021). If an ILV for one box did not show enough variation (e.g. if only males solved the Percussive box, the ILV ‘sex’ did not show variation), that ILV had to be dropped, as NBDA could not fit it to the model. Since we only had dominance rank values (calculated as Elo-ratings, using the package ‘EloRating’ in R 3.6.3, see Neumann et al., 2011; R Core Team, 2013) for 2019, rank was not included in 2018. Thus, for the model testing for the Dropping box across 2018 and 2019, we included the following as ILVs: stone-handling profile, age (as a binary variable, with ‘juvenile/subadult’ and ‘adult’ as attributes), sex, exposure to the task and whether an individual had already solved the Percussive box before opening the Dropping box; for the model testing for the Percussive box in 2019, we included the following as ILVs: stone-handling profile, sex, dominance rank, exposure to the task and whether an individual had already solved the Dropping box before opening the Percussive box. We did not include the data for the Percussive box in 2018 because only one individual solved the box in this study period and thus there was no evidence of social learning, as only one independent innovation occurred.

Each ILV was fitted to the model in an unconstrained fashion. In other words, the effects of ILVs on asocial learning and/or social transmission were assumed to be independent (Hasenjager et al., 2020; Hoppitt & Laland, 2013). For instance, an individual's stone-handling profile could affect asocial learning but have no explanatory role in social transmission. We used Akaike information criterion (AIC) to determine the best model and calculated model-averaged estimates and Wald's 95% confidence intervals for each parameter included in the analyses (Hasenjager et al., 2020). Since Wald's 95% confidence intervals for social transmission parameters can be misleading, due to asymmetrical uncertainty (i.e. social transmission parameters often have more certainty in the lower limit than in the upper limit, and Wald's 95% confidence intervals are more reliable for symmetric uncertainty; see Hasenjager et al., 2020), we used profile likelihood to calculate 95% confidence intervals for social transmission (Morgan, 2010). In one instance (i.e. ILV = ‘Social Percussive stone-handling profile’, in Percussive box 2019), we were unable to calculate confidence intervals. To interpret the contribution of social transmission to explaining learning, we report the estimated percentage of events that occurred by social transmission (Hasenjager et al., 2020).

As previously mentioned, NBDA provides a powerful way to assess the likelihood and contribution of social and asocial learning in the acquisition of a target behaviour. However, it comes with at least two limitations. First, NBDA only provides information on the learning mechanisms for the first occurrence of the target behaviour, here stone-assisted actions as means to open a puzzle box, but it does not provide any information about the processes underlying the subsequent expression of the behaviour by an individual. Second, and more specifically associated with our study, we ran separate diffusions for each puzzle box, which limited the ILVs we could select per box (due to the intrinsic variation associated with ILVs for each box type, e.g. if only males solved one of the puzzle boxes, there would be no intrinsic variation in the ILV ‘sex’). Thus, we decided to run a more comprehensive multilevel model to (1) explore the expression of successful stone-assisted actions at the puzzle box beyond an individual's first production and (2) to investigate the impact of all ILVs on both puzzle boxes and study periods.

Multilevel model

To investigate the impact of ILVs on both puzzle boxes and study periods, and beyond an individual's first production, we constructed a multilevel regression model following Bernoulli distribution, using a Bayesian framework, using the package ‘brms’ (Bürkner, 2017) in R 3.6.3 (R Core Team, 2013). The model included weakly informative priors (mean = 0, SD = 1) to limit the role of prior assumptions into the model (for a discussion of prior selection in Bayesian inference, see Lee & Vanpaemel, 2018). We modelled whether the following variables affected the likelihood that an individual would solve a box using stone-assisted actions: (1) whether an individual had ever been observed manipulating stones outside the experimental sessions (i.e. presence/absence of recorded stone-handling activity for an individual); (2) an individual's stone-handling profile, matching the corresponding box type (e.g. Percussive stone-handling profile for Percussive box); (3) age/sex (as a categorical variable, with ‘juvenile/subadult females’, ‘juvenile/subadult males’, ‘adult females’ and ‘adult males’ as attributes); (4) dominance rank; (5) box type (as a binary variable, with Dropping box and Percussive box as attributes); (6) individual's (experimental) trial number; (7) whether an individual's trial had been interrupted by the occurrence of agonistic, affiliative or sexual interactions (as a binary variable); (8) how many times an individual had previously solved the same box.

Individual's identity, study period (i.e. year) and experimental session number were modelled as random effects. Because we only had dominance rank for 2019, we first constructed one model with all variables but dominance rank, which included the entire data set across the two study periods. Then, we constructed another model with all the variables, which only included the 2019 data set (i.e. the study period during which dominance rank was available). As a result, for the model including dominance rank, we removed the study period from random effects because only the 2019 data set was included in this model. Leave-one-out cross-validation (conceptionally close to an adjusted R^2 measure; Vehtari et al., 2017) and posterior predictive check were used to estimate the variance explained by the model. All $\hat{R}$s = 1.0, which confirmed model convergence (Gelman & Shirley, 2011).

Scatterplots of the Markov chain Monte Carlo drawn from the model (Gabry et al., 2019) were used to check for multicollinearity (Webber et al., 2020). To interpret the output from the model, we report 95% credible intervals for each variable and probability of direction (pd) estimates for the independent variables. Pd estimates can range from 0.5 to 1.0 and indicate the certainty of the direction (negative or positive) of an effect (with pd ~ 97.50%, pd ~ 99.50% and pd ~ 99.95% corresponding to weak, moderate and strong evidence for an effect, respectively; Henzi et al., 2021; Makowski et al., 2019). R code is available as Supplementary Material S5.

Ethical Note

This research was noninvasive and the monkeys' participation in the field experiments was voluntary. Balinese longtailed macaques living in Ubud are highly habituated to humans. Our study was conducted in accordance with the Indonesian Ministry of Research and Technology, the Provincial Government of Bali and the local district authorities. It was approved by the institutional Animal Welfare Committee of the University of Lethbridge (Protocol number 1906).

RESULTS

Stone-handling Profiles and Stone-directed Actions Performed at the Dropping Box and Percussive Box

We conducted 285 experimental sessions (2018: 96 sessions; 2019: 189 sessions). There were 140 different individuals who participated across the two study periods, and 21 individuals solved either puzzle box (i.e. 15% of the individuals; Table 1). Specifically, 17 out of 116 individuals solved the Dropping box (i.e. 15% of the individuals) and 11 out of 123 individuals solved the Percussive box (i.e. 9% of the individuals).

When considering the individuals that solved the Dropping box more than once, we found a statistically significant difference in the duration of actions belonging to the macrocategory Dropping (hereafter, dropping actions) in an individual's stone-handling profile and in the stone-assisted actions performed across trials and directed at the Dropping box (Wilcoxon's signed rank test: $Z = 78.00$, $N = 12$, $P = 0.002$). Dropping actions directed at the Dropping box lasted significantly longer (mean ± SD = 34.9 ± 26.1%) than dropping actions during stone-handling activity (1.6 ± 2.5%).

When considering the individuals that solved the Percussive box more than once, we found a statistically significant difference in the duration of actions belonging to the macrocategory Percussive (hereafter, percussive actions) in an individual's stone-handling profile and in the stone-assisted actions performed across trials and directed at the Percussive box (paired sample t test: $t_6 = -3.45$, $N = 7$, $P = 0.014$). Percussive actions directed at the Percussive box lasted significantly longer (58.1 ± 38.9%) than percussive actions during stone-handling activity (19.5 ± 17.3%).

Information Diffusion (i.e. NBDA)

For the Dropping box, we found strong evidence that individuals used social information to learn how to solve the box. In 88% of the models in NBDA, there was evidence of social learning. On average, 44.89% (lower 95% CI = 30.55%) of learning events followed the observation network. For the individuals that solved the Dropping box primarily via social learning, there was no effect of stone-handling profile, sex, age or whether they had solved another box on social transmission. For the individuals that learned how to solve the Dropping box using primarily asocial information, we found an effect of whether they had previously solved the Percussive box (Table 2). If an individual had previously solved the Percussive box, it was 2.1 times more likely to solve the Dropping box asocially than individuals that had not previously solved the Percussive box. We found no effect of stone-handling profile, sex, age or exposure to the task on asocial learning.

For the Percussive box (2019 only), we found almost no evidence of social transmission. Only 3.48% of the models in NBDA showed an effect of social learning. For individuals that learned how to solve the box using asocial information, we found an effect of stone-handling profile and exposure to the task (Table 3). If an individual had a higher Percussive stone-handling profile, it was 1.6 times more likely to solve the Percussive box asocially than individuals with lower Percussive stone-handling profiles. Individuals that had been exposed more to the Percussive box were 3.8 times more likely to learn asocially compared to animals with less exposure. We found no effect of asocial or social learning, sex, dominance rank or whether an individual had previously solved the Dropping box.

Table 2
Diffusion through the observation network for the Dropping box

Parameter	Model-averaged estimate (±95% CIs)	Backtransformed effect (±95% CIs)	Akaike weight	ΔAIC
Visual observation network[a]	2.546 (0.349, 15.157)	44.889 (30.550)[b]	0.066	0.000
ILVs asocial transmission				
Dropping SH profile	0.061 (−0.143, 0.819)		0.023	2.117
Sex (females)	−7.272 (−27469.620, 27428.820)		0.053	0.431
Age (juveniles/subadults)	0.417 (−0.518, 3.791)		0.040	1.029
Another box solved[a]	0.740 (0.535, 1.412)	×2.096 (×1.707, ×4.106)[c]	0.066	0.000
Exposure to the task	0.238 (0.251, 1.388)		0.043	0.858
ILVs social transmission				
Dropping SH profile	−0.059 (−1.089, 1.030)		0.025	1.979
Sex (females)[a]	−0.444 (−3.733, 0.758)		0.066	0.000
Age (juveniles/subadults)	−1.471 (−25.456, 19.820)		0.041	0.965
Another box solved	0.073 (−0.137, 0.725)		0.053	0.431

CI = confidence interval; AIC = Akaike information criterion; ILVs = independent level variables; SH: stone handling. All variables were scaled to assist with model fit. Age is relative to juveniles/subadults; sex is relative to females.

[a] Variables that were found in the best model.

[b] Backtransformed effects for visual observation network estimate represent the percentages of events transmitted socially using the best performing model, with the average percentage of events from all models in parentheses.

[c] Backtransformed effects for significant variables found in the best performing model. For example, if an individual had previously solved another puzzle box, the probability of solving the Dropping box increased by a factor of 2.096.

Table 3
Diffusion through the observation network for the Percussive box (2019 only)

Parameter	Model-averaged estimate (±95% CIs)	Backtransformed effect (±95% CIs)	Akaike weight	ΔAIC
Visual observation network	0.004 (0.000, 7.997)		0.005	7.728
ILVs asocial transmission				
Percussive SH profile[a]	0.481 (0.168, 1.292)	×1.617 (×1.182, ×3.639)[b]	0.261	0.000
Sex (males)	−0.053 (−1.087, 0.403)		0.052	3.216
Dominance rank[a]	0.370 (−0.011, 1.704)		0.261	0.000
Another box solved	0.010 (−0.341, 0.591)		0.040	3.759
Exposure to the task[a]	1.326 (0.830, 1.889)	×3.764 (×2.293, ×6.616)[b]	0.261	0.000
ILVs social transmission				
Percussive SH profile	0.001		0.003	8.913
Sex (males)	0.000 (−1.775, 1.663)		0.001	10.954
Dominance rank	0.017 (−0.398, 2.960)		0.005	7.728
Another box solved	0.008 (−1.858, 4.095)		0.004	8.451

CI = confidence interval; AIC = Akaike information criterion; ILVs = independent level variables; SH: stone handling. All variables were scaled to assist with model fit. Sex is relative to males.

[a] Variables that were found in the best-fitting model.

[b] Backtransformed effects for significant variables found in the best model. For example, as exposure increased, the probability of solving the Percussive box increased by a factor of 3.764.

Table 4
Posterior estimates of the likelihood of solving either puzzle box

Effect	Parameter	Estimate	Est. error	Lower 95% CI	Upper 95% CI	Pd (%)
Population level effects	Intercept (adult males)	−3.10	1.69	−6.20	0.65	95.10
	Adult females	−0.67	0.58	−1.81	0.47	87.60
	Juvenile/subadult males	−0.39	0.63	−1.66	0.84	73.27
	Juvenile/subadult females	−0.68	0.86	−2.39	0.93	78.37
	Presence/absence of SH activity	0.02	0.98	−1.93	1.96	50.07
	Box-matching SH profile	0.53	0.18	0.18	0.89	99.80
	No. of boxes previously solved	0.17	0.06	0.06	0.28	99.93
	Box type (PB)	−1.27	0.39	−2.05	−0.52	99.97
	Trial number	0.05	0.02	0.02	0.09	99.97
	Trial interrupted	−1.14	0.27	−1.68	−0.61	100.00
	Dominance rank[a]	0.78	0.45	−0.07	1.67	96.50
Group level effects	SD(ID)	2.19	0.43	1.47	3.17	100
	SD (date)	0.25	0.20	0.01	0.72	100
	SD (study period)	1.38	1.52	0.03	5.39	100

CI = credible interval; Pd = probability of direction; PB = Percussive box. Population level effects and group level effects correspond to fixed effect factors and random effect factors, respectively, in frequentist approach. Number of observations: 1202; LOO-adjusted $R^2 = 0.59$.

[a] 2019 only; number of observations: 742.

ILVs Beyond First Production (i.e. Multilevel Regression Model)

The model found variation in group level variables (Table 4). Specifically, there was high variation across individual identities and study periods, whereas little to no variation was found in date. Overall, individuals were very unlikely to solve the box (Table 4). For the individuals that did solve it, we found strong evidence that the Percussive box was less likely to be solved than the Dropping box (pd = 99.97%; Fig. 2). Although there was a level of uncertainty associated with the Dropping box (i.e. as indicated by the spread of

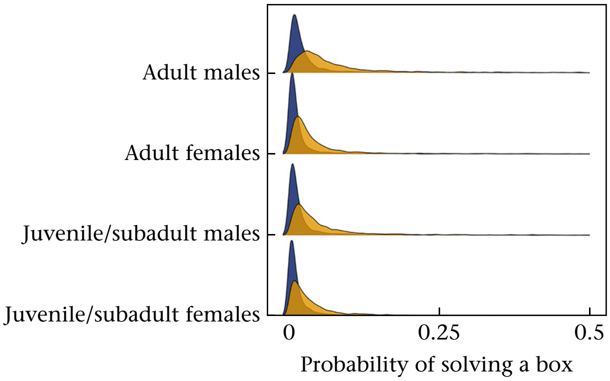

Figure 2. Probability of solving the Dropping box (orange) and the Percussive box (blue) for different age/sex classes. Density plots present the range of probability predicted by the model, with the height of the density curve indicating the predicted probability and the spread of the curve indicating its uncertainty (see Table 4). Probability scale is reduced and ranges from 0 to 0.5.

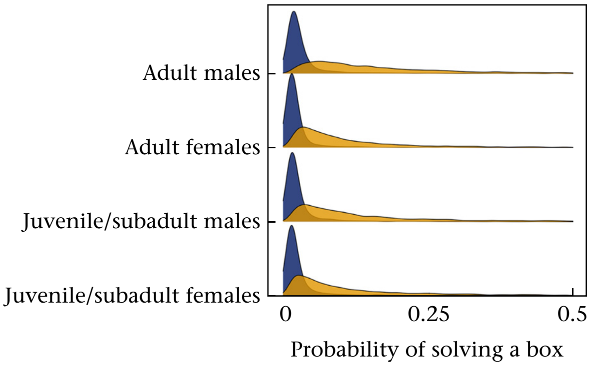

Figure 3. Probability of solving a puzzle box by matching stone-handling profile (i.e. Dropping stone-handling profile for the Dropping box; Percussive stone-handling profile for the Percussive box) for different age/sex classes. Density plots for the high stone-handling profiles (orange) and low stone-handling profiles (blue) present the range of probability predicted by the model, with the height of the density curve indicating the predicted probability and the spread of the curve indicating its uncertainty (see Table 4). Probability scale is reduced and ranges from 0 to 0.5.

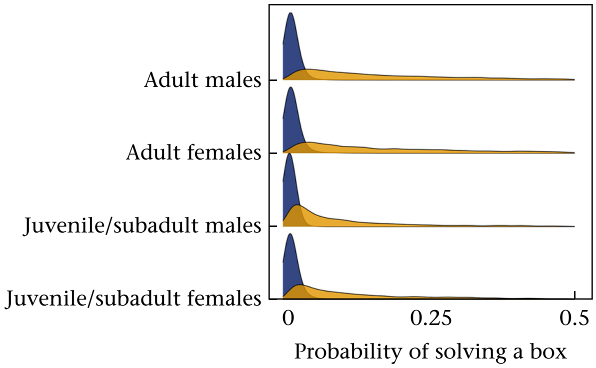

Figure 4. Probability of solving a puzzle box by dominance rank for different age/sex classes. Density plots for high rank (orange) and low rank (blue) present the range of probability predicted by the model, with the height of the density curve indicating the predicted probability and the spread of the curve indicating its uncertainty (see Table 4). Probability scale is reduced and ranges from 0 to 0.5.

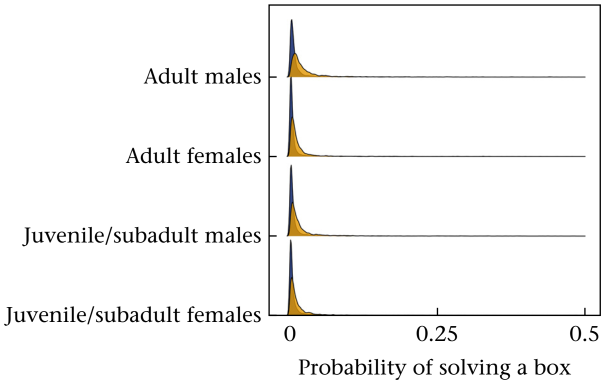

Figure 5. Probability of solving a puzzle box in individuals whose trials were interrupted (e.g. due to agonistic or sexual interactions) or not, and for different age/sex classes. Density plots per trials not interrupted (orange) and trials interrupted (blue) present the range of probability predicted by the model, with the height of the density curve indicating the predicted probability and the spread of the curve indicating its uncertainty (see Table 4). Probability scale is reduced and ranges from 0 to 0.5.

the orange curve in Fig. 2), the height of the density curve for the Percussive box suggests that the Percussive box was less likely to be solved across age/sex classes.

We found no evidence that the presence or absence of stone-handling activity (independently of a stone-handling profile) influenced the likelihood that an individual would solve either the Dropping box or the Percussive box (pd = 50.07%; Table 4). However, box-matching stone-handling profile (e.g. a Percussive stone-handling profile for the Percussive box) affected the likelihood of solving the box. Specifically, individuals with higher box-matching stone-handling profiles were more likely to solve the box than individuals with lower box-matching stone-handling profiles (pd = 99.80%; Fig. 3).

We found weak evidence that an individual's dominance rank influenced the likelihood to solve a puzzle box (pd = 96.50%; Table 4, Fig. 4); specifically, lower-ranking individuals were less likely to solve the puzzle boxes, but there was not enough evidence to suggest that higher-ranking individuals were more likely to solve the puzzle boxes. Additionally, we found strong evidence that an individual's trial number (pd = 99.97%; Table 4) and whether they had previously solved the box (pd = 99.93%; Table 4) influenced their likelihood of solving a box again. The more trials, and the more times individuals had solved the box, the more likely they were to solve again. We also found strong evidence that if an individual's trial was interrupted, this affected its likelihood of solving a box (pd = 100.00%; Fig. 5); specifically, if an individual's trial was interrupted, that individual was less likely to solve a puzzle box. Lastly, there was no evidence that solving a puzzle box was influenced by age/sex (pd < 95%; Table 4).

Acquisition Curves of Age/Sex Classes That Solved the Dropping Box or Percussive Box

We described how several individuals of different age/sex classes acquired the puzzle box solution. In Supplementary Material S6, we provide a detailed description for (1) a middle-ranking adult male, named Wayan Flange, who was the first individual to solve both the Dropping box and the Percussive box, (2) two high-ranking adult dominant males, Temple and Obelix, (3) three adult females of various dominance ranks, Lunge, S9 and S10, and (4) two juvenile/subadult males, Ketut and Sick Boy, who only solved the Dropping box.

DISCUSSION

In this study, we used a combination of descriptive, frequentist and Bayesian frameworks to test whether an individual's stone-handling profile could reliably predict its ability to solve an experimentally induced foraging task, whose solution required the functional and action-specific use of stones as tools. Despite methodological differences, the convergent evidence from these three different approaches provides a compelling case for the role of stone-handling profiles (and other individual attributes) in the expression of instrumental stone-directed actions used to solve a foraging task. We found strong evidence that the individuals who were able to open a puzzle box with stones more than once expressed longer box-matching stone-directed actions at the box, compared to the same actions performed during their respective stone-handling activity (i.e. playful manipulation of stones). This result suggests that individuals were probably not ‘playing’ with stones on the boxes. Additionally, when considering which characteristics would make individuals more likely to solve a puzzle box, we found that an individual's stone-handling profile predicted, to some extent, the likelihood of opening a puzzle box with stone-directed actions. Specifically, we found that a higher Percussive stone-handling profile predicted an individual's first solution at the Percussive box (Prediction 2 was supported). However, we found that a higher Dropping stone-handling profile did not predict an individual's first solution at the Dropping box. When looking at individual experience across trials (including after solving a puzzle box for the first time), an individual with a higher box-matching stone-handling profile (i.e. a Dropping stone-handling profile for the Dropping box and a Percussive stone-handling profile for the Percussive box) was more likely to solve the corresponding puzzle box (Prediction 1 was partly supported). Taken together, our results provide some support for the affordance learning theory, but they also suggest an interplay between several individual level variables in generating the solution to the puzzle boxes. Below we discuss the contribution of each variable/mechanism separately; lastly, we provide a general discussion of the main findings of this study.

The Role of Stone-handling Activity in the Acquisition of Stone-tool Use

The key aim of the current study was to evaluate the contribution of the daily expression of an individual's stone-handling activity in this individual's performance at a foraging task, whose solution required the use of stones as tools. In line with a perception–action approach, whereby spontaneous manipulation of objects provides opportunities for individuals to familiarize themselves with the properties of these objects and use them for novel tasks, including as tools to solve problems (Lockman, 2000), we found that an individual's stone-handling profile contributed to predicting (1) the first solution to the Percussive box and (2) the overall solutions to both the Dropping box and the Percussive box. Specifically, an individual with a higher box-matching stone-handling profile (e.g. a Percussive stone-handling profile for the Percussive box) was more likely to solve the corresponding box, compared to an individual with a lower box-matching stone-handling profile. Additionally, as an individual engaged in more experimental trials, its stone-directed actions performed at the box became increasingly specialized and matched the box type (e.g. percussive actions for the Percussive box), a feature that is common in functionally constrained actions (Stephens & Krebs, 1986). When comparing the box-matching stone-handling profile to the relative duration of similar stone-assisted actions at a box (i.e. percussive actions on the Percussive box), we found that individuals were displaying longer stone-assisted actions at the box compared to the same actions expressed during their stone-handling activity. Although these results do not strictly demonstrate the facilitatory effect of object play in the acquisition of tool use, they suggest that qualitative and quantitative aspects of object play (i.e. stone-handling profiles) may contribute to the emergence of tool use. A recent conceptual analysis by Leca and Gunst (2023) offers a compelling hypothesis for how stone-handling activity holds an exaptive potential for stone-tool use to emerge given its low-cost, autotelic, arbitrary, structurally variable and combinatorially flexible nature. It is noteworthy that other stone-directed actions in the stone-handling behavioural repertoire of the population we studied may have been co-opted into stone-tool use in the sexual behavioural domain (Cenni et al., 2020, 2022) and in the foraging behavioural domain, for drinking (Cenni, Thierry, et al., 2023). In line with the exaptive potential of stone-handling activity, the stone-directed actions directed at the puzzle box to release the food reward may constitute another example of stone-handling actions co-opted into tool use in the foraging behavioural domain.

As it emerged from the descriptive account of how individuals acquired the box solution, we should emphasize that in some instances, solving the box with stones appeared to be accidental. For example, the first time Obelix opened the Dropping box, he did not immediately realize that the box had been opened and he did not clearly show an understanding of the action–outcome contingencies (Supplementary Material S6). This is in line with the view that behavioural innovation, like some forms of tool use, may emerge from accidental circumstances, provided an adequate set of enabling conditions (context, coincidence and consequence; Wasserman, 2021). For instance, in Japanese macaques, an adult female was repeatedly observed flossing her teeth with hair, and although this tool-assisted behaviour may be perceived as seemingly functional (in an evolutionary sense), further analyses showed that flossing was temporally associated with grooming, rather than foraging, suggesting that it emerged as a by-product of grooming activity (Leca et al., 2010b). In our case, object play (and stone-handling activity more specifically) may provide an individual with a large pool of behavioural variants that are highly arbitrary in their respective expression, where chance (coincidence), given the right circumstances (context), like the ones afforded by the puzzle boxes, can occur, and lead to the emergence of behavioural innovations, such as stone-tool use, that may be eventually acquired and repeated (consequence; Wasserman, 2021).

Interestingly, when looking at how juvenile/subadult males acquired the stone-assisted solution to the boxes, they often appeared to exhibit play-like behaviour. Indeed, stone-directed actions by juvenile/subadult males seemed less focused and less directed at the puzzle box (and distributed across the experimental area) and occurring in the presence of several individuals of similar age also performing stone-directed actions; these characteristics are typical of play-like behaviours in this age/sex class and are in line with the normal activity budget of this age class (Peterson et al., 2021). Additionally, such social settings were generally associated with relatively low levels of competition for access to the box (C. Cenni, personal observation; see Supplementary Material S7). It is possible that individuals of different ages acquire relevant information differently; for immature individuals, the perception of action–outcome contingencies of a food-baited box may result from playing with the experimental apparatuses. However, more analyses are needed to test this hypothesis.

Lastly, it is worth discussing why we found a stronger effect of the Percussive stone-handling profile in comparison to the Dropping stone-handling profile in predicting the likelihood of solving a puzzle box with stones. To assess the monkeys' ability to transition from playing with stones to using them as tools, when we designed the experimental apparatuses for the foraging tasks, we chose boxes whose solutions required stone-directed actions similar to the ones commonly expressed while performing stone-handling behaviour. This deliberate approach served as a test for the affordance learning theory. Stone-handling behavioural patterns that comprise the behavioural macrocategory named ‘Dropping’ have been documented in the daily practice of the stone-handling repertoire of Balinese longtailed macaques living in Ubud (Bunselmeyer et al., 2022; Pelletier et al., 2017). However, when looking at the distribution of dropping actions across individuals, these actions were much less frequent than other behavioural macrocategories, such as percussive actions (i.e. Dropping stone-handling profile: 2018: 1.1 ± 2.4%; 2019: 0.9 ± 2.1%; Percussive stone-handling profile: 2018: 7.4 ± 10.3%; 2019: 7.9 ± 11.9%). Thus, dropping actions and the Dropping box may not have been the most appropriate targets to test the relationship between stone-handling activity and stone-assisted actions during a foraging task. A future study should consider testing different types of puzzle boxes to include a larger variety of stone-handling behavioural patterns and stone-handling behavioural patterns that constitute a larger proportion of individual stone-handling repertoires, such as ‘tapping’ (cf. Cenni et al., 2020, 2022). However, possible ceiling effects should be avoided by not choosing stone-handling behavioural patterns that are frequently expressed by most individuals and for which there would be little or no inter-individual variance.

Motivational Processes

The results of the current study provide evidence for the role of motivational processes in the acquisition of tool use to solve a foraging task. In this regard, we found that individuals who had previously solved the Percussive box were 2.1 times more likely to solve the Dropping box, and individuals who had a longer exposure to the Percussive box (that is, they came back and approached the experimental area across multiple days) were 3.8 times more likely to solve the Percussive box. Additionally, when looking at individual trajectories of task acquisition, we found that individuals that solved the puzzle boxes more than once showed sustained interest in the puzzle boxes. This was demonstrated by (1) individuals being subject to social constraints (i.e. lower-raking individuals) waiting around a puzzle box for other individuals monopolizing access to the apparatus to leave and (2) persistent behaviour, with individuals continuing to manipulate the puzzle boxes unless disturbed by others (i.e. repeatedly dropping stones inside the Dropping box, if the first stone did not open the box, or repeatedly pounding on the Percussive box with a stone to open it). Indeed, we found that when an individual lost interest in the puzzle box (e.g. when this individual inspected or mounted nearby females), its likelihood of solving the box decreased. For instance, as shown in Supplementary Material S6 (Fig. S2c and d), Obelix had a fluctuating curve across trials for both the Dropping box and the Percussive box, and he only occasionally solved the box. When looking at the type of actions he performed at the puzzle box, Obelix consistently displayed dropping actions for both the Dropping box and the Percussive box, which suggests that he did not spend time tinkering with alternative stone-directed actions to solve the box. The main difference between his trials and trials of other individuals that habitually solved the box was Obelix's frequent loss of interest for the puzzle box, mainly to inspect nearby females, and his lack of persistence in opening the box; in one instance, after dropping a stone in the Dropping box, which did not open the box, he lost interest and he did not repeat the action a second time.

Motivational processes are fundamental for innovative behaviours to be expressed (Laland & Reader, 1999; Sol et al., 2012). In experimental settings, the manipulation of extrinsic motivators to ensure animals' interest in the task is paradigmatic in the study of animal (and human) behaviour (Yerkes, 1907). As a result, much attention has been given to the motivators associated to the task (cf. Tennie & Call, 2023). However, the motivational state of individuals significantly contributes to the performance at a task (e.g. Sol et al., 2012), and our results are in line with this view. Additionally, motivation may include a stable and personality-like individual component (i.e. some individuals may have a more consistent motivation throughout their lifetimes than others), and these differences may reflect the expression of innovative behaviours (Sol et al., 2011). Specifically, previous studies have shown that behavioural syndromes are likely to impact an individual's performance in foraging tasks (e.g. Laland & Reader, 1999) and an individual's time budget (e.g. Kluiver et al., 2022). The latter point is particularly relevant for the daily expression of stone-handling activity and the high degree of interindividual variation and (to some extent) intraindividual consistency found in the expression of stone-handling activity in this population (Cenni, 2022). Object play is by definition intrinsically motivated, and varying levels of predisposition to engage in stone-handling behaviour may reflect sustained interest in the task independently of the quality of the food reward. Further studies should explore how motivational differences in object manipulation affect the acquisition of tool use (see Pellis et al., 2019 for a kinematic approach to distinguishing differentially motivated forms of object manipulation). This area of research offers promising insights into the information monkeys acquire under different motivational states (Chertoff, 2021).

Social Influences and Social Learning

Our study aims to assess the validity of affordance learning theory, by introducing an ecologically relevant behaviour not already present in the population's repertoire (for examples of a perception–action framework applied to a population of bearded capuchin monkeys that spontaneously use stone-tool use to crack nuts, see: Fragaszy et al., 2023; Resende et al., 2021). Specifically, we induced stone-tool use in the foraging domain of longtailed macaques that do not routinely display this behaviour but have the cognitive potential to do so (Muhammad et al., 2023). Additionally, we investigated the nonmutually exclusive contribution of social influences in the acquisition of task-related solutions, as these are likely to play a large role in explaining tool use acquisition (e.g. Falótico, 2022; Holzhaider et al., 2010; Whiten et al., 2022). On the one hand, we found that the acquisition of the Dropping box was significantly mediated by social transmission. Indeed, for the Dropping box, 44% of learning events could be attributed to social learning. On the other hand, we found no evidence of social transmission in the acquisition of the Percussive box. We propose two possible explanations for the differential reliance on social transmission to solve the two puzzle boxes. First, in the Dropping box, action–outcome contingencies are temporally closer than in the Percussive box. Indeed, when an individual drops a stone into the Dropping box, the internal platform is likely to collapse and the food reward can be readily released, making the association between action and outcome almost immediate. Conversely, to open the Percussive box, an individual needs to repeatedly pound a stone onto the cement tile, and several iterations of these object-assisted instrumental actions might be needed to crack the tile and access the food reward. As an individual is operating on the tile, conspecific witnesses might lose interest and disengage visual attention from the Percussive box. A second possible explanation is that, in the Percussive box, social transmission may be hindered by the characteristics of the task. Indeed, even if individuals acquired the necessary information to open the Percussive box via direct observation, a minimum physical strength is required to access the Percussive box (see Physical and Social Constraints below). This may explain why no juvenile/subadult individuals solved the

Percussive box. Additionally, a minimum amount of time is needed to access the food reward in the Percussive box because an individual (often) has to repeatedly pound a stone on the tile to crack it. Each action produces a loud sound that is likely to attract the attention of higher-ranking individuals that will in turn monopolize the box. Lastly, we found that individuals who had a longer exposure to the Percussive box (that is, they came back and approached the experimental area across multiple days) were 3.8 times more likely to solve the box. Exposure to the task may reflect local enhancement opportunities (Hasenjager et al., 2020; Hobaiter et al., 2014; Nord, 2021). In the specific context of stone-directed manipulation, a field experiment demonstrated that indirect social inputs, including stimulus or local enhancement brought about by stone-handling artefacts (e.g. piles of stones left on the ground by previous stone handlers) contributed to the long-term maintenance of stone-handling traditions in Japanese macaques (Leca et al., 2010a). It is thus likely that various social influences mediated the acquisition of the solutions to the Dropping box and the Percussive box by our study subjects.

Our findings do not provide a definitive support for either explanation. However, it is noteworthy that by the end of the experimental period (August 2019), most monkeys had witnessed direct solutions to both puzzle boxes; yet, even when given the opportunity (i.e. when having sufficiently long and undisturbed access to the box), not all individuals solved the foraging task with stones. In fact, only 15% of the individuals manipulating the box solved the tasks by using stones. Therefore, social influences alone are unlikely to explain success at the puzzle boxes. This is consistent with observations on tool-using longtailed macaques living in Koram Island, Thailand, in which distribution of tool use is likely explained by a combination of social and inheritance factors (Reeves et al., 2023). Additionally, (at least) the first monkey is likely to have solved the task in the absence of social learning, although social influences can still play a role in the emergence of innovations, by lowering an individual's level of neophobia, or by directing an individual's attention to salient details of the task, via stimulus/local enhancement (e.g. Benson-Amram & Holekamp, 2012). Lastly, in some cases, individuals who saw a puzzle box being solved with a specific technique (e.g. percussive action to solve the Percussive box) used a different stone-assisted technique to solve the same box, which they repeatedly performed across trials. For instance, despite Obelix having observed the solving of the Percussive box with percussive actions, he continuously performed dropping actions to open the Percussive box (Supplementary Material S6). Taken together, these findings suggest a likely interplay between asocial and social learning in the acquisition and expression of behavioural innovations, as documented in other species (e.g. Gajdon et al., 2011). Additionally, these results indicate that indirect and non-copying forms of social learning (e.g. stimulus/local enhancement) might be sufficient for the acquisition and expression of stone-tool use in this population (see Tennie et al., 2020). At the same time, even though direct social influences, such as the one afforded by the observation of the box solution, may not be necessary, they could speed up (or be responsible for) the acquisition of stone-tool actions for some individuals (cf. Price et al., 2009).

We acknowledge that one possible limitation of the current study is that we only considered observational networks in the context of the last action that led the subjects to solve the box. Future analyses should explore the information an individual acquires throughout another individual's trial. In other words, it would be important to examine whether a series of actions performed on the puzzle box by another individual provides relevant social cues for witnesses to solve the puzzle box.

Physical and Social Constraints

Even though our experimental design did not allow us to control for physical and social constraints associated with the tasks, this limitation reflects ecologically valid problems these animals regularly face in their environment. No juvenile/subadult individuals were able to open the Percussive box; we observed a few instances of juvenile/subadult individuals repeatedly pounding a stone on the box, sometimes marginally cracking the tile, but not making a hole through the tile or opening the puzzle box. To open the Percussive box, a minimum level of physical strength and sensorimotor coordination are probably required; similar developmental pathways are observed in the acquisition of instrumental object manipulation in habitually tool-using species. In the case of stone tool-assisted nut-cracking behaviour performed by capuchin monkeys, it takes more than 2 years to gain the necessary physical and physiological maturation to master the behaviour (Resende et al., 2008).

In addition to physical constraints, some individuals were prevented from accessing the puzzle boxes, usually by more dominant individuals (mostly males) monopolizing the access to the puzzle boxes. As a result, we found some evidence that lower-ranking individuals were less likely to solve the box. Additionally, we found strong evidence that the likelihood of solving a puzzle box decreased if an individual's trial was interrupted, mostly due to social disturbance (e.g. agonistic interactions, sexual interactions); this suggests that social constraints had a major effect on task acquisition. The dynamics observed at the box mirror the natural landscape in which these animals learn. Because more dominant individuals are more likely to monopolize access to resources (e.g. food or mates), lower-ranking individuals are generally more likely to express behavioural innovation, as a necessity to differentiate their niches (necessity drives innovation hypothesis; Reader & Laland, 2001). In our field experiments, the monopolization of the puzzle boxes by dominant individuals may have hindered the ability of more subordinate individuals to solve the boxes.

In conclusion, because of the shorter time required to open the Dropping box (i.e. in most cases one suitable stone would open the box in a single insertion), and the looser constraints associated with the physical requirements to solve the Dropping box, it is not surprising that more individuals solved the Dropping box compared to the Percussive box. Future investigations should consider how social constraints affect task acquisition, also comparing the stress level of individuals in the presence of individuals of different social ranks and whether stress affects task performance (see Sosnowski et al., 2022 for an example of performance deficit due to stress in an experimental task in capuchin monkeys). Alternatively, several puzzle boxes could be installed to control for social constraints and task monopolization by dominant individuals (e.g. Canteloup et al., 2020).

General Discussion, Limitations and Future Directions

Several theories hold that object play and tool use are proximately linked, in their developmental pathways and underlying sensorimotor and cognitive mechanisms (see Bjorklund, 2016; Lockman, 2000). However, despite numerous attempts, findings actually connecting object play and tool use across taxa are inconsistent (Smith, 2010). In a recent study, Allison et al. (2020) investigated the relationship between object play and innovative problem solving in two otter species. Specifically, they tested whether rock-juggling behaviour, a form of stone-handling activity (i.e. object play) documented across several otter species (Bandini et al., 2021), differed in frequency and facilitated the solution of novel extractive food puzzles in (1) Asian small-clawed otters, *Aonyx cinereus*, a species that habitually uses extractive behaviours to forage on crabs and shellfish (Kruuk, 2006), and (2) smooth-coated otters, *Lutrogale perspicillata*, which rely less on dextrous movements for foraging (Allison et al., 2020). Contrary to their expectations, they found no differences in rock-juggling frequency between species and no relationship between object play frequency and the solution to novel food puzzles (that did not require the use of tools). In agreement with previous findings obtained from Asian small-clawed otters (Pellis, 1991), the authors suggested that object play may not be linked to innovative problem solving in these two otter species but could be an example of misdirected foraging (Allison et al., 2020). On the one hand, none of the species tested by Allison et al. (2020) regularly use stones as tools in the wild. Indeed, the only species in which stone-tool use is currently known is the sea otter, *Enhydra lutris* (Fujii et al., 2017), which has developed bodily adaptations for stone-tool use, such as retractive claws and object-carrying pouches between the forelimbs and chest (Kenyon, 1969). On the other hand, to explain the acquisition of tool use, any relevant differences in object play may not be found in the total time allocated to overall playful activity but in the qualitative components of playful manipulation, such as the preference for certain actions expressed.

Taken together, our results suggest that there is a proximate relationship between object play and tool use, but that (1) there is substantial interindividual variation in how object play and tool use may be connected and (2) the links between these two activities are mediated by a number of confounding factors (see also Bjorklund & Gardiner, 2011; Vandenberg, 1981). The complex interplay between several individual level variables (e.g. stone-handling profiles, physical and social constraints) may explain why only 15% of individuals that participated in the field experiments solved the puzzle boxes using stones. Nevertheless, our study provides some support for affordance learning theory, suggesting that qualitative and quantitative differences in stone-handling activity affect the expression of tool use. In our investigation, we considered stone-handling profiles as continuous variables, rather than identifying a threshold for a high stone-handling profile for a specific macro-category (e.g. a high Percussive stone-handling profile). We believe this approach is a powerful way to circumvent the differential expression of stone-handling behavioural actions across individuals. Indeed, some stone-handling behavioural actions (e.g. ‘Clack’) are rare across individuals, and even when a given individual appears to perform these actions regularly, they still constitute a small proportion of stone-handling actions in that individual's repertoire compared to other stone-handling behavioural patterns (Cenni, 2022).

One of the potential limitations of this study is that, in 2019, we provided three puzzle boxes, a Dropping box, a Percussive box and a Rubbing box. The Rubbing box consisted of a rectangular parallelepiped Lexan transparent box (30 × 15 × 10 cm) with a metallic frame on top, through which a lid was inserted to close the box. The lid consisted of a Lexan layer measuring 30 × 15 × 1 cm, on top of which a thin net-textured silicone layer was glued. Inside the box, there was a food reward (e.g. pieces of fruit or raw egg), which could be accessed by sliding the lid through the metallic frame by rubbing stone(s) against the lid. Due to the net texture of the surface of the lid, the friction generated by rubbing actions with suitable stones (i.e. stones with a grainy texture) facilitated the opening of the box. However, during experimental sessions with the Rubbing box, we encountered several problems associated with the malfunctioning of the Rubbing box (e.g. dirt gathered by individuals while manipulating the Rubbing box jammed the sliding mechanism; repetitive pounding actions on the metallic frame pressed and blocked the sliding lid). Therefore, after 20 days of unsuccessful experimental attempts, we removed the Rubbing box from this study. However, we cannot rule out the possibility that some individuals may have acquired information from the manipulation of the Rubbing box and/or the witnessing of other individuals solving this puzzle box, which may have contributed to explaining the solving of other puzzle boxes. In the future, more attention will be given to designing experimental apparatuses with lower chances of malfunctioning.

Another avenue to explore how stone-assisted actions differ across contexts (specifically, between the expression of stone-handling activity and that of stone-assisted actions at the puzzle boxes) is to compare the type of stones used at the box. We have not yet explored the degree (if any) of stone selectivity displayed by individuals, a fundamental feature of skilled tool use that has been reported in habitual tool users (e.g. Chappell & Kacelnik, 2002; Visalberghi et al., 2009). We have previously mentioned that the expression of specific stone-handling behavioural patterns is likely to be arbitrary, and macaques use stones of various sizes and textures to perform stone-handling behaviour (Cenni et al., 2021; Leca et al., 2008b). However, during the instrumental expression of stone-assisted self-directed genital tapping and rubbing, adult females of the present population of Balinese longtailed macaques were observed expressing a moderate degree of selectivity, by preferentially using stones of rough texture and angular shape (Cenni et al., 2022). Future analyses will assess the degree of stone selectivity at the puzzle boxes, which is expected to be higher in a fitness-enhancing context (i.e. foraging) than in a questionably adaptive and self-pleasurable form of tool use (i.e. masturbation; Cenni et al., 2021, 2022; see also Cenni, Wandia, et al., 2023).

Author Contributions

Camilla Cenni: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing, Investigation. **Christina Nord:** Formal analysis, Writing – review & editing, Visualization. **Jessica B.A. Christie:** Data curation, Writing – review & editing, Investigation. **I. Nengah Wandia:** Project administration, Resources. **Jean-Baptiste Leca:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing, Validation, Investigation, Project administration, Resources.

Data Availability

The data for this study are available as Supplementary material.

Declaration of Interest

The authors declare no conflicts of interest.

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Supplementary Material

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