# ON THE PROXIMATE LINKS BETWEEN OBJECT PLAY AND TOOL USE IN THE CONTEXT OF STONE HANDLING BEHAVIOR IN BALINESE LONG-TAILED MACAQUES


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ON THE PROXIMATE LINKS BETWEEN OBJECT PLAY AND TOOL USE
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**DEDICATION**

To all the Wayan Flanges, and the Sultans, whose stories are unknown.

## ABSTRACT

Several theories on the origins and evolution of instrumental object-assisted actions hold that object play facilitates tool use, through enhanced perception of an object's properties and potential for manipulation. However, the data-based findings actually connecting these activities are conflicting. In this thesis, I explored the links between object play and tool use at a proximate level, that is by looking at their mechanisms and structural differences. Using a combination of observational and experimental methods, I studied a culturally maintained form of object play named stone handling (SH) performed by Balinese long-tailed macaques. First, I assessed inter-individual variation and intra-individual consistency in the expression of SH behavior, and whether the physical properties of the objects being manipulated (i.e., stone size) affected an individual's expression of SH activity. Second, I tested whether SH in this population has the exaptive potential to turn into tool use, spontaneously in the sexual domain, as a form of self-directed tool-assisted masturbation, and via experimental induction in the foraging domain, as extractive tool-assisted foraging techniques to open novel food-baited puzzle boxes. Overall, my findings demonstrate that, due to the intrinsic characteristics of play behavior, such as its combinatorial flexibility, SH may be exapted into tool use under certain motivational domains, and qualitative and quantitative features of playful object manipulation, that is the *types* and duration of different actions, covary with the expression of instrumental object-assisted solutions. Future investigations aiming to explore the relationship between object play and tool use should focus on structural components of these two activities.

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# CHAPTER 1: GENERAL INTRODUCTION

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"In short, the road to tool use entails much more than technical reasoning skills – motor skills must be refined; grips must be strengthened; and muscles and joints must be coordinated."

Lockman et al. (2020, p.33)

"By its very nature, tool using (or the incorporation of objects into skilled activity) required a chance to achieve the kind of wide variation upon which selection could operate."

Bruner (1972, p. 693)

Tools and other utilitarian artifacts pervade humans' lives. They have played such a pivotal role in theories of human evolution (R. W. Byrne, 1997; S.T. Parker & K. R. Gibson, 1977) that tool use has traditionally been considered a behavioral indicator of complex and flexible cognition. While this early promise has long triggered and maintained keen scientific interest for the study of tool use in non-human animals, it may also have revived some naïve anthropomorphic and even anthropocentric biases, particularly when studying species that are evolutionarily close to humans (Burghardt, 2007). It is noteworthy that not all cases of tool use necessarily imply high levels of cognitive sophistication, and we should not automatically attribute some of our psychological characteristics to other tool-using species, just because tools are part of our human identity. In fact, tool use is a broad functional category of behaviors that includes a wide range of actions directed to various objects, and whose cognitive substrates may differ substantially across species (Beck, 1980; Shumaker et al., 2011). Among the species-specific factors underlying the expression of tool use, ecological stimuli, social influences, psychological traits (e.g., cognitive processes, motivational determinants, personality attributes), and anatomical features differentially contribute to engaging in the use of objects as tools (Sanz et al., 2013).

First, I will provide definitions of tool use – following a list of relatively consensual criteria – and description of some of its variants. Then, I will review the main ingredients that allow for the expression of tool use across taxonomic groups, distinguishing between extrinsic factors (e.g., stimuli from the physical and social environments) and intrinsic factors (e.g., psychological processes and anatomical features). Focusing on the proximate causes of tool use (i.e., mainly mechanisms) may help generate further inquiries about its ultimate consequences (i.e., its adaptive nature). Indeed, the challenges associated with longitudinal designs and correlational tests between tool use and individual fitness benefits make it extremely difficult to unequivocally demonstrate the adaptive value of tool use, as measured by increased survival rate and reproductive success (Biro et al., 2013; Dawkins, 1986, but see Izar et al., in press, for compelling evidence on the fitness benefits associated with nut-cracking behavior in capuchin monkeys).

Following the "design-feature argument", in which the detailed structure of a given behavior is matched against the requirements of its hypothesized function (Martin & Caro, 1985; Moran, 1985; Pellis & Pellis, 1998), one way to circumvent the lack of evidence for the fitness-enhancing value of tool use is to conduct an in-depth structural analysis of this behavior. The heuristic power of the behavioral structure-function interface is reflected in the following statement by Pellis and Pellis (1998): "[…] behavioral description informs functional inference, which in turn, influences further description" (p. 115). For instance, kinematic and biomechanical analyses of patterns of grip and hand movement capabilities across different primate species are indicative of evolutionary scenarios about stone tool technology in ancestral hominins (Heldstab et al., 2016).

### 1.1. Defining tool use

More than 60 years after Jane Goodall's pioneering observations of a chimpanzee fashioning and using a stick to extract termites in Gombe, Tanzania, the debate around the appropriate characterization of the term "tool use" is still open. Because the definitions of tool use range from a focus on the *goal* of the action (i.e., the functional consequences of the tool-assisted behavioral patterns being performed), to the *means* of the action (i.e., the structural details of these behaviors), to the condition of the *object* employed, there is no universal consensus among researchers about what constitutes tool use, and what constitutes (object-assisted) problem-solving. These differences in perspectives stem from conceptually and methodologically divergent approaches across academic disciplines (e.g., ethology, psychology, anthropology), and this disagreement is often referred to as the "tool use paradox" (Crain et al., 2013).

Arguably, one of the most widely adopted definitions of tool use was provided by Shumaker and colleagues (2011). With a focus on the *goal* of the action, tool use is defined as "the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool."

(Shumaker et al., 2011, p. 5). With a focus on different functional features of a tool, alternative definitions consider tool use a form of problem-solving that includes the instrumental use of an object (e.g., St. Amant & Horton, 2008). For example, according to Shumaker et al. (2011), a weighing scale cannot be categorized as a tool because this object does not alter the form, the position, or the condition of another object or the user. However, under St. Amant and Horton's (2008) functional definition, using a weighing scale to detect an object's weight is a way to mediate the flow of information, and as such, it is a form of tool use.

Another criterion for tool use focuses on the condition of the utilised *object*. The same object may be either freely manipulable or attached to a substrate, which potentially affects its action-mediated use. For many authors, a Californian sea otter pounding a stone onto a shellfish to break it open is an example of tool use (Hall & Schaller, 1964), whereas a wrasse pounding a shell onto a rock to open it (Bernardi, 2012) is not. Clearly, those behavioral patterns (i.e., the pounding actions) are structurally similar, but because the rock used by the wrasse is attached to a substrate (i.e., the ocean floor), they are put into separate functional categories by Shumaker et al. (2011). In line with this argument, "true tool-using" avian species (following the definition by Shumaker et al., 2011; e.g., an Egyptian vulture breaking open an egg by dropping a stone on it) have larger residual brain sizes (regressed against body weight) than bird species using attached objects that do not qualify as tools (e.g., a sea gull dropping an egg on a seashore boulder; Lefebvre et al., 2002).

However, some researchers have disagreed about how structurally similar object-assisted actions may be characterized as being functionally so different. By focusing on the biomechanics of tool use, their approach proposes an embodied theory that shifts the focus of study from the object (i.e., the tool) or the goal, to the *action* (i.e., “to tool” as a verb; Fragaszy & Mangalam, 2018; Mangalam & Fragaszy, 2016). “Tooling is deliberately producing a mechanical effect upon a target object/surface by first grasping an object, thus transforming the body into the body-plus-object system, and then using the body-plus-object system to manage (at least one) spatial relation(s) between a grasped object and a target object/surface, creating a mechanical interface between the two” (Fragaszy & Mangalam, 2018, p. 194). Behaviors that have been historically recognized as tool use, such as a chimpanzee climbing on top of a pile of wooden boxes to reach for a hanging banana (Köhler, 1925), do not qualify as tooling, because the tool has to be grasped (with the hand or the mouth; Fragaszy & Mangalam, 2018). In a slightly different view, although partly supporting this action-based approach, some researchers argue that this embodied theory of tool use downplays the role of cognitive processes underlying these object-assisted actions. They claim that tool use is not only about manipulating an object to achieve a goal, but also about understanding the action-relevant physical properties of this object in the context of achieving this goal (i.e., embodied cognition; Osiurak et al., 2010; Osiurak & Badets, 2016; Osiurak & Danel, 2018). In fact, human patients with a left brain-damaged condition, known as apraxia, that results in an impairment of coordinated movements associated with tool use attempt to perform daily actions using inappropriate tools, or display inappropriate actions with everyday tools (e.g., trying to cut a tomato with a comb, or rubbing a hammer on a nail instead of pounding; Osiurak & Danel, 2018). Consistent with the initial objective to dissociate ourselves from the anthropocentric views that have pervaded tool use research in the past decades, I adhered in this thesis to the action-based approach proposed by Fragaszy and Mangalam (2018), as this may further our understanding of the causal mechanisms underlying the expression of tool use within and across species.

### 1.2. Different forms of tool use

Even though the behavioral specializations broadly acknowledged as tool use are sporadic in their phylogenetic distribution and relatively rare, it is noteworthy that they are expressed by evolutionarily distant species (Hunt et al., 2013). However, the systematic comparison of tool use propensities across species often requires the distinction between *stereotyped* and *flexible* tool use. Stereotyped tool use entails limited to no inter-individual variation in the form or frequency of actions directed to similar objects, whereas flexible tool use implies the use of different tools, applied to different contexts, to achieve different goals, with a dissociation of mean-end between action and purpose (Boesch, 2013; Hunt et al., 2013).

Stereotyped tool use has been typically associated with invertebrates and fish, because of the relatively low cognitive abilities it requires (Alcock, 1972). However, birds and mammals can also use tools stereotypically (e.g., anting in Passeriformes, a behavior that consists in whipping insects onto one's feathers; Beck, 1980; stone-throwing behavior in Egyptian vultures to break into eggs; Barcell et al., 2015; Thouless et al., 1989). Yet, considering tool use in invertebrates as exclusively stereotyped would be an oversimplification. Octopuses have one the largest and most complex nervous systems of all invertebrates, and their brain-body weight ratio exceeds that of most fishes and reptiles (Zullo & Hochner, 2011). They use tools in many ways, from defensive water jets for prey capture to object-sheltering as an anti-predatory strategy, to object-handling serving the purpose of moving away unwanted items, and those examples may be characterized as flexible tool use (Finn et al., 2009; Mather, 2008; Packard, 1972; Shumaker et al., 2011). Stereotyped tool use is performed by all the members of a given species and sometimes by several species within a given genus, with extremely low levels of behavioral variation in the form and frequency across individuals. For instance, the hunting strategy of pit-building antlions (i.e., throwing sand at their prey once it fell inside a pit to prevent it from escaping; Guillette et al., 2009; Pierce, 1986), resembles the prey-burying of *Sphecinae* digger wasps, a closely related genus, which compress sediments on top of their nest after putting prey inside to feed their offspring. A possible explanation for this consistency is that stereotyped tool use develops from pre-existing behaviors (e.g., flicking sand randomly to maintain the pits in antlions, placing objects to cache the entrance in digger wasps; Alcock, 1972; Brockmann, 1985), and are acquired (almost exclusively) asocially, and without (much) learning (Hunt et al., 2013). Lastly, stereotyped tool use is generally context-specific (i.e., the same object or action is not employed to attain different goals). For instance, Egyptian vultures do not place stones to hide food from competitors, or do not throw them at predators to drive them away.

Instances of flexible tool use have been mostly reported in animal taxa displaying relatively high cognitive abilities, such as corvids and primates (Lefebvre et al., 1997; Reader & Laland, 2002). Although flexible tool use may originate from pre-existing schemata (e.g., caching behavior in New Caledonian crows closely resembles the developmentally acquired combination of objects that precedes tool use; Amodio et al., 2018; Kenward et al., 2011; Rutz & St Clair, 2012), a considerable amount of time and practice is spent to learn how to successfully use tools, via individual and observational learning, which may partly explain the high degree of inter-individual variation in the expression of flexible tool use (Hunt et al., 2013). In juvenile capuchin monkeys, the fullblown and successful form of stone-assisted nut-cracking behavior emerges after more than two years of unsuccessfully percussing nuts and nutshells against substrates, and upon observational learning from proficient nut-cracking individuals (de Resende et al., 2008, Eshchar et al., 2016). Termite-fishing behavior in chimpanzees shares similar acquisition patterns, and individuals successfully master this complex tool-aided foraging technique after five years of practice (Lonsdorf, 2006).

The strong positive correlation found between relative brain size and the ability to use different objects instrumentally, in various contexts, and to reach different goals support the hypothesis that flexible tool use requires advanced cognitive skills (Navarrete et al., 2016; Reader & Laland, 2002). Species that can flexibly manipulate different objects to solve functionally similar or different problems tend to outperform closely related non-tool-using species in cognitive tasks testing for physical cognition (Chappell & Kacelnik, 2002; but see Emery & Clayton, 2009), causal reasoning (Emery & Clayton, 2004), working memory (Haidle, 2010), and self-control (Evans & Westergaard, 2006; Laumer et al., 2019). When comparing pit-assisted hunting behavior in antlions, sponge-assisted rostrum-covering in dolphins, twig-assisted termite-extraction in chimpanzees, stone chopper-assisted meat-processing technique in Oldowan hominins, and spear-making/using technology in prehistoric humans, there was an increase across species in the ability to hold information for later usage (i.e., working memory), expressed by an increase in problem-solution distances (Haidle, 2010). When using tools, humans can understand the cause-and-effect relationships among objects (i.e., causal material reasoning); other taxonomic groups capable of performing object-assisted instrumental actions in diverse contexts may be relying on similar cognitive processes (Boesch & Boesch-Achermann, 2000; Hunt et al., 2013; Johnson-Frey, 2003).

Intriguingly, some captive members of non-typically tool-using species are able to use objects as tools and possess cognitive skills similar to closely-related species with a propensity for tool use in the wild (e.g., bonobos, Boose, et al., 2013; Gruber et al., 2010; C. Jordan, 1982; see Samuni et al., 2022 for an example of tool use in three wild communities of bonobos; keas, Auersperg et al., 2011; see Goodman et al., 2018 for an example of tool use in a wild population of keas; rooks, Bird & Emery, 2009). One way to experimentally test for the mental ability to represent the physical properties of objects (i.e., physical reasoning) is to use the two-trap tube task (Bird & Emery, 2009; Seed et al., 2006; Visalberghi & Limongelli, 1994), a revised version of the tube-trap task. In its original version, the tube-trap task consists of a transparent tube, with food placed in the center and an underside trap into which the food will fall if moved into it. To access the reward, an individual must maneuver an already inserted stick-tool to extract the food out of the tube while avoiding the trap. The two-trap tube task has an additional non-functional trap in which food can pass over a solid base, and the subject must detect the correct side to avoid the functional trap and retrieve the food reward. When tested on the two-trap tube task, New Caledonian crows (i.e., a typical tool-using species in the wild) successfully used a stick-tool to extract the food reward; interestingly, six out of seven captive rooks (i.e., members of the corvid family that do not appear to use tools in the wild) performed similarly (Emery & Clayton, 2009; Seed et al., 2006; Taylor et al., 2009). Tool use may be an evolutionary by-product of other adaptive cognitive abilities, rather than an originally adaptative mental trait (Kacelnik, 2009; Meulman et al., 2013). What is perhaps even more surprising, is that highly proficient tool users in the wild, like chimpanzees, fail popular tests for causal reasoning, like the trap tube task (Seed at al., 2009; Völter & Call, 2014). Chimpanzees learn to avoid the trap after around 80–100 trials (Limongelli et al., 1995;

Povinelli, 2000), but do not appear to transfer knowledge between different trap problems (Martin-Ordas et al., 2008). Indeed, when the trap is inverted (i.e., the trap tube task is ineffective), chimpanzees keep adopting the previously learned strategy (Reaux & Povinelli, 2000). Similar results have been found in humans, and the effectiveness of the trap tasks for testing for causal understanding has been questioned. In the end, researchers are left with an outstanding question: Is causal reasoning necessary to use objects as tools (and if so, to what extent)? These results should also make us cautious when considering the assumption that tool use in humans and non-human animals has a common evolutionary origin and followed similar cognitive pathways of expression.

A necessary ingredient for the expression of flexible tool use is the *propensity* to manipulate objects, which is not only a reflection of anatomical features, but emerges from a combination of psychological processes determined by extrinsic and intrinsic factors (Call, 2013). Indeed, capuchin monkeys and squirrel monkeys have similar hands, but they markedly differ in their manipulative propensities and their abilities to use tools (E. J. Jordan et al., 2020). Unfortunately, there is no clear consensus on the definition of the term “manipulative propensity”, and systematic cross-species comparisons are made difficult by the use of different operational definitions (but see Heldstab et al., 2016 for attempts to systematize these cross-species comparisons). Manipulative propensity has been measured in terms of *amount* of object manipulation (i.e., frequency or duration; Brunon et al., 2014; Chevalier-Skolnikoff, 1989; Jalles-Filho, 1995), *complexity* of object manipulation (e.g., number of object combinations), or *variety* in the types of object-directed actions (e.g., Kenward et al., 2011; Westergaard & Fragaszy, 1987). As such, a given species’ manipulative propensity may affect its ability to efficiently use tools across different contexts (i.e., flexibly). In the next sections, different extrinsic and intrinsic stimuli influencing the propensity and ability to use objects as tools are reviewed.

## 1.3. Extrinsic factors affecting the propensity to manipulate objects instrumentally

### *1.3.1. Ecological factors*

Food availability is one of the main drivers in the propensity to manipulate objects, and thus it is not surprising that most instances of tool use occur within the behavioral domain of foraging activities (Shumaker et al., 2011). According to the Ecological Necessity hypothesis (Fox et al., 1999), tool use may have emerged as a need to exploit novel and hard-to-process food sources due to resource scarcity. Food scarcity may be due to ecological factors (e.g., seasonality; Melin et al., 2014), social factors (e.g., dominant individuals having priority of access to main food resources; Fox et al., 1999) and intrinsic factors (e.g., higher physiological demand during pregnancy and lactation; Bronson, 1989). The diet of chimpanzees living at Bossou, Guinea, mainly consists of fruit pulp, but during periods of fruit scarcity, these animals rely on oil-palm nuts and pits, which are processed by two types of tool use: nut-cracking and pestle-pounding behaviors (Yamakoshi, 1998). The rates of tool use increase from 10% to over 30% during fruit scarcity, which indicates that tool-assisted extractive foraging is a necessary behavioral strategy for this population.

According to the Ecological Opportunity hypothesis, individuals should have the opportunity to use tools (e.g., presence of instrumentally relevant objects, or food sources that can be exploited by tool use; Fox et al., 1999). The population of orangutans living at the Suaq Balimbing Research Station, in Sumatra, has significantly higher tool-assisted insect foraging rates than other populations of orangutans living in different sites (Fox et al., 2004). The abundance of insects at the Suaq Balimbing Research Station is higher compared to other sites, which supports the idea that propitious circumstances may have driven tool invention in this population.

Considering the previous two hypotheses, the need and opportunity to access embedded and rich food sources during seasonal periods of food scarcity in species with omnivorous diets and extractive foraging strategies may have selected for the emergence and refinement of specific object-assisted food-procurement behavioral patterns, including tool use (see also: Technical Intelligence hypothesis; S. T. Parker & K. R. Gibson, 1977). In capuchin monkeys, extractive foraging strategies follow seasonal patterns, with the tool-aided exploitation of embedded invertebrates concentrated during periods of food scarcity (Melin et al., 2014). However, the Technical Intelligence hypothesis has been challenged mainly because tool use is rare and its phylogenetic distribution is patchy among extractive foraging and generalist primate species (i.e., only a few populations of capuchins, cercopithecines, and great apes routinely use objects as tools in the wild, Tomasello & Call, 1997). Similarly, alternative ecological and functional hypotheses only partly explain the occurrence of tool use across phylogenetically related species (Koops et al., 2015a). Thus, although those hypotheses remain generally valid, ecological factors and the evolution of complex extractive foraging skills alone cannot explain the emergence and spread of tool use behavior in the wild (van Schaik et al., 1999).

### *1.3.2. Social factors*

The social influences an individual is exposed to, may also drive the expression of the instrumental manipulation of objects as tools. Several food-provisioned groups of Japanese macaques have been reported to customarily engage in a form of culturally maintained, playful and seemingly functionless stone manipulation called stone handling

(Huffman, 1984; Huffman & Quiatt, 1986; Leca et al., 2007a). However, it has been argued that the relatively relaxed dominance style of the captive Takahama group of Japanese macaques housed at the Kyoto University Primate Research Institute might have facilitated the innovation and diffusion of the spontaneous and functional use of stone tools in this primate species, possibly derived from the daily practice of stone handling; indeed, unaimed stone-throwing behavior, mainly expressed during periods of high disturbance, may function to amplify the performer's agonistic display (Leca et al., 2008a). Such differential social environments may alter not only the context of expression, but also the functional significance, of other tool use variants (Boesch, 2013). In chimpanzees, the leaf-clipping behavioral pattern is a tool-assisted communication signal that consists for an individual in repeatedly nipping leaf blades with its incisors and lips without eating any part of the leaf. This sound-producing display is culturally-mediated and acquired different social meanings that can be population-specific: (1) in Mahale, Tanzania, it is a socio-sexual display that serves the function of attracting potential mates and attracting the attention of offspring to initiate movement (Huffman, personal communication); (2) whereas in Bossou, Guinea, it is used to initiate social play interactions and group movement (Huffman, personal communication); and (3) in Taï, Ivory Coast, it is an important mediator in the context of within-group male-male competition (Boesch, 1996).

According to the Opportunity for Social Learning hypothesis, higher levels of within-population social tolerance led to greater manipulative propensities, because behavioral innovations, like tool use, can spread and be maintained across individuals (van Schaik et al., 2003). Social tolerance allows potential learners to be exposed to the mere presence of skilled group members (i.e., social enhancement), to the presence of tool artefacts previously employed by successful tool users (i.e., stimulus enhancement), and in some cases to demonstrators of the tool-assisted actions (e.g., emulation, imitation, and possibly teaching; Coussi-Korbel & Fragaszy, 1995; van Schaik et al., 2003). The comparative analysis of behavioral data from captive rhesus, long-tailed and Tonkean macaques showed a significant positive correlation between species-specific levels of social tolerance and the time spent manipulating novel objects, including tool use (Thierry et al., 1994). Similarly, the Goualougo Triangle chimpanzee population, in the Republic of Congo, characterized by a relatively complex tool-use repertoire, including instances of coaction (i.e., when an individual allows another to touch either the hand or part of the tool during use), exhibits levels of social tolerance and spatial proximity that are higher than in other populations of chimpanzees (Sanz & D. B. Morgan, 2013). Relaxed social environments enhance opportunities for behavioral coordination among group members, visual feedback from tool-using conspecifics, and access to the physical traces left at tool-using sites by previous tool users. Such favorable circumstances are conducive to direct and indirect social learning of tool use. In an experimental study aiming to explore the social processes underlying the acquisition of novel object-directed actions in captive capuchin monkeys, seven out of nine subjects preferentially touched the area of the apparatus previously manipulated by their group members (Matthews et al., 2010). Likewise, during an object-choice task, New Caledonian crows preferentially selected the tools previously used by a conspecific demonstrator, compared to other novel objects (Kenward et al., 2006). However, extrinsic factors alone do not suffice to explain the phylogenetic distribution of tool use behavior and a given species' propensity to manipulate objects in either playful or instrumental ways. Intrinsic factors, such as motivational processes, morphological adaptations, and individual history, play a vital role in a subject's proclivity for object manipulation and tool use.

## 1.4. Intrinsic factors affecting the propensity and the ability to manipulate objects

### *1.4.1. Intrinsic motivation and the role object play in tool use*

Broad structural similarities across various object-oriented activities (i.e., exploratory, playful, and instrumental ones) have been found in an extensive comparison of 74 species of non-human primates (Torigoe, 1985). More specifically, the overall execution by adult long-tailed macaques of a probably functional activity (i.e., pounding an edible object – a hard-shelled nut – on a hard substrate) and a seemingly non-functional one (i.e., pounding a non-edible object – a stone – on a hard substrate) has very similar basic sequential movement components (i.e., upswing, adjustment, and strike; Pellis et al., 2019). Likewise, the fundamental motor building blocks of stone tool-assisted nut-cracking behavior in chimpanzees include actions that are typically observed in explorative and playful object manipulation in this species (Koops et al., 2015a). Moreover, several experimental studies in non-human primates and children found positive correlations between the frequency of non-instrumental (playful) object manipulation and measures of success in subsequent problem-solving tasks involving the use of these objects as tools (e.g., shorter latency to succeed for the subjects with previous object-handling experience; Birch, 1945a; Fragaszy & Visalberghi, 1989, 1990; Gajdon et al., 2014; Polizzi di Sorrentino et al., 2014). For example, the ability to join sticks together to make and use raking tools in order to access out-of-reach food was improved by the prior playful manipulation of sticks in captive chimpanzees (Birch, 1945a).

The spontaneous manipulation of objects in a non-functional way (i.e., play) may contribute to an individual's propensity to use these objects in functional contexts (Huffman & Quiatt, 1986; Koops et al., 2015a). In a free-ranging and coastal population of Burmese long-tailed macaques in Thailand that routinely use stone tools to crack open shellfish, developmental data reveal some level of playful manipulation of lithic material by juvenile monkeys before they learn to use stones instrumentally (Tan, 2017). In this species, percussive stone-tool use may be facilitated by exploratory and non-instrumental stone-directed actions gradually incorporated into foraging activity. In an experimental study addressing the role of motivational processes (and previous experience) in tool use performance in great apes, extrinsic motivation (i.e., food reward as an external foraging trigger) had a negative/inhibitory effect on tool-assisted problem-solving success, whereas intrinsic motivation (i.e., the internal neophilic drive to explore a novel, even empty, apparatus) shortened the latency to solve the tool-use task (Ebel & Call, 2018). This result is consistent with studies showing that (1) high extrinsic motivation (i.e., higher interest in, and attraction to, a visible food reward during a test) decreases problem-solving performance, and (2) individuals in an atypical hunger state (e.g., due to food deprivation) performed more poorly in a food-rewarded tool task than individuals in a typical hunger state (Birch, 1945b).

Play behavior, including object play, that is the (mainly solitary) manipulation of inanimate objects in a spontaneous and seemingly functionless way (Power, 1999), is also intrinsically rewarding (Rius et al., 2018), which may contribute to the maintenance of object-directed activities, particularly during the development. First, the frequency of object play is age-dependent: juveniles spend significantly more time playing with objects than adults (Fagen, 1981). Second, the acquisition of flexible tool use is gradual and proceeds through several developmental stages; in long-lived animal species, such as primates, it takes years for an individual to master specific and complex tool-use skills (de Resende et al., 2008; Lonsdorf, 2006). During such a lengthy acquisition period, object-directed play may serve the function of maintaining high levels of intrinsic motivation (e.g., sustained interest in, and attention to, objects) in unskilled youngsters, before they can be externally rewarded as proficient tool users. Among great apes, who need several years of practice before mastering tool use (Lonsdorf, 2006), chimpanzees and humans are the most frequent and versatile tool using species; interestingly, juvenile chimpanzees and children also engage in significantly more object play than immature bonobos, which are their most closely related species, and a species that is not proficient in tool use (Koops et al., 2015a, 2015b). However, the propensity to manipulate objects is constrained by the physical *ability* to do it, which depends on the individual's anatomy and physical strength.

### *1.4.2. The role of anatomical features in tool use structure*

While psychological processes affect the propensity to manipulate objects, anatomical features constrain object-directed actions. Not surprisingly, the most complex and various tool use repertoires are found in primates, and more specifically in humans, followed by great apes, whose hands possess the greatest potential for movement *complexity* and *dexterity* (i.e., grip and grasping postures; Bardo et al., 2017; Marzke, 2013; Shumaker et al., 2011). Manipulative complexity has been structurally defined in various ways, including manipulation pattern diversity (Torigoe, 1985; van Schaik et al., 1999), object-substrate combination (Fragaszy et al., 2004a; Torigoe, 1985; van Schaik et al., 1999; Visalberghi & Fragaszy, 2006), and bimanual asymmetric coordination (Heldstab et al., 2016; Leca et al., 2011; van Schaik et al., 1999). In a comparative study across 36 non-human primate species, it was measured by the cumulative ranking of occurrence of different categories of object manipulation, based on unimanual/bimanual actions, synchronous/asynchronous use of hands and fingers, and whether the same/different objects were handled (Heldstab et al., 2016). Species displaying more complex types of object manipulation (e.g, tool use) were also able to engage in lower levels of manipulation categories (e.g., grasping and holding; Heldstab et al., 2016). However, hands are not necessary for efficient tool use; morphological characteristics of the beak (e.g., depth, shape) play a major role in the manipulative complexity of tool-using birds (e.g., New Caledonian crows, Kenward et al., 2006; Goffin's cockatoos, Auersperg et al., 2014).

Dexterity is the ability to solve a motor task precisely, quickly, and effectively (Bernstein, 1996). The same action can be performed more or less dexterously, and an individual with higher manipulative complexity may still act with little dexterity, (e.g., a naïve individual learning a new handling skill). Dexterity requires sensori-motor coordination, which needs to be greater when the action is more complex (i.e., there is a higher number of degrees of freedom to control the moving parts of the body; Bernstein, 1996; Fragaszy & Mangalam, 2018; Mangalam & Fragaszy, 2016, 2018). Dexterity in tool use necessitates a high spatiotemporal organization of the movements performed by the body-plus-tool system (e.g., hand-plus-tool in primates, beak-plus-tool – occasionally coordinated with the foot – in corvids). However, an individual's relationship with a tool does not only result from the propensity and the ability to manipulate this object; it is also affected by the functional properties of this object. Indeed, through a variety of object-directed activities, the performer also *experiences* the tool.

### *1.4.3. The role of experiential learning in the acquisition of tool use*

Inter-individual variation in the expression of object-directed activities, including flexible tool use, exists across most taxonomic groups (G. Byrne & Suomi, 1996; Kappeler & Kraus, 2010). In capuchin monkeys, individuals vary considerably in their tool use rate and success in experimental tasks, regardless of their age and sex classes (Fragaszy et al., 2004b). In chimpanzees, tool-assisted foraging techniques, such as ant-dipping and termite-fishing, are acquired by individuals at different ages, and some individuals never master them (Humle et al., 2009). In the Suidae family, tool use has only been observed in few individuals in a captive population of Visayan warty pigs, and the use of sticks and bark as part of nest-building sequences was mainly expressed by lower-ranking group members including some adult females (Root-Bernstein et al. 2019). Exposure to, and *experiential learning* with, objects may play an important role in the emergence of inter-individual variation in tool use (Bateson, 2014; Bruner, 1972; Bjorklund, 2016).

Tool use acquisition is a continual developmental process in which an individual's understanding of the spatiotemporal relations between objects is mediated by exploratory interactions with the environment, through affordance learning (E. J. Gibson, 1988; Lockman, 2000). Affordances arise from the relation between a specific individual and a specific environment, with respect to achieving goals (J. J. Gibson, 1979). For example, a stone affords throwing to an Egyptian vulture, pounding to a sea otter, and knapping to an Oldowan ancestral human. Likewise, object properties may be perceived differently by members of the same species. According to the Affordance Learning theory, the perception of an object's physical properties determines its potential for manipulation, affording the means for goal-oriented behaviors (E. J. Gibson, 1988; Lockman, 2000). Watching a toddler banging an object on the ground is likely to be interpreted by parents and educators as playful practice for the future functional use of this object as a tool. Most flexible forms of tool use are acquired through long periods of time, during which the learner tinkers with the tool and the possibly functional consequences of its tool-mediated actions. During this critical phase of trial-and-error learning, individuals may perform irrelevant or incorrect actions, express an incomplete or misordered sequence of actions, use inappropriate tools or substrates, and apply their actions towards the wrong goal. Tool use acquisition proceeds through a developmental process of gradual elimination of unsuccessful attempts and honing of successful behavioral strategies.

From the perspective of the Affordance Learning theory, it might not be highly relevant to distinguish between an individual attempting to use an object as a tool and an individual engaging in object play. This view stems from an ecological approach to the acquisition of tool use (E. J. Gibson, 1988), which is better explained by a progressive specificity in perceiving and acting on the material world rather than by a sudden insight into the instrumental consequences of object-directed actions. Developmental data indicate that, as children acquire further haptic experience (i.e., tactile feedback about the physical properties of objects; e.g., Bourgeois et al., 2005; Fontenelle et al., 2007; E. J. Gibson & A. S. Walker, 1984; Morgante & Keen, 2008; Palmer, 1989), they become more selective in their object exploration. At the age of 6 months (i.e., when functionally-directed object manipulation has not fully emerged yet), infants engage in discriminate exploration when interacting with different objects, by modifying their actions depending on the object's properties; for instance, they wave a bell with a clapper more often and more intensely than a bell without a clapper, or they squeeze a spongy toy more than a hard one (Palmer, 1989).

In the Sonso chimpanzee community in Uganda, where the use of sticks as tools has not been reported, growing individuals show decreasing interest in, and manipulation of, sticks, whereas they preferentially explore other objects that are later used as tools (Lamon et al., 2018). Likewise, during the acquisition of stone tool-assisted nut-cracking behavior, capuchin monkeys gradually learn to select and match the appropriate stones with the appropriate food targets based on the physical properties of these objects (e.g., size, weight, hardness, and resistance) as well as the geographical distance between them (Spagnoletti et al., 2011; Visalberghi & Neel, 2003).

Exposure to, and experience with, objects in a non-instrumental context not only contribute to discovering information about the properties of these objects, but also help refine the executive control when handling them in a functional manner, through practice and acquisition of manipulative dexterity (Lockman, 2000). By repeatedly performing similar object-directed actions in an exploratory context, individuals acquire the sensori-motor coordination needed to become skilled tool users. As human infants develop, their object-mediated banging actions (i.e., the repetitive striking of a surface through up-down motion of the arm while grasping an object) become less structurally variable, and their movements gradually acquire the biomechanical characteristics of proficient tool-assisted percussive actions (e.g., hammering; Kahrs et al., 2012, 2013). Even though juvenile chimpanzees are capable of performing some of the behavioral building blocks of the stone tool-assisted nut-cracking activity, they will not master the complete and successful behavioral sequence until they reach adolescence (Inoue-Nakamura & Matsuzawa, 1997). In captive rhesus macaques, repetitive tool-using actions gradually create novel neural projections in the brain areas that process and integrate information about the visual and somatosensory status of the training body-plus-tool system (i.e., visual, frontal, and parietal cortex; Hihara et al., 2006). Arguably, the Affordance Learning theory (J. J. Gibson, 1979; E. J. Gibson, 1982) is a promising and integrative theoretical approach to understand the proximate causes of tool use.

Several theories on the origins and evolution of instrumental object-assisted actions hold that object play and tool use are linked at the proximate levels (i.e., in their developmental pathways and underlying sensorimotor and cognitive mechanisms; see Bjorklund, 2016; Lockman, 2000). These views fall under the "play ethos", that is the zealous position that long assumed the manyfold functions of play, which is widely accepted (and mostly unquestioned) across disciplines and scholars, and lies at the core of Western educational systems (P. K. Smith, 2010). Its essence is clearly reflected in the words, among many others, of Tudor-Hart (1955): "Play is the very essence of life and the only means whereby the infant can learn anything. It remains the chief means of learning well into school years, certainly until reading has been completely mastered" (p. 10). The "play ethos" has gained increasing support in Western educational politics from the 1960s and 1970s, being advocated by eminent educational, developmental, and cognitive psychologists, as well as by the growing toy industry. However, despite several attempts, findings connecting object play and tool use across taxa are sparse and conflicting (P. K. Smith, 2010).

Many correlational and experimental studies aiming to test whether play led to cognitive and social benefits in children have failed to replicate significant findings (reviewed in P. K. Smith, 1988, 2010). Specifically, it is not clear whether the shortcomings of the "play ethos" are theoretical or methodological in nature. If the former, the "play ethos" should be re-evaluated, by testing whether different *types* of play may contribute to cognitive, social, and anatomical development, rather than by blindly assuming the putative benefits of play as facts (P. K. Smith, 1988). If the latter, methodological limitations, such as possible experimenter biases, selective interpretations of results, and the use of inappropriate control groups, should be addressed, although "[i]t is difficult to see how one could design any other procedures to test the play ethos, which would have superior ecological validity without losing so much control of relevant variables that interpretation would become highly problematical" (P. K. Smith, 1988, p. 222). Indeed, to date, no studies have tested the validity of the Affordance Learning theory in an ecologically relevant scenario. One of the challenges of testing this framework in a population that habitually uses tools is to parse out whether playful manipulation facilitates the acquisition of tool use from the alternative but non-mutually exclusive possibility that tool use acquisition is primarily explained by a species' cognitive repertoire in the physical domain (i.e., a *Zone of Latent Solutions* within which individuals have the potential to invent novel solutions to novel ecological problems; Tennie et al., 2009). One way to circumvent the aforementioned limitation is to experimentally study populations of non-human animals that are not known to habitually use tools, but for which habitual tool use is documented in the wild in other groups. In the following section, I introduce more extensively stone handling behavior, a form of object play that constitutes an ideal behavioral candidate to test the validity of the Affordance Learning theory in an ecologically relevant model.

### 1.5. Stone handling behavior

Stone handling (SH) is a culturally maintained form of object play that involves the non-instrumental manipulation of one or more stones in a versatile way (Huffman, 1984;

Leca et al., 2007a; Nahallage et al., 2016). SH behavior was first reported in Japanese macaques (Huffman, 1984) where it has been studied for over four decades, making it, to date, one of the longest investigated behavioral traditions in monkeys (Huffman et al., 2008; Leca et al., 2012). From its first observation, SH has been reported in several captive and free-ranging provisioned populations across four macaque species belonging to the *Fascicularis* group (Albanese et al., 2022; Leca et al., 2007a; Nahallage et al., 2016; Pelletier et al., 2017). Additionally, two recent reports outside the *Macaca* genus documented the expression of SH behavior in captive geladas (*Theropithecus gelada*; Cangiano & Palagi, 2020), and across most otter species, where SH has been reported in captive groups and wild populations (Allison et al., 2020; Bandini et al., 2021). In macaques, SH is thought to have emerged as a behavioral by-product of relaxed selective pressures on foraging afforded by food provisioning (Huffman & Quiatt, 1986; Leca et al., 2008b).

Interestingly, although SH is mainly performed on the ground in non-human primates, and stones are clearly necessary for its expression, neither terrestriality nor stone availability are sufficient drivers to explain the presence of SH activity in a population (Leca et al., 2008c). Although mainly solitary, SH behavior is socially learned, making it a cultural phenomenon. In Japanese macaques, SH first spread through horizontal (from peer to peer), then vertical (from mothers to infants) and horizontal (in the absence of SH mothers) transmission pathways, and there seems to be a critical period for individuals to acquire SH behavior (Huffman, 1984; Huffman & Hirata, 2003; Nahallage et al., 2007a,b); similar acquisition pathways are likely to occur in other species (but more data are needed to validate this claim). Additionally, SH behavior is culturally maintained through direct and indirect social learning and influence mechanisms; indeed, the presence of SH artifacts and stones transported across *play stations* may enhance the performance of this behavior at these specific locations and the affordances associated with lithic objects (Huffman & Quiatt, 1986; Leca et al., 2010a; Quiatt & Huffman, 1993). In long-tailed macaques, response facilitation may contribute to the routine expression of SH behavior within pairs of individuals (Sciaky et al., 2022). SH behavior constitutes an ideal candidate to test the Affordance Learning theory for several reasons.

First, SH is characterized by substantial behavioral variability, with group-specific SH repertoires comprising up to 45 behavioral patterns of varying complexity (Leca et al., 2007a,b). Indeed, the playful nature of the SH activity means that stones are flexibly manipulated in an arbitrary way, where no combination of actions is a “mistake”, which is likely to generate a versatile pool of actions (Leca, 2015). Second, contrary to most instances of object play, that mainly occur during juvenescence (Fentress, 1983), SH is expressed across age and sex classes, which provides a great opportunity to test the links between different forms of object manipulation without the confounding effect of immaturity (see Pellis et al., 2019). Third, being defined as a playful activity, SH is likely to be intrinsically motivated, which may (a) explain its maintenance in several groups (Huffman & Hirata, 2003; see also R. W. Byrne, 2015), and (b) provide individuals with opportunities to learn the properties of the objects manipulated (Huffman & Quiatt, 1986; see also Birch, 1945b; Ebel & Call, 2018). Fourth, in Japanese macaques, SH behavior has been co-opted into stone tool use in the social domain; in one group, stone-throwing was used by several individuals to augment agonistic displays (Leca et al., 2008a). Thus, SH may have the exaptive potential to be transformed into the functional use of stones as tools (Leca & Gunst, accepted).

Furthermore, a special case should be built for the expression of SH behavior in long-tailed macaques. First, due to their anatomy and propensity to manipulate objects, long-tailed macaques are extremely dexterous, with their behavioral repertoire including more combinatorial and percussive actions than any other species within the *Fascicularis* group (Heldstab et al., 2016; Pelletier et al., 2017; Torigoe, 1987). Second, coastal populations of Burmese long-tailed macaques in Thailand habitually use stones as tools to extract seafood from shells (Gumert et al., 2009), which suggests that this species has the cognitive potential to express stone tool use in (at least) the foraging domain. Lastly, in a free-ranging population of long-tailed macaques, living at the Sacred Monkey Forest in Ubud, Bali, Indonesia, the SH tradition has been established for at least three decades, and is characterized by a complex repertoire of actions, spread across age/sex classes (Pelletier et al., 2017; see Fuentes, 1992; Wheatley, 1988 for early reports of possible SH behavior), making SH behavior amenable to quantitative testing in relation to the ecological validity of the Affordance Learning theory.

### 1.6. Outline of this thesis

In this thesis, I reported the findings obtained from a combination of observational and experimental studies conducted in 2018 and 2019 in Ubud, Bali, Indonesia, in an effort to understand the proximate relationships between object play and tool use. To do so, I focused on the SH behavior of a population of Balinese long-tailed macaques.

Chapter 2 examines whether these monkeys exhibit substantial inter-individual variation and intra-individual consistency in their expression of SH behavior, and whether we can identify the presence of individual SH profiles, which may arise from quantitative and qualitative differences in the expression of stone-directed actions. Specifically, I evaluated whether SH *versatility* (i.e., the total number of different SH behavioral patterns displayed by an individual), SH *evenness* (i.e., the degree of similarity in the distributions of different SH behavioral patterns displayed by an individual), and SH *preference* (i.e., the preference of some individuals for certain SH behavioral patterns) showed significant inter-individual and intra-individual variation across individuals of different age/sex classes.

As previously mentioned, the performance of specific SH behavioral patterns is largely arbitrary, and thus, no wrong stone-directed actions can be expressed. However, actions are likely to be constrained by structural features, associated with the object being used. On the basis of Newell's constraint model (1986), which holds that objects' physical characteristics influence the form that actions take, Chapter 3 explores whether differences in stone-directed actions can be explained by the size of the stones used to perform SH. In this chapter, I tested the Object Affordance hypothesis, whereby the expression of SH behavioral patterns is mediated by the size of the stones being manipulated. Specifically, I tested whether SH *versatility* (i.e., the total number of different SH behavioral patterns displayed *across* individuals) differed across stone sizes, and whether the duration of different SH behavioral patterns varied across stone sizes.

After providing the building blocks for characterizing an individual's expression of SH behavior in Balinese long-tailed macaques, I tested whether in this species, SH behavior has the exaptive potential for tool use to emerge, and whether it is therefore valid to address the Affordance Learning theory in this primate model. In Chapter 4 and Chapter 5, I focused on two stone-directed actions (and a few additional behavioral variants), that are part of the SH repertoire of Balinese long-tailed macaques living in Ubud, namely the repetitive tapping and rubbing of stones onto the inguinal and genital area of both males and females, which may constitute an example of self-directed tool-assisted masturbation in this population. Chapter 4 and Chapter 5 tested the Sex Toy hypothesis, which proposes that these genital stone-tapping and stone-rubbing actions are two forms of self-directed tool-assisted masturbation. Specifically, in Chapter 4, I compared the behavioral structure of SH sequences with and without genital stone-tapping and -rubbing to infer the instrumental nature of these actions in males; this research is grounded in three characteristics of play, namely variability, repeatability, and exaggeration (Burghardt, 2005). In Chapter 5, I investigated the physiological and behavioral correlates of these actions, in both males and females, to see whether genital stone-tapping/-rubbing are sexually motivated. Taken together, these two chapters aimed to test whether SH behavior may have been co-opted into stone-tool use in Balinese long-tailed macaques in the sexual domain, as a form of self-directed tool-assisted masturbation.

After building a strong case for why SH behavior constitutes an ideal candidate to evaluate the Affordance Learning theory (J. J. Gibson, 1979; E. J. Gibson, 1982), in Chapter 6, I presented findings from a series of field experiments aiming to induce stone-tool use in the foraging domain, by providing novel food-baited puzzle boxes whose solution required the use of stones as tools. First, I assessed whether the action-specific use of stones was instrumental (in other words, whether individuals that opened the puzzle boxes with stones used stones as tools, or as playthings, to operate the experimental apparatuses).

Second, I explored which individual level characteristics (including an individual's SH profile), both at the asocial and social levels, made individuals more likely to solve the puzzle boxes. Lastly, I provided a detailed description of the acquisition curves in individuals of different age and sex classes that solved the puzzle boxes.

Chapter 7 is a general discussion of the findings of this thesis and extends the current literature on the proximate links between object play and tool use. In this chapter, I discussed the limitations of the current project and how they may inform future research.

# CHAPTER 2: INTER-INDIVIDUAL AND INTRA-INVIDUAL VARIATION IN STONE HANDLING BEHAVIOR

A modified version of this chapter has been submitted for publication in the journal *Animal Cognition*, with the title: "Does object play have an individual signature in long-tailed macaques (*Macaca fascicularis*)? Inter-individual variation in stone handling behavior". At the time of the thesis submission, the manuscript was in review.

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## 2.1. Abstract

Inter-individual variability in behavioral expression is more than statistical noise around the so-called "average individual": it is phylogenetically widespread and selectively meaningful. To appreciate the mechanisms and evolutionary significance of behavioral variability across individuals, fine-grained descriptive analyses of behaviors are needed. We studied stone handling (SH) behavior in long-tailed macaques, a form of object play characterized by a broad range of largely non-instrumental and probably arbitrary stone-directed actions. We explored whether individuals differed in quantitative and qualitative

aspects of their SH activity, such as *versatility, evenness*, and *preference* (i.e., the total number, the similarity in the distributions, and the preference for certain SH behaviors, respectively) and whether these differences were consistent over time. Cross-sectional analyses showed that individuals differed in *versatility, evenness,* and *preference*, and these differences were only partially explained by age. When resampling the same individuals across different days, intra-individual variation in SH *versatility, evenness,* and *preference* was lower than inter-individual variation. Our results suggest that SH in long-tailed macaques is characterized by behavioral idiosyncrasy and individual signature; these features are a potential source of adaptive variability and could serve as an exaptive reservoir for the possible emergence of stone tool use.

## 2.2. Introduction

"…the average animal which emerges may have a set of features that were not possessed by any single individual in the group."

Slater (1981, p. 46)

Behavioral variability, which describes the diversity in behavioral responses to environmental situations, has been at the core of a dramatic paradigm shift in the field of animal behavior. After being considered mere statistical noise around the so-called "average animal", behavioral variability became a genuine research topic, overwhelmingly reported at different hierarchical levels, including lineage, species, population, inter-individual, and intra-individual levels, and recognized as a driver of species survival, acting as an important component in the expression of an individual's behavioral repertoire (for an extensive review see Kappeler & Kraus, 2010). As a result, special attention has been given to *which* behavioral traits are more subject to variation, and why, as reflected in Slater's (1981) words: "This variation in variability presents a challenge which is particularly important at a time when interpreting behavior in terms of natural selection is the fashion: does variability exist because it is irrelevant as far as selection is concerned or because selection actively encourages it?" (p. 47). To answer this question, it is crucial to first understand (through in-depth behavioural description) the degree of behavioural variability among individuals of the same species sharing similar environments (e.g., belonging to the same population) and the ways in which this variability is expressed, and thereby appreciate the contribution of extrinsic (Chapman & Rothman, 2009) and intrinsic (Boogert et al., 2018; Rowe & Healy, 2014; Thornton & Lukas, 2012) sources of variation.

To this end, an ideal candidate behavior is play. Indeed, play is defined as intrinsically variable (Burghardt, 2005) and has been, at least theoretically, linked to learning and flexibility, allowing individuals either to train for unexpected situations (Spinka et al., 2001), refine their motor skills (Byers & C. Walker, 1995), or experience contextual, environmental and object properties, through affordance learning (Lockman, 2000). Among the types of play that are relevant to behavioral variability, object play, a form of non-instrumental, pleasure-driven, and *process*-oriented object manipulation, is of particular interest, because (1) it shares structural and functional similarities with an evolutionarily significant form of instrumental object-directed actions, that is tool use, and (2) the phenotypic (i.e., sensorimotor and cognitive) variability associated with object play may be beneficial for the development, expression, and evolution of tool use (i.e., Affordance Learning theory; E. J. Gibson, 1988; Lockman, 2000). Thus, characterizing the degree of behavioral/structural variability associated with object play is a necessary step to evaluate whether object play may facilitate the expression of instrumental object manipulation.

In capuchin monkeys (*Sapajus apella*), that are known for their extensive manipulative skills, analyses of frequencies and duration of playful actions revealed individual differences in manipulative profiles. Sex and age partly explained differences in overall frequency of object manipulation, but they were not predictive of play styles (i.e., presence or absence of certain behaviors). Additionally, during the observation period, individuals showed a strong manipulative stability over time, with similar actions directed towards different objects, suggesting the presence of individual consistency in qualitative aspects of object play (G. Byrne & Suomi, 1996). Similarly, in children, cross-situational stabilities and stylistic characters (i.e., qualitative features of behaviors, that were either idiosyncratic or common to a restricted group of individuals) of object play across objects were detected in free object play sessions, while considering sex and age differences (McCall, 1974). As reported in other forms of object play in non-human primates (e.g., G. Byrne & Suomi, 1996; Leca et al., 2007a,b), the frequency of overall manipulation was predicted by age (i.e., younger individuals consistently played more than older ones), but as individuals grew older, stylistic variables started to diverge, and infants adopted different play strategies, independently of their age and sex, or the type of toy used, with several subjects displaying idiosyncratic styles of play (McCall, 1974). Thus, relevant individual differences in playful object manipulation may not be found in the total time allocated to overall object play, but in the qualitative structural components of playful manipulation. However, most work has been conducted on infants and juvenile individuals, and confounding variables such as "immaturity" (i.e., the sensorimotor constraints acting on developing individuals) make the investigation of the manipulative patterns of object-directed activities challenging (but see Pellis et al., 2019 for a notable exception). More systematic and comparative structural analyses aiming to characterize qualitative aspects of object play and differences in manipulative styles in a broader range of species and across age classes are needed to assess whether there is (if any) behavioral variability in styles of object-directed play.

Stone handling (SH), a form of culturally learned stone-directed play exhibited by several macaque species (Nahallage et al., 2016) is an ideal candidate behavior for characterizing object play variability for three main reasons. First, it is performed by male and female monkeys throughout their lifespan, making this behavior amenable to quantitative and systematic comparison across age classes, by controlling for the confounding effect of sensorimotor constraints acting on immature individuals. Second, it is characterized by a vast range of SH behaviors (i.e., stone-directed actions that can be assigned to mutually exclusive behavioral categories defined in the SH repertoire) reminiscent of foraging activity (e.g., biting, pounding, rubbing, wrapping; Supplementary Material S2.1 in Appendix A; Leca et al., 2007a; 2011; Pelletier et al., 2017). Third, previous findings have shown that extrinsic factors (i.e., the size of the stones handled) affect the expression of quantitative and qualitative aspects of stone play, such as SH *versatility* (i.e., the total number of different SH behaviors) and duration of certain SH behaviors, *across* individuals in Balinese long-tailed macaques (*Macaca fascicularis*), through the perception of stone affordances (Cenni et al., 2021).

In this study, we explored whether quantitative and qualitative aspects of object play, namely SH *versatility* (i.e., the total number of different SH behaviors displayed by an individual), SH *evenness* (i.e., the degree of similarity in the distributions of different SH behaviors displayed by an individual), and SH *preference* (i.e., the preference of some individuals for certain SH behaviors) show inter-individual and intra-individual variation. These variables were chosen because (a) SH *versatility* and duration of SH behaviors (which is part and parcel of the way SH *preference* was measured) were previously observed to be meaningful quantitative and qualitative variables in describing the SH activity at the population level (Cenni et al., 2021), (b) these variables could be standardized across individuals, independently of an individual's recorded SH activity, and (c) SH *evenness* could provide a meaningful and complementary layer of description on an individual's SH activity, that is amenable to standardization across individuals, independently of an individual's recorded SH activity. To investigate inter-individual and intra-individual variation, we described the individual distribution of SH behaviors performed by free-ranging Balinese long-tailed macaques of different sex and age classes and discussed whether, when looking at the three variable of interests, (1) individuals differ in quantitative and qualitative aspects of their SH activity, (2) differences (if any) are predicted by age, (3) those features are consistent within an individual's repertoire, and (4) the structural variability associated with SH is higher across individuals than within individuals. To interpret the results, we looked at differences in SH *versatility*, SH *evenness*, and SH *preference* between- and within-individuals. Lastly, we discussed possible sources of individual variability in the SH activity of this primate species.

## 2.3. Methods

### *2.3.1. Study population and site*

We studied a population of free-ranging, urban-dwelling, habituated, and provisioned Balinese long-tailed macaques, living in and around the Sacred Monkey Forest Sanctuary in Ubud, central Bali, Indonesia. The study site is a forested area surrounded by human settlements and Hindu temples. Depending on the study period, the study population totalled between 700 and 1000 individuals and was comprised of five to seven neighbouring groups with overlapping home range areas (Giraud et al., 2021; Kluzinski, 2016). The monkeys were provisioned at least three times per day with fruits and vegetables by the temple staff.

### *2.3.2. Data collection and study subjects*

Observations were conducted during the dry season, between May and August 2016, 2018, and 2019, between 08:00 and 18:00. SH activity occurred in all seven groups of this primate population, and across all age and sex classes (Pelletier et al., 2017). In this study, we sampled 40 individually identified subjects, 20 females and 20 males from two groups of comparable sizes (i.e., groups totaling around 100 individuals per group; Table 2.1), equally distributed across five age classes, namely young juveniles (aged 1 to 2 years) old juveniles (aged 2 to 3 in females and 2 to 4 in males), subadults (adolescents individuals aged 3 to 4 in females and 4 to 6 in males), young adults (aged 4 to 6 in females, and 6 to 11 in males), and old adults (aged 6 or more in females and 11 or more in males; Brotcorne et al., 2015; Shively et al., 2012).

All the SH sequences used in this study were video-recorded with a digital camera (Sony Full HD Handycam Camcorder). Visibility conditions allowed for good quality video records to be obtained. SH sequences were collected by CC, JBAC, YVdP, CIW, and three field research assistants using focal animal sampling and *ad libitum* sampling methods (Altmann, 1974). During focal sampling, the subject was continuously filmed for 15 minutes, independently of its activity. If the focal subject performed SH during the last two minutes of the focal follow, the observation was extended for five minutes, or longer if SH was still in progress (cf. Huffman, 1996). During *ad libitum* sampling, the subject was filmed if performing SH. The data used in this study were collected as part of a broader field research season that included a series of field experiments on the same study group aiming to test whether stone tool use is facilitated by SH activity. During daily sessions (mean number = 3 sessions/day, mean duration = 1 hour 30 min/day), we tested and video-recorded the study subjects' ability to solve food-retrieval tasks whose respective solutions require the functional and action-specific use of stones as tools. The experimental devices consisted of food-baited transparent Plexiglas boxes, each with a different built-in opening mechanism. Each box could be opened by performing either stone-pounding (Box#1) or stone-inserting/dropping actions (Box#2). Less than 2% of the SH sequences used in this study were recorded during the field experiments. In these cases, the subject was not operating the experimental apparatus, and even though the SH activity occurred within five meters of the box, it was spontaneous. Whenever possible, the subjects were filmed from the front or side, within 3-5 meters, and about two-meter square in-frame.

**Table 2.1** – *Number of Days of Data Collection per Subject, Total Duration of SH Activity Recorded for Each Subject Across Multiple Days, and Mean SH Duration (± SD) per Day and per Subject.*

| Subject | Sex | Age | Obs. day | Tot SH (mm:ss) | M SH (mm:ss) | Resampled | Obs. day | Tot SH (mm:ss) | M SH (mm:ss) |
|---|---|---|---|---|---|---|---|---|---|
| Cipria | Female | Young juvenile | 11 | 30:57 | 02:49 (± 02:59) | | | | |
| Gnome | Female | Young juvenile | 4 | 25:53 | 06:28 (± 06:02) | | | | |
| Lady-Qui-Louche | Female | Young juvenile | 9 | 31:27 | 03:30 (± 03:15) | | | | |
| Megamind | Female | Young juvenile | 8 | 30:48 | 03:51 (± 03:11) | | | | |
| Benji | Male | Young juvenile | 9 | 28:18 | 03:09 (± 04:54) | | | | |
| Gennaro | Male | Young juvenile | 6 | 30:09 | 05:02 (± 04:17) | x | 3 | 34:07 | 11:23 (± 05:47) |
| Morty | Male | Young juvenile | 6 | 30:53 | 05:09 (± 02:56) | | | | |
| Scarface | Male | Young juvenile | 10 | 31:08 | 03:07 (± 04:05) | | | | |
| Grinch | Female | Old juvenile | 4 | 35:06 | 08:47 (± 01:07) | x | 4 | 30:44 | 07:41 (± 06:17) |
| Kappa | Female | Old juvenile | 3 | 34:45 | 11:35 (± 16:39) | | | | |
| Kyla | Female | Old juvenile | 3 | 32:42 | 10:54 (± 07:12) | | | | |
| Pirata | Female | Old juvenile | 2 | 32:58 | 16:33 (± 05:21) | | | | |
| Bass | Male | Old juvenile | 5 | 30:21 | 06:05 (± 05:25) | | | | |
| C-17 | Male | Old juvenile | 4 | 31:59 | 08:00 (± 04:22) | x | 4 | 30:01 | 07:30 (± 04:30) |

**Table 2.1** (continued)

| Subject | Sex | Age | Obs. day | Tot SH (mm:ss) | M SH (mm:ss) | Resampled | Obs. day | Tot SH (mm:ss) | M SH (mm:ss) |
|---|---|---|---|---|---|---|---|---|---|
| Lookout | Male | Old juvenile | 8 | 30:55 | 03:52 (± 03:02) | | | | |
| Sick Boy | Male | Old juvenile | 4 | 37:28 | 07:30 (± 05:40) | | | | |
| Duchess | Female | Subadult | 4 | 35:50 | 08:58 (± 10:04) | x | 12 | 33:11 | 02:55 (± 01:54) |
| Encrenca | Female | Subadult | 3 | 30:41 | 10:14 (± 15:19) | | | | |
| Langur | Female | Subadult | 4 | 30:47 | 07:42 (± 07:07) | | | | |
| S3 | Female | Subadult | 6 | 19:18 | 02:56 (± 03:34) | | | | |
| Charlie | Male | Subadult | 4 | 39:05 | 10:03 (± 09:08) | | | | |
| Littlefinger | Male | Subadult | 6 | 33:30 | 05:35 (± 03:38) | | | | |
| Pinocchio | Male | Subadult | 7 | 30:11 | 04:19 (± 04:14) | x | 5 | 29:25 | 05:53 (± 03:21) |
| White Eyebrows | Male | Subadult | 4 | 40:23 | 10:06 (± 09:31) | | | | |
| Beardy | Female | Young adult | 7 | 24:36 | 04:06 (± 03:02) | | | | |
| Musty | Female | Young adult | 5 | 30:12 | 06:02 (± 05:43) | | | | |
| Punk | Female | Young adult | 5 | 31:21 | 07:50 (± 02:41) | | | | |
| S12 | Female | Young adult | 3 | 35:50 | 11:57 (± 02:56) | x | 3 | 30:18 | 10:06 (± 02:16) |
| Danger | Male | Young adult | 5 | 30:45 | 06:09 (± 07:21) | | | | |
| Ramsey | Male | Young adult | 7 | 30:20 | 04:20 (± 04:23) | x | 7 | 30:12 | 04:19 (± 03:00) |
| Ronald | Male | Young adult | 4 | 31:02 | 07:46 (± 01:34) | | | | |
| Temple Baggy | Male | Young adult | 3 | 35:54 | 11:58 (± 10:12) | | | | |
| Baffo | Female | Mature adult | 4 | 40:05 | 13:22 (± 17:34) | | | | |
| Sorry | Female | Mature adult | 4 | 30:55 | 07:44 (± 03:20) | x | 6 | 30:06 | 05:01 (± 09:11) |
| T5 | Female | Mature adult | 5 | 40:37 | 07:01 (± 03:19) | | | | |
| Yetta | Female | Mature adult | 4 | 33:23 | 08:21 (± 05:04) | | | | |
| Anvil | Male | Mature adult | 3 | 30:28 | 10:09 (± 06:32) | x | 4 | 30:17 | 07:35 (± 05:29) |
| Baggy | Male | Mature adult | 7 | 29:31 | 03:41 (± 02:56) | | | | |
| Nigel | Male | Mature adult | 5 | 34:26 | 05:44 (± 04:49) | | | | |
| Splash | Male | Mature adult | 2 | 40:08 | 20:04 (± 07:32) | | | | |

*Note.* Tot = total duration (in minutes, and seconds) of SH activity. For resampled subjects: additional number of days of resampled SH activity, and total and mean SH duration.

### *2.3.3. Data coding*

To explore whether quantitative and qualitative aspects of SH activity differed *between* individuals, we used 40 subjects, 20 females and 20 males (Table 2.1). For each of these 40 subjects, the first author (CC) scored on average 32 minutes of total SH activity (M = 32:23 ± 04:18), which belonged to different SH sequences collected across multiple days. Each subject was exclusively observed within one field season (i.e., between May and August of either 2016, 2018, or 2019). To explore whether quantitative and qualitative aspects of SH activity differ *within* individuals, we used 9 of the 40 subjects, 4 females and 5 males (Table 2.1), one per sex/age classes. For each of these 9 subjects, the first author (CC) scored on average an additional 31 minutes of total SH activity (M = 30:56 ± 01:36), which belonged to different SH sequences collected within the same year, but across multiple days, and that were independent from the SH activity used to explore whether aspects of SH behavior differ *between* individuals; in other words, the resampled SH activity did not share any SH behaviors with the original SH activity, used to investigate between-individual differences. We were unable to resample any young juvenile females because no additional 30 minutes of SH activity were available. Although our analyses used only *behavior*s (within sequences) rather than *sequences* per se (i.e., our analyses did not consider the sequential organization of behaviors), SH sequences were coded in their entirety, unless the total SH activity of an individual already exceeded 30 minutes (i.e., 10 SH sequences out of 233). CC used the same SH ethograms produced by Pelletier et al. (2017) and Cenni et al. (2021) and used *The Observer XT 15* (Noldus Information Technology, The Netherlands) to score the SH behaviors for each subject. During the scoring process, we detected new behavioral variants of the stone-directed actions described by Pelletier et al. (2017). Given that SH is a culturally maintained form of object play, it is not surprising that the behavior undergoes transformation over time (Huffman & Quiatt, 1986; Leca et al., 2012). Therefore, the operational definitions of SH behavior in the Balinese long-tailed macaques living in Ubud were updated and can be found in the Supplementary Material S2.1 in Appendix A. Video references of SH behavior in three old juveniles Balinese long-tailed macaques can be found in Supplementary Material S2.2 in Appendix A.

To assess reliability of video scoring when testing whether quantitative and qualitative aspects of SH activity differed *between* individuals (total sample duration: 21 hours and 35 minutes), we calculated an inter-scorer reliability test for CC and JBL when transcribing the same samples of SH video records, involving a total of 2 hours and 16 min of SH activity across 21 SH sequences, with a total of 2542 SH behaviors performed (i.e., 10.50% of total sample; Cohen's k = 0.96; see Martin & Bateson, 1993). To assess reliability of video scoring when testing whether quantitative and qualitative aspects of SH activity differed *within* individuals (total sample duration: 4 hours and 38 minutes), we used the duration-sequence option of *The Observer XT 15* to assess intra-scorer reliability for CC when transcribing the same samples of SH video records, involving a total of over 49 min of videos containing SH activity across the 9 individuals used to test within-individual differences, with a total of 1015 SH behaviors performed (i.e., 17.60% of total sample; k = 0.89; see Martin & Bateson, 1993).

#### *2.3.4. Data analysis*

The quantitative and qualitative aspects of SH activity we evaluated were (1) SH *versatility*, defined as the total number of different SH behaviors displayed by an individual, (2) SH *evenness*, defined as the degree of similarity in the distributions of different SH behaviors displayed by an individual, and (3) SH *preference*, defined as the preference of some individuals for certain SH behaviors (i.e., measured by the relative duration of SH behaviors across individuals). Thus, while SH *versatility* and SH *evenness* were calculated *within* an individual, and subsequently compared *between* individuals, SH *preference* was a metric already calculated by considering the duration of SH behaviors *across* individuals.

***Rarefaction analysis***

To evaluate and compare SH *versatility* and SH *evenness* between and within individuals, we used a rarefaction analysis to generate rarefaction curves, calculated through *EcoSim* software (Gotelli & Entsminger, 2011). Rarefaction analysis is a technique commonly used by ecologists to measure species diversity on individual levels (i.e., the cumulative number of different species found in a sample of individuals) and to estimate the predicted number of species from a sub-sample of individuals (Gotelli & Colwell, 2001). By repeatedly and randomly resampling a pool of *N* individuals, rarefaction analysis generates the expected number of species in a smaller collection of *n* individuals, randomly drawn from *N* (Simberloff, 1978). Iteration produces a mean and variance of species expected in each smaller subset of individuals and allows researchers to generate rarefaction curves and to compare the expected species presence in two or more samples that differ in total abundance of individuals (Gotelli & Colwell, 2001). First, to generate rarefaction curves, the number of expected species of smaller subsets are plotted, as the full dataset *N* gradually rarefies. Second, to explore differences, rarefaction curves are compared at the maximum common abundance level available to the curves that are being compared (e.g., black dotted lines in Figure 2.1-2.2).

To apply the use of rarefaction analysis to estimate SH *versatility* and SH *evenness*, we treated SH behaviors (e.g., Clack, Pound, Rub) within an individual's repertoire as species, and the total abundance of SH behaviors performed (e.g., the total number of Clack, Pound, Rub, being recorded) as individuals. As a result, the rarefaction analysis allowed us to compare individuals differing in overall SH abundance, to measure whether, at equal SH abundance (i.e., the *total* number of SH behaviors performed by all compared individuals), some individuals expressed a greater number of *different* SH behaviors than others. We performed the rarefaction analysis at the individual level (i.e., individual-based rarefaction method). Further details about the application of rarefaction analysis to behavioral repertoires can be found in Cenni et al. (2021) and Peshek and Blumstein (2011).

To quantify SH *versatility*, rarefaction analysis was applied directly to SH behaviors (as commonly used in ecological samples when trying to evaluate species richness; Gotelli & Entsminger, 2011). To quantify SH *evenness*, rarefaction analysis was applied after calculating Probability of Interspecific Encounter (PIE; Hurlbert, 1971), an index predominantly used in ecology that gives the probability that two randomly sampled individuals from *N* belongs to two different species. PIE is calculated as follows:

$$PIE = \left(\frac{N}{N-1}\right)\left(1 - \sum_{i=1}^{S} p_i^2\right)$$

where *N* is the total number of individuals, *S* is the total number of species, and *p(i)* represents the proportion of the entire sample represented by the species *i*. PIE is a simple index of *evenness* that can be easily interpreted as a probability, and it is relatively unbiased by small sample size (Hurlbert, 1971). Higher values of PIE identify a higher similarity in the distributions of different SH behaviors displayed by an individual (i.e., higher values of PIE characterize high SH *evenness*). Thus, SH *evenness* was obtained from the rarefaction analysis applied to the PIE index calculated for SH behaviors within an individual's repertoire, and it was expressed as a number ranging from 0 to 1.

***Duration of SH behavioral patterns***

To evaluate and compare SH *preference* for SH behaviors, first we extracted for each subject the relative duration (to an individual's total SH activity duration) of the 38 SH behaviors, as defined by Pelletier et al. (2017) and Cenni et al. (2021), from the event-log files generated from *The Observer XT 15*. Then, to determine whether individuals differed in their SH *preference* (i.e., whether they spent more time than other individuals exhibiting certain SH behaviors), we used Z-scores, as a way to indicate how many standard deviations an individual deviated from the mean of the group (i.e., all 40 subjects). When the distribution of a given SH behavior did not meet normality, data were log-transformed, to allow for the interpretation of Z-scores. When the distribution of a SH behavior did not meet normality after log-transformation, we used its original distribution to interpret Z-scores. Non-normal distributions were positively skewed, meaning that values greater than + 1.96 still represented individuals that significantly deviated from the mean of the sample. We acknowledge that for non-normal distributions, the cut-off point identifying individuals that significantly deviated from the sample average might be smaller than + 1.96; however, we interpreted as significantly different only individuals with Z-scores greater than + 1.96. Because our aim was to evaluate individuals that spent more time than average exhibiting certain SH behaviors, we did not consider Z-scores lower than – 1.96.

***2.3.5. Ethical statement***

This study was exclusively observational and minimally invasive. 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 #1906).

## 2.4. Results

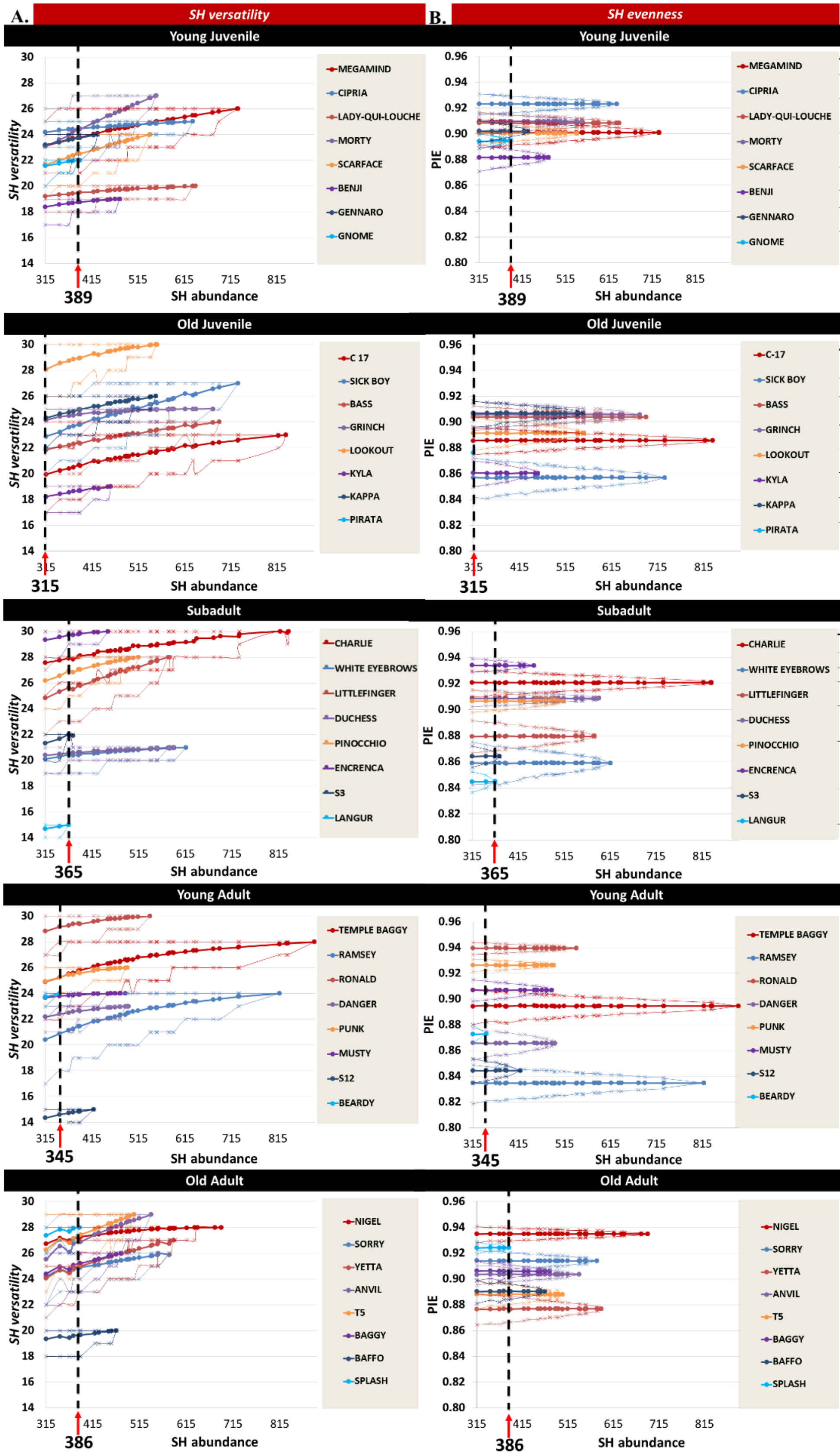
### *2.4.1. Between-individual comparison*

#### *Rarefaction analysis*

At common abundance level, we found a difference in the estimates for SH *versatility* between individuals, which ranged from low to high (Figure 2.1A). Figure 2.1A shows the rarefaction curves for SH *versatility* for all individuals, across age classes. For instance, in young adults, at equal abundance level (i.e., 345), the total number of different SH behaviors for Ramsey (a lowly versatile stone handler), Temple Baggy (a moderately versatile stone handler), and Ronald (a highly versatile stone handler) were 21 (95% C. I. 18 – 23), 25 (95% C. I. 22 – 28), and 29 (95% C. I. 27 – 30), respectively.

At common abundance level, we found a difference in the estimates for SH *evenness* between individuals, which ranged from low to high (Figure 2.1B). Figure 2.1B shows the rarefaction curves for SH *evenness* for all individuals, across age classes. For instance, in young adults, at equal abundance level (i.e., 345), the SH *evenness* for Ramsey (a highly skewed stone handler), Temple Baggy (a moderately skewed stone handler), and Ronald (a lowly skewed, or even, stone handler) was 0.835 (95% C. I. 0.821 – 0.848), 0.895 (95% C. I. 0.882 – 0.907), and 0.940 (95% C. I. 0.935 – 0.944), respectively (i.e., higher values of SH *evenness* indicate a more evenly distributed SH activity).

**Figure 2.1 –** *Rarefaction Curves for SH Versatility (i.e., the Total Number of Different SH Behaviors; A.) and SH Evenness (i.e., the Degree of Similarity in the Distributions of Different SH Behaviors; B.) as a Function of SH Abundance (i.e., the Total Number of All SH Behaviors Performed), and SH Preference (i.e., the Preference of Some Individuals for Certain SH Behaviors; C.) for 40 Individuals Across Age Classes.*




C. **SH preference**

| Subject | SH element |
|---|---|
| Megamind | None |
| Cipria | Pick Up<br>Push-Through |
| Lady-Qui-Louche | Carry<br>Gather<br>Scatter |
| Morty | Move Push/Pull<br>Scatter<br>Wrap |
| Scarface | Lick<br>Slap |
| Benji | None |
| Gennaro | Bite<br>Pound-Drag |
| Gnome | Carry<br>Grasp<br>Lick |

| Subject | SH element |
|---|---|
| C-17 | Roll with Fingers<br>Tap |
| Sick Boy | None |
| Bass | Slap |
| Grinch | Shake in Hands |
| Lookout | Clack |
| Kyla | Move Push/Pull<br>Tap |
| Kappa | Cuddle<br>Lick |
| Pirata | Rub |

| Subject | SH element |
|---|---|
| Charlie | Slam |
| White Eyebrows | Pound |
| Littlefinger | None |
| Duchess | Cover<br>Roll in Hands |
| Pinocchio | Roll<br>Toss-Walk<br>Throw |
| Encrenca | Flint<br>Grasp-Walk<br>Pick Up<br>Shift in Hands |
| S3 | Grasp-Walk<br>Pound<br>Scatter |
| Langur | None |

| Subject | SH element |
|---|---|
| Temple Baggy | Lick<br>Toss-Walk<br>Throw |
| Ramsey | Groom<br>Roll with Fingers |
| Ronald | Move in Mouth<br>Roll with Fingers<br>Shake in Hands<br>Shift in Hands<br>Toss-Walk |
| Danger | Pound<br>Sniff |
| Punk | Carry |
| Musty | None |
| S12 | Cuddle |
| Beardy | None |

| Subject | SH element |
|---|---|
| Nigel | Rub Together<br>Rub with Hands |
| Sorry | Rub Together<br>Slap |
| Yetta | Flint<br>Throw |
| Anvil | Groom<br>Pick and Drop<br>Rub with Hands<br>Throw |
| T5 | Shake in Hands |
| Baggy | Move in mouth |
| Baffo | Roll in Hands<br>Slam |
| Splash | Dislodge<br>Move in mouth<br>Pound-Drag<br>Push-Through<br>Tap |

*Note*. The lighter lines with crosses as markers represent the 95% confidence intervals. At equal abundance level (e.g., in young juveniles, 389; vertical dotted black line), rarefaction curves differ in SH *versatility* and SH *evenness*.

***Duration of SH behavioral patterns***

We found a statistically significant difference in SH *preference* for SH behaviors across individuals. Among the 36 SH behaviors expressed by the 40 sampled subjects, 35 SH behaviors (i.e., 97%) had at least one individual exhibiting SH *preference*; in other words, at least one individual per SH behavior differed in its expression of that SH behavior more than two standard deviations from the study sample average. Figure 2.1C shows SH *preference* for all individuals, across age classes. Z-scores identifying SH *preference* for all individuals are reported in Supplementary online Table S2.3 in Appendix A. Highlighted Z-scores point out to SH behaviors that were preferred by certain individuals (i.e., Z-score > + 1.96; green cells in Table S2.3).

***2.4.2. Within-individual comparison***

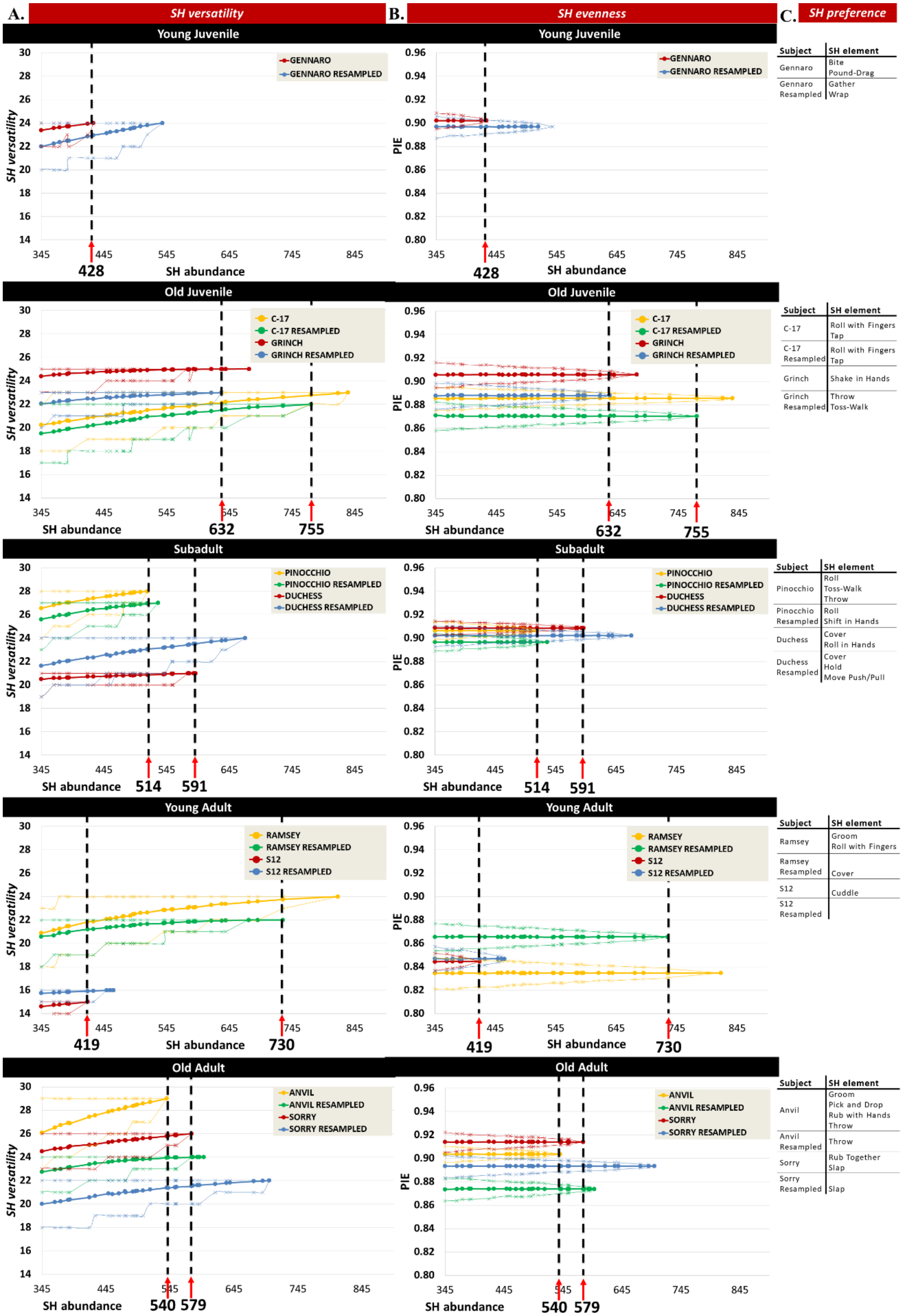
***Rarefaction analysis***

When resampling the SH activity of the same subject on different days, we found some degree of within-individual consistency in SH *versatility* (i.e., the rarefaction curves of resampled individuals were overall more similar than the rarefaction curves of different individuals; Figure 2.1A; Figure 2.2A). Figure 2.2A shows the rarefaction curves for SH *versatility* of original and resampled SH activity for 9 individuals, across age classes. For instance, in young adults, at equal abundance level (i.e., 419), the number of different SH behaviors for the original and the resampled SH activity for the subject named “S12” were 15 (95% C. I. 15 – 15) and 16 (95% C. I. 15 – 16), respectively, whereas at equal abundance level (i.e., 730), the number of different SH behaviors for the original and the resampled

SH activity for Ramsey were 24 (95% C. I. 23 – 24) and 22 (95% C. I. 22 – 22), respectively.

When resampling the SH activity of the same subject on different days, we found some degree of within-individual consistency in SH *evenness* (i.e., the rarefaction curves of resampled individuals were overall more similar than the rarefaction curves of different individuals; Figure 2.1B; Figure 2.2B). Figure 2.2B shows the rarefaction curves for SH *evenness* of original and resampled SH activity for 9 individuals, across age classes. For instance, in young adults, at equal abundance level (i.e., 419), the SH *evenness* for the original and the resampled SH activity for S12 was 0.845 (95% C. I. 0.845 – 0.845) and 0.847 (95% C. I. 0.841 – 0.852), respectively, whereas at equal abundance level (i.e., 730), the SH *evenness* for the original and the resampled SH activity for Ramsey were 0.835 (95% C. I. 0.830 – 0.839) and 0.866 (95% C. I. 0.866 – 0.866), respectively.

**Figure 2.2 –** *Rarefaction Curves for Original and Resampled SH Versatility (i.e., the Total Number of Different SH Behaviors; A.) and SH Evenness (i.e., the Degree of Similarity in the Distributions of Different SH Behaviors; B.) as a Function of SH Abundance (i.e., the Total Number of All SH Behaviors Performed), and SH Preference (i.e., the Preference of Some Individuals for Certain SH Behaviors; C.) for 9 Individuals Across Age Classes.*


A.
SH versatility
B.
SH evenness
C.
SH preference
Young Juvenile
GENNARO
GENNARO RESAMPLED
428
Subject
SH element
Gennaro
Bite
Pound-Drag
Gennaro Resampled
Gather
Wrap
Old Juvenile
C-17
C-17 RESAMPLED
GRINCH
GRINCH RESAMPLED
632
755
C-17
Roll with Fingers
Tap
C-17 Resampled
Roll with Fingers
Tap
Grinch
Shake in Hands
Grinch Resampled
Throw
Toss-Walk
Subadult
PINOCCHIO
PINOCCHIO RESAMPLED
DUCHESS
DUCHESS RESAMPLED
514
591
Pinocchio
Roll
Toss-Walk
Throw
Pinocchio Resampled
Roll
Shift in Hands
Duchess
Cover
Roll in Hands
Duchess Resampled
Cover
Hold
Move Push/Pull
Young Adult
RAMSEY
RAMSEY RESAMPLED
S12
S12 RESAMPLED
419
730
Ramsey
Groom
Roll with Fingers
Ramsey Resampled
Cover
S12
Cuddle
S12 Resampled
Old Adult
ANVIL
ANVIL RESAMPLED
SORRY
SORRY RESAMPLED
540
579
Anvil
Groom
Pick and Drop
Rub with Hands
Throw
Anvil Resampled
Throw
Sorry
Rub Together
Slap
Sorry Resampled
Slap
SH versatility
PIE
SH abundance

*Note*. The lighter lines with crosses as markers represent the 95% confidence intervals. At equal abundance level (e.g., in the subject named "GENNARO", 428; vertical dotted black line), rarefaction curves marginally differ in SH *versatility* and SH *evenness* of resampled individuals.

***Duration of SH behavioral patterns***

When resampling the SH activity of the same subject on different days, we found a within-individual consistency in SH *preference* for at least one SH behavior in 5 out of 9 individuals. Figure 2.2C shows a comparison of SH *preference* for all 9 individuals in their original and resampled SH activity. For instance, in the originally sampled SH activity, Pinocchio displayed SH *preference* for Roll, Toss-Walk, and Throw. After resampling its SH activity, Pinocchio displayed SH *preference* for Roll and Shift in Hands. Thus, Pinocchio maintained SH *preference* for Roll across resampled SH activities. Z-scores identifying SH *preference* for resampled individuals are reported in Supplementary online Table S2.4 in Appendix A. Highlighted Z-scores point out to SH behaviors that were preferred (i.e., Z-score > + 1.96; green cells in Table S2.4) by individuals in their original and resampled SH activity.

## 2.5. Discussion

Our results provide the first in-depth characterization of quantitative and qualitative aspects of SH activity in long-tailed macaques at the individual level. We found that multiple features of SH activity, such as SH *versatility*, SH *evenness*, and SH *preference*, differed across individuals, and those differences were not markedly predicted by age (but see SH *versatility* in young juveniles and old adults). We also found that, when resampling the same individual across different days, quantitative and qualitative aspects of its SH activity could vary across resampled SH activity, but when looking at the overall magnitude of within-individual variation (i.e., for all resampled individuals) in SH *versatility*, SH *evenness*, and SH *preference* across original and resampled SH activity, differences were smaller than those observed between individuals. In other words, within-individual differences in SH *versatility*, SH *evenness*, and SH *preference* were smaller than these differences between individuals.

First, when looking at the distribution of the rarefaction curves across age classes (Figure 2.1), we found that overall young juveniles and old adults displayed lower variation in SH *versatility* than other age classes (i.e., at common abundance level, the range of SH *versatility* in young juveniles and old adults was smaller than in other age/sex classes). This result may reflect sensorimotor constraints faced by individuals during their development (Fentress, 1983). Conversely, older juveniles, subadults, and young adults displayed the greatest variation in SH *versatility*. These findings are consistent with previous research investigating the developmental correlates of object manipulation complexity (Greer & Lockman, 1998; Nahallage et al., 2016). Manual complexity tends to increase with age as a result of improved affordance detection through versatile manipulation and refined sensorimotor coordination through practice (Lockman, 2000) and acquired dexterity for complex actions reflect the capacity to express more diverse actions (Nahallage & Huffman, 2007a). For instance, in Japanese macaques, infants initially exhibit only basic SH behaviors, such as Bite, Cuddle, and Hold (Nahallage & Huffman, 2007a,b). As they grow into juvenescence and early adulthood, there is an increase in the diversity and complexity of their stone-directed manual actions (measured by the level of bimanuality, as well as coordination and symmetry in hand use), with the acquisition of SH behaviors, such as Grasp, Swipe, and Flint by older juveniles, subadults, and young adults (Leca et al., 2007a,b; 2010a; 2011; Nahallage & Huffman, 2007a,b; Nahallage et al., 2016). Once they reach full maturity, and particularly senescence, the diversity and complexity of SH behaviors decrease, which may reflect behavioral conservatism (Nahallage & Huffman 2007a) or possible degradation of motor skills (Leca et al., 2011).

Second, we found some degrees of consistency in features of SH activity when resampling the same individual across different days. These findings, together with reports of idiosyncratic behaviors in SH activity expressed by only one or a few individuals (Pelletier et al., 2017; see also Leca et al., 2007a in Japanese macaques) suggest some levels of individual signature in SH activity. Inter-individual differences in behavior that are consistent over time may emerge as an adaptation to individual responses under different environmental conditions (Sih et al., 2015). Research on behavioral syndromes and animal personality highlights how individual repeatability over time and correlations between various behaviors, such as boldness, sociability, and aggressiveness, may be favored when those traits contribute to consistent differences in survival, both in terms of reproduction and growth (Biro & Stamps 2008). Behavioral idiosyncrasy in object play that persists over time may be beneficial in the acquisition and mastering of efficient instrumental actions, such as flexible tool use, in which individual differences are often documented (Boesch, 2013). For instance, in the chimpanzee population living in Loango, Gabon, the extraction of honey from underground bee nests showed consistent inter-individual differences that might be partly explained by the behavioral variability associated with their foraging repertoire (Estienne et al., 2017). Successful honey extraction techniques consist of the repetition, in an orderly sequence, of a few effective behaviors, selected from a remarkable behavioral repertoire size of 14 fundamental foraging actions that are reorganized at the individual level into functional patterns and that differ across individuals (Estienne et al., 2017). Through a systematic and multivariate comparison of SH activity across age and sex classes, our results show that SH behavior in Balinese long-tailed macaques is highly variable between individuals, and it has some repeatability at the individual level (which is consistent with the idea that SH activity is play; Burghardt, 2005). Given that in our study population, two SH behaviors possibly co-opted into tool use in a sexual context (i.e., repeated stone-tapping and stone-rubbing onto the genital area as a form of object-assisted solitary masturbation in male long-tailed macaques; Cenni et al., 2020), further studies should be conducted to evaluate whether (a) there are individual differences in the expression of stone-instrumental actions, and if so, (b) whether these differences covary with individual differences in SH activity. However, we do acknowledge that only a few individuals were resampled across different days; a larger dataset with several resampling of SH activity per individual would provide a clearer understanding of intra-individual consistency in SH activity.

It is noteworthy that we found some variation when resampling the same individual. Previous findings in long-tailed macaques revealed that the expression of SH activity in this population was impacted by the physical properties of the stone(s) manipulated (i.e., size; Cenni et al., 2021). Specifically, SH *versatility* and the duration of SH behaviors were affected by the size of the stone(s) handled. In this study, it was not possible to control for the physical properties of the stones being manipulated by individuals. Still, it is likely that extrinsic features of the objects used contributed to explaining between- and within-individual differences. Additionally, the behavioral context of expression of SH activity could affect the performance of an individual's playful manipulation (Leca et al., 2008a,b). In contrast with findings obtained in some free-ranging and provisioned groups of Japanese macaques, in which the expression of SH is strongly temporally associated with food provisioning (Leca et al., 2008b), SH activity in the free-ranging and provisioned population of long-tailed macaques at Ubud seems to be motivationally distinct from foraging (Pellis et al., 2019), and its expression occurs throughout the day. Future studies should evaluate the contribution of extrinsic factors in mediating the individual expression of SH across different days. For instance, despite representing a minimal part of our sample (less than 2%), the experimental devices occasionally provided on the same study group aiming to test whether stone tool use is facilitated by SH activity may have influenced the expression of SH activity at the individual level; this possibility, however, has yet to be tested.

Lastly, intrinsic factors, such as visual attention (Chertoff, 2021), but also possibly motivational processes and emotional responses, are likely to moderate the performance of SH behavior at the individual level. Due to the playful and cultural nature of SH in macaques, this activity is also likely to retain some level of arbitrariness in its expression (Leca et al., 2011). Indeed, the huge majority of SH behaviors are not instrumental and probably not reinforced by direct or tangible benefits to the performers; for example, the stones are typically not used as physical agents to achieve a particular foraging goal (but see Cenni et al., 2020 and Leca et al., 2008a for possible benefits of a few SH behaviors in the sexual and social domains). Contrary to stone tool use, there are no optimal SH behaviors and no possible "mistake" in expressing SH by gathering stones into a pile, clacking two stones together, pounding a stone onto another stone, rubbing a stone on the ground, or any other stone-directed actions. Thus, it is reasonable to assume that most SH behaviors are not the primary targets of natural selection. The results from this study indicate that such relaxed functional constraints on a material culture in a non-human primate species may result in arbitrary variation in the expression of playful stone-directed actions, that are probably more influenced by unselected biases, such as whim or individual preference, than by necessity. Our findings are consistent with the view that behavioral arbitrariness is usually a function of individual experience but can also be influenced culturally through social interactions with other group members (Stephenson, 1973).

Previous findings in Japanese macaques have shown that SH is socially acquired (Nahallage & Huffman, 2007a,b) and culturally maintained (Huffman, 1996; Leca et al., 2010a), through direct and indirect social influences, but little is known about the learning mechanisms underlying the composition of an individual's SH repertoire. Several studies across macaque species in captive and free-ranging settings have reported the ability to re-innovate instrumental forms of object-assisted actions under appropriate context, suggesting that individual learning is an important mode of acquisition of tool use (Bandini & Tennie, 2020; Macellini et al., 2012). The high degree of idiosyncrasy in SH profiles indicates that similar processes of individual learning, together with affordance learning mechanisms (Cenni et al., 2021), may be involved in the acquisition of non-instrumental forms of object manipulation, such as SH.

Many theories on the origins and evolution of behavioral variability hold that flexibility may have a key role in evolutionary changes by (1) increasing the availability of exploitable niches (Bolnick et al., 2003; Duckworth, 2009), (2) providing coping mechanisms to mitigate the negative consequences of new and unpredictable environmental challenges (Bateson, 2014; 2015; Bruner, 1972), (3) preventing strong directional selection to equally act on all individuals via a pool of behavioral solutions available (Sih et al., 2015), and (4) offering affordances (i.e., opportunities to perceive environmental features as being action-relevant), which affects an individual's speed of acquisition of functional tasks (Wu et al., 2014). As suggested by Sutton-Smith (2001), playful activities are good candidates for such exaptive processes: "the metaphors for play as a model of variability is too close to be ignored […] If quirkiness, redundancy, and flexibility are keys to evolution, then finding play to be itself quite quirky, redundant, and flexible certainly suggests that play may have a similar biological base” (pp. 221 and 224). Under relaxed selective pressures on foraging (e.g., food provisioning), the behavioral variability associated with SH is likely to maintain in some macaque populations a reservoir of stone-directed behaviors that could be subsequently co-opted into stone tool use, if new environmental conditions arise (Huffman & Quiatt, 1986; Leca et al., 2008a). Thus, SH would be a source of originally blind but ultimately adaptive variability.

At least three SH behaviors were possibly co-opted for beneficial effects in the domain of stone tool use: one in a social context (i.e., unaimed stone-throwing to augment the effect of agonistic display in Japanese macaques; Leca et al., 2008a) and two in a sexual context (i.e., repeated stone-tapping and stone-rubbing onto the genital area as a form of object-assisted solitary masturbation in male long-tailed macaques; Cenni et al., 2020). Within macaque populations in which the SH tradition has been established for decades, the customary performance and cultural transformation of SH activity, along with individual SH signatures allowing for behavioral tinkering, may have enhanced the perception by these monkeys of the affordances of stones as objects with action-relevant properties and, over time, facilitated the functional recycling of stones from playthings to tools. This argument is in line with the Affordance Learning Theory proposed by Lockman (2000), and the view that cultural evolution is one of the best explanations for the rapid propagation of learned, arbitrary, and originally non-functional behaviors in social animals (Boesch, 1996; Leca, 2015). A follow-up study will experimentally test the relationships between SH variability and the innovation of stone tool-assisted foraging solutions at the individual level.

The rarefaction analysis, an ecologically-based method used to evaluate species diversity and evenness, proves to be an innovative and powerful tool to explore quantitative components of behavioral repertoires (Cenni et al., 2021; Peshek & Blumstein, 2011). First, it allows to assess whether behavioral repertoires have been exhaustively sampled (i.e., by looking at whether rarefaction curves reached their asymptote). This application, however, was beyond the scope of the current study. Second, it allows to compare different individuals (or populations) of the same species, which are expected to express similar behaviors, but for which total sampled duration may not be the same. This last point is extremely appealing, as it offers a possibility to explore repertoire differences when sampling effort does not allow an equal representation for the sampled individuals (e.g., when focal animal sampling methods are not possible). The main caveat associated with rarefaction analysis is that, unless the complete samples for the rarefaction curves are representative of the population from which they are drawn, rarefaction analysis does not allow for the statistical comparison across curves. Indeed, the confidence intervals obtained are conditional to the sample, and therefore mainly informative about the statistical differences across samples collected. Additionally, it does not allow for extrapolation to a larger sample size (like accumulation curves), but it only interpolates to a smaller sample size. Future studies should apply unconditional variance to statistically compare rarefaction curves based on their confidence intervals (see Colwell, 2013; Colwell & Elsensohn, 2014; Hsieh et al., 2016). Nonetheless, the present study provides a key contribution to the necessary descriptive account of individual variability in play behavior in animals. It is also significant for future investigations aiming to elucidate the proximate and ultimate forces acting on behavioral variability.

## CHAPTER 3: HOW STONE AFFORDANCES AFFECT THE EXPRESSION OF STONE HANDLING BEHAVIOR

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### 3.1. Abstract

Object affordances play a major role in action expression, (1) providing opportunities to generate potential solutions to instrumental problems, and (2) shaping and constraining the motor actions available to an individual. The playful manipulation of objects can facilitate individual acquisition of functional object-assisted actions, through affordance learning. We tested the Object Affordance hypothesis in free-ranging long-tailed macaques. This hypothesis holds that the physical properties associated with stone size afford different stone-directed actions, in the context of stone handling (SH) behavior, a form of culturally maintained stone play from which stone tool use can emerge. We predicted that higher SH *versatility* (i.e., total number of different SH behavioral patterns expressed) and higher duration of the SH behavioral pattern "Pound" would be associated with the manipulation

of medium-sized stones, followed by small stones and then large stones. Our data partly supported these predictions. Both medium-sized and small-sized stones afforded the highest SH *versatility*, and a higher duration of "Pound" than large stones. As expected, duration of "Pound" was higher with medium than small stones, but the difference was not statistically significant. Our results were consistent with Newell's Constraint Model, which emphasizes the role of objects' physical properties in limiting and enhancing the expression of actions directed to these objects. The relaxed selective pressures acting on SH behavior may enhance the expression of a range of actions directed towards stones of different sizes that could facilitate the emergence of instrumental solutions and may contribute to understanding and better explaining the evolution of lithic technology in early humans.

### 3.2. Introduction

Acting selectively based on available information is an adaptive component of problem-solving and instrumental object manipulation (i.e., tool use; Shumaker et al., 2011) because it allows individuals to tailor effective behavioral responses to local environmental features (Fragaszy et al., 2010; Stephens & Krebs, 1986). There are several extrinsic (e.g., ecological, social) and intrinsic (e.g., anatomical, motivational, cognitive) variables that affect selectivity in tool-assisted actions (Cenni & Leca, 2020a). Among the ecological factors, object *affordances* (i.e., the physical properties of objects that determine their potential for manipulation; J. J. Gibson, 1979) play a major role in shaping and constraining the efficiency of instrumental object-directed actions. Indeed, affordances mediate motor acquisition and expression (1) by limiting the actions available to an individual, through the structural constraints associated with both the object and the user (Newell, 1986; Newell & K. Jordan, 2007; Newell et al., 1989), and (2) by creating opportunities to experience actions, enabling affordance learning (Bourgeois et al., 2005; Fontanelle et al., 2007; Lockman, 2000; Palmer, 1989).

Perceiving the affordances of objects, through visual exposure and manual contact, increases the efficiency of instrumental object manipulation (Randerath et al., 2011), by facilitating action expression. Human participants were tested across three conditions in the performance of an instrumental object-assisted task (Randerath et al., 2011). In the pantomime condition, all object affordances related to the task were hidden (both visually and manually) and participants were asked to perform the actions needed to accomplish the task (e.g., hammering a nail or scooping soup into a plate) without having visual or haptic (i.e., tactile) contact with the tools. In the demonstration condition, the participants were asked to reproduce the actions needed to accomplish the task while having only visual access to the tool, used by a demonstrator. Lastly, in the use condition, the participants were asked to perform the actions needed to accomplish the task while having both visual access to, and haptic contact with, the tool. As expected, the results showed that the pantomime condition was the most prone to errors. The information provided by object affordances increasingly facilitated the expression of tool-use task, from the demonstration condition to the use condition, in which the task was performed almost normally, suggesting that access to object-related information is a crucial feature for the appropriate expression of instrumental actions (Randerath et al., 2011).

Newell’s Constraint Model (1986) holds that objects’ physical characteristics influence the form that actions take, both by promoting and inhibiting different levels of action semantics, such as grip configuration, which is an embedded characteristic of action (Napier, 1956; van Elk et al., 2009). In a study by Newell and colleagues (1989) exploring the influence of object constraints in action expression, preschoolers and adults were tested on their ability to grasp a series of cubes differing in sizes, from smaller to larger than the palm of their hands, and the variability in grips, number of hands and number of fingers used to control differently-sized objects, in relation to hand size. Object-to-hand-size ratio was a significant predictor for the number of hands and fingers touching the cubes, and, interestingly, this relation was independent of age. As expected, the total number of fingers in contact with the cubes increased as objects became larger, but the constraints associated with large cubes limited the versatility of grip patterns, with only a few grips being exhibited when grasping large objects. When handling very large cubes, the physical constraints eliminated the majority of possible configurations between fingers and thumbs, suggesting that the number of potential actions available with large objects would decrease. In contrast, medium-sized objects allowed for the greatest variability in numbers of fingers involved in grasping, which may afford a higher number of potential actions, when several combinations of grip patterns are possible (Napier, 1956; Newell et al., 1989).

Similarly, six primate species were tested on their grasping strategies and number of fingers used to control spherical objects, in relation to object's volume (Pouydebat et al., 2009). To grasp small objects, subjects preferentially used two fingers, whereas larger objects (which did not exceed the length of the subject's hand) were controlled with more fingers and a greater variety of grip configurations that could potentially afford a higher number of actions. Specifically, in cercopithecids, such as macaques and baboons, power grip was the preferred grasping configuration for larger objects, whereas precision grip (i.e., the grasping of the object with the distant phalanx of thumb and index finger) was more likely adopted to grasp small objects (Pouydebat et al., 2009). These results are in line with findings in long-tailed macaques, *Macaca fascicularis,* a species known for its extensive manipulative capacities (Heldstab et al., 2016; Pelletier et al., 2017; Torigoe, 1987), in which some populations instrumentally manipulate stones of different sizes in the context of tool-assisted extractive foraging (Gumert et al., 2009). Power grips were reported to be preferentially adopted in pounding actions directed towards large stones (approximately the size of an individual's palm or larger), whereas precision grips were more likely used to grasp smaller stones (Gumert et al., 2009). Thus, qualitative features of an object, such as size and volume, may be used as predictors for subsequent individual differences in the performance of functional object-directed actions. Understanding the role of objects' physical properties in the expression of actions is crucial to investigate how objects available in an individual's environment afford different functional motor actions, by limiting and enhancing the performance of suitable solutions for instrumental tasks.

To further explore the relationships between object affordances and action expression in instrumental object manipulation, one may investigate how the physical properties of objects influence non-instrumental forms of object manipulation, such as object play, often claimed to be proximately and ultimately linked with tool use (Lockman, 2000). In long-tailed macaques, Zou and colleagues (2017) examined the exploratory and non-instrumental behavioral patterns directed towards novel objects of different sizes (i.e., a basketball ball and a tennis ball), to determine how the physical properties of novel objects mediate the expression of object-directed actions. Interestingly, they found no significant variation in the overall time spent manipulating these two objects across subjects, but marked inter-individual differences emerged in the relative duration of several behavioral actions directed towards the objects; for example, a tennis ball was rolled, held and bitten more often than a basketball ball (Zou et al., 2017). Thus, meaningful differences caused by the physical properties of objects that can predict differential action expression in a population may not be found in the total time allocated to their non-instrumental handling (i.e., the overall duration of play with different objects), but in the qualitative structural components of object-directed playful handling (i.e., relative durations of differential manipulative actions expressed towards different objects).

Stone handling (SH) is a form of culturally maintained stone-directed play in several macaque species (Nahallage et al., 2016). This behavior is a good candidate to explore object affordances in play, for at least four reasons. First, SH is characterized by a vast repertoire of stone-directed actions, including several SH behavioral patterns (i.e., stone-directed actions that can be assigned to mutually exclusive behavioral categories defined in the SH repertoire) reminiscent of foraging activity (e.g., Bite, Pound, Rub, Wrap; Leca et al., 2007a, 2011; Pelletier et al., 2017). Second, according to the definitions used by Pelletier et al. (2017), long-tailed macaques rely on different manual grips to control and perform SH behavioral patterns (i.e., SH behavioral patterns require using a different numbers of fingers), with some SH behavioral patterns requiring a power grip (e.g., Pound), whereas others necessitate a precision grip (e.g., Pick and Drop) to be expressed. Third, previous studies indicated that three SH behavioral patterns may have been co-opted into stone-tool use under different motivational domains: one in Japanese macaques (*Macaca fuscata*) in a social context (i.e., unaimed stone-throwing to enhance the effect of agonistic display; Leca et al., 2008a), and two in long-tailed macaques in a sexual context (i.e., repeated stone-tapping and stone-rubbing onto the genital area as a form of object-assisted solitary masturbation; Cenni et al., 2020). Fourth, these macaques play with stones of various sizes, weights, and textures, which provides opportunities for different stone-directed actions to emerge, and possibly contributes to explaining the great variety of behavioral elements in a given species' SH repertoire.

To explore the role of object affordances in the expression of object-directed playful actions, we examined SH behavioral patterns involving stones of different sizes in free-ranging Balinese long-tailed macaques. Our objective was to assess whether various stone sizes differentially afforded SH behavioral patterns. We tested the Object Affordance hypothesis, whereby the expression of SH behavioral patterns was mediated by the size of the stones being manipulated; in other words, the selection, diversity, and duration of the SH behavioral patterns performed by the monkeys should covary with the size of the stones they playfully handle. To do so, we compared SH behavioral patterns directed towards small, medium and large stones. From this hypothesis, in line with Newell's Constraint Model (1986), we generated two predictions. First, we predicted that SH *versatility* (i.e., defined as the number of different SH behavioral patterns displayed across subjects) would differ across stone sizes. Specifically, handling a medium-sized stone should be associated with the greatest SH *versatility*, followed by small stones and large stones (i.e., large stones should afford the smallest number of different SH behavioral patterns; Prediction #1). Second, in line with previous findings in long-tailed macaques on grip patterns during the performance of instrumental stone-pounding (Gumert et al., 2009), we predicted that SH behavioral patterns requiring power grip (i.e., Pound) should be preferentially performed with medium stones, followed by large stones and small stones. In other words, object-directed actions requiring all fingers and thumb to be expressed, as well as control over the object, should be more likely performed using medium stones, followed by large stones and small stones (Prediction #2). Finally, in line with previous findings about the different manual grips expressed in the SH repertoire of long-tailed macaques (cf. Pelletier et al.,

2017) and in light of Newell's Constraint Model (1986), which emphasizes how objects' physical properties affect the expression of actions directed to these objects, we discussed the distribution of different SH behavioral actions across stone sizes. To assess whether different SH behavioral patterns are preferentially associated with specific stone sizes, we measured the relative durations of each SH behavioral pattern (in relation to the overall duration of SH activity) directed towards stones of different sizes.

## 3.3. Methods

### *3.3.1. Study population and site*

We observed a population of free-ranging, urban-dwelling, habituated and provisioned Balinese long-tailed macaques inhabiting the Sacred Monkey Forest Sanctuary in Ubud, central Bali, Indonesia. The area is forested and surrounded by human settlements and Hindu temples. In 2019, the population of long-tailed macaques living in Ubud totalled over 1000 individuals and was comprised of seven neighbouring groups with overlapping home range areas (Giraud, 2021). During the study period, the monkeys were provisioned at least three times per day with fruits and vegetables by the temple staff.

### *3.3.2. Data collection and study subjects*

Observations were conducted during the dry season, from May to August 2018 and 2019, between 08:00 and 17:00. SH behavior occurred in all seven groups of this primate population, and across all age and sex classes (Pelletier et al., 2017). In this study, we sampled 37 individually identified subjects, 15 females and 22 males, belonging to the same group, which counted around 200 individuals. Of the 37 sampled subjects, 13 were old juveniles (aged 2 to 3 in females and 2 to 4 in males), 9 were subadults (adolescents individuals aged 3 to 4 in females and 4 to 6 in males), and 15 were adults (aged 4 or more in females, and 6 or more in males; Brotcorne et al., 2015). We selected individuals two years old or older because in Japanese macaques, a phylogenetically close species, within the same *Fascicularis* sub-genus group of *Macaca*, previous findings showed that at this age individuals already exhibit all SH behavioral patterns (Nahallage & Huffman, 2007a). No senile individuals were sampled, since previous findings showed that in aging individuals the complexity of the SH repertoire gradually decreases, possibly due to the degradation of their motor coordination (Nahallage et al., 2016). It is noteworthy that continued SH practice into old age was proposed to help stave off dementia through the maintenance of synaptic connections via enhanced and continuous object manipulation activities; however, this hypothesis has not been tested yet (Nahallage et al., 2016). All the SH sequences used in this study were video recorded with a digital camera (Sony Full HD Handycam Camcorder). SH sequences were collected by CC and two field research assistants using *ad libitum* sampling method (Altmann, 1974): the subject was filmed if performing SH. Whenever possible, the subjects were filmed from the front or the side, within 3-5 meters, and about two-meter square in-frame, to ensure excellent visibility conditions and to obtain good quality videos.

For each subject, we collected the stones used by the monkeys to perform SH activity. To determine stone size, CC and two field research assistants measured the length along the longest line of the stone with the use of a caliper. Because our subjects varied in age and consequently in hand size, we used two measures to characterize stone size, (1) absolute stone length, expressed in cm, and (2) relative stone size, inferred by comparing the size of the stone to the subject's palm. A *small* stone was defined as being smaller than the subject's palm of hand and characterized by a length < 3 cm (M ± SD: 2.15 ± 0.47 cm, ranging from 0.70 to 2.90 cm). A *medium* stone was defined as being of similar size to the subject's palm with a length varying between 3 and 5 cm (3.99 ± 0.54 cm, ranging from

3.00 to 5.00 cm). A *large* stone was defined as being greater than the subject's palm and characterized by a length > 5 cm (7.92 ± 1.51 cm, ranging from 5.40 to 11.00 cm). After being collected and measured, all stones were video recorded, to allow for a later match between the stone and the corresponding SH bout.

***3.3.3. Data analysis and statistics***

For each of the sampled subjects, we selected three two-minute SH sequences, truncated from longer independent SH bouts (i.e., they belonged to distinct SH bouts collected on different days). Thus, a SH bout represented the display of SH activity with possible pauses for up to 120 seconds (Huffman, 1996; Leca et al., 2007a), whereas a SH sequence represented a truncated two-minute segment of a longer SH bout. For five subjects, two of the selected SH sequences were truncated from SH bouts collected on the same day, and for three out of these subjects, the selected SH sequences were truncated from the same SH bout, but they did not overlap in time (i.e., two SH sequences did not share any SH behavioral patterns). In each of these SH sequences, the subject manipulated at least a *small* stone, a *medium* stone and a *large* stone, respectively, independent from each other: each stone was used in a single SH sequence (see three video examples of an individual manipulating a small, medium and large stone on different days in Supplementary Materials S3.1 in Appendix B). Regarding the three subjects whose selected SH sequences were truncated from the same SH bout, two selected stones were present in both SH sequences. Additionally, whenever possible, we ensured that the small, medium and large stones manipulated by one subject were not manipulated by another subject. In two cases, the same stone was manipulated by two subjects on two separate SH bouts recorded on the same day. Thus, in total, we selected 36 small, 37 medium, and 36 large stones. In the selected SH sequences, a subject could use more than one stone to perform

SH within the same SH sequence, or the stone of interest could be combined with objects other than stones (e.g., locally available hard-shelled nuts, that are commonly manipulated but almost never consumed and usually discarded), but we only scored the SH behavioral patterns directed to the selected stone (i.e., the selected small, medium and large stone, respectively). The SH behavioral patterns that require at least two stones to be performed (e.g., Clack, Flint, Rub Together) were scored if the stone of interest was used together with other stones or objects to perform them. In the end, the selected SH sequences contained on average 1 minute and 42 seconds (± 25 seconds) of SH activity (i.e., the overall SH behavior displayed in a SH sequence) with the selected stone. SH sequences were chosen and truncated on the basis of optimal visibility conditions, to ensure that all the behavioral elements directed to the stone of interest could be reliably identified. For a SH sequence to be eligible, the stone used should be matched with the video-record available for the stone collected. If more than one SH sequence was eligible for selection, SH sequences were chosen at random, with the use of a random number generator. If a SH bout was longer than two minutes, the beginning of the truncated SH sequence was randomly selected with the use of a random time generator. In each video-recorded SH sequence, the first author (CC) scored all the SH behavioral patterns performed by the subject with the stone of interest and used the same SH ethogram as in Pelletier and colleagues (2017) to generate event-log files (i.e., series of consecutive SH behavioral patterns), by using *BORIS* software (Friard & Gamba, 2016). During the scoring process, we detected two stone-directed actions not previously described by Pelletier and colleagues (2017). Given that SH is a culturally maintained form of object play, it is not surprising that the behavior may undergo transformation (Huffman & Quiatt, 1986; Leca et al., 2012). The two newly described SH behavioral patterns were named “Push-Through” and “Slam”.

Operational definitions and video references of these two new SH behavioral patterns can be found in Supplementary Material S3.2–S3.3 in Appendix B. To assess reliability of video scoring, we calculated an inter-scorer reliability test for CC and JBL when transcribing the same samples of SH video records, involving a total of 24 SH sequences (i.e., 22% of the sample; k = 0.95; Martin & Bateson, 1993).

To test Prediction #1 (i.e., medium-sized stones should be associated with the greatest SH *versatility*, followed by small stones and large stones), we used the "rarefaction analysis" to generate rarefaction curves, calculated through *EcoSim* software (Gotelli & Entsminger, 2001). Rarefaction analysis is a technique commonly used by ecologists to characterize the species composition of ecological samples, based on the cumulative number of individuals belonging to different species found in a sample, and to estimate the predicted number of species in a sub-sample of individuals (Gotelli & Colwell, 2001). By repeatedly resampling a large pool of *N* individuals, the expected number of species in a smaller collection of *n* individuals, drawn at random from *N*, can be generated (Simberloff, 1978). Rarefaction curves are plotted from the number of expected species found in smaller subsets, and they move from right to left, as the full dataset *N* increasingly rarefies. A rarefaction curve describes, on the *y* axis, species *versatility*, defined as the total number of different species found across a collection of individuals, providing confidence intervals that, if complete samples are representative of the population from which they were drawn, allow for statistical comparisons between samples. Rarefaction analysis has been previously used to characterize animal behavioral repertoires (Peshek & Blumstein, 2011). To apply the rarefaction analysis to estimate SH *versatility*, defined as the total number of different SH behavioral patterns displayed across subjects, we treated SH behavioral patterns (e.g., Bite, Pound, Wrap) within an individual's repertoire as species, and the total abundance of SH behavioral patterns performed (e.g., the total number of Bite, Pound, Wrap, recorded; i.e., SH abundance) as individuals. As a result, SH *versatility* was calculated as a function of SH abundance (Figure 3.1).

We performed sample-based rarefaction analysis to compare SH *versatility* across small, medium and large stone sizes (cf. Gotelli & Colwell, 2001). A sample-based rarefaction preserves the heterogeneity that comes from comparing individuals differing in the SH *versatility* (i.e., performing a different number of SH behavioral patterns than other individuals) associated to a stone size. In fact, although sample-based rarefaction computes the expected sampled SH *versatility* as a function of SH abundance, it maintains the relationship between an individual's SH *versatility* and its SH abundance. Operationally, a sample-based rarefaction curve is generated by repeatedly resampling and pooling a smaller sample of individuals and computing the mean and variance for the SH *versatility* found across smaller subsets of individuals, depending on their relative SH abundance. The main function of this rarefaction analysis is that it allows for the comparison of rarefaction curves belonging to different stone sizes with different SH abundance, by calculating the expected SH *versatility* for smaller SH abundances. To do so, sample-based rarefaction curves representing SH *versatility* for different stone sizes can be compared at the maximum common abundance level available to the curves that are being compared (black dotted lines in Figure 3.1). Because we compared three rarefaction curves, we considered two maximum common SH abundance levels, one for the stone size associated with the smallest SH abundance (i.e., SH *versatility* associated to the curve with the smallest SH abundance was compared to SH *versatility* associated to the other two curves), and one for the stone size associated with the second smallest SH abundance (i.e., SH *versatility* associated to the curve with the second smallest SH abundance was compared to SH *versatility* associated to the curve with the highest SH abundance). At equal abundance levels, the 95% Confidence Intervals (95% C. I.) allow for statistical comparisons between samples. We do acknowledge that C. I. are conditional to the sample, and thus mainly informative of the relative sample collected. However, similar length of sampled SH sequences and number of individuals sampled suggest that our samples for stone size may be representative of the population. Further details about the application of rarefaction analysis to behavioral repertoires can be found in Peshek and Blumstein (2011).

To test Prediction #2 (i.e., "Pound" should be more likely performed using medium stones, followed by large stones and small stones), we extracted for each subject the relative duration (i.e., in relation to the cumulative duration of SH activity) of Pound expressed with each stone size from the generated event-log files. Additionally, we examined the relative duration of SH behavioral patterns across stone sizes that comprised 1% or more of the overall sampled SH activity. To compare the duration of SH behavioral patterns directed to stones of different sizes, we used a Friedman test with Dunn's post-hoc tests for multiple pairwise comparisons and Bonferroni correction to control for type I errors (Siegel & Castellan, 1988).

#### *3.3.4. Ethical statement*

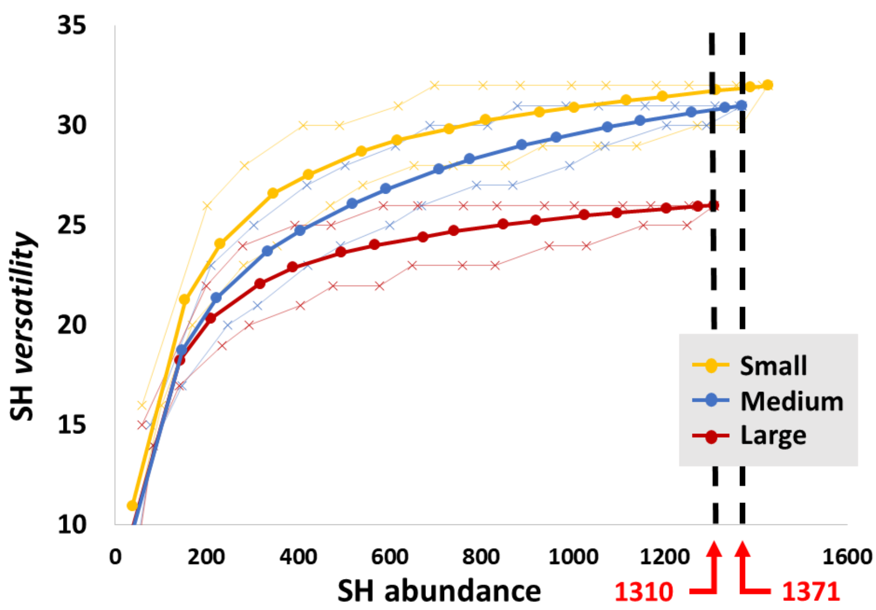
This research was exclusively observational and non-invasive. Our study was conducted in accordance with the Indonesian Ministry of Research and Technology, the Provincial Government of Bali, and the local district authorities. It was approved by the institutional Animal Welfare Committee of the University of Lethbridge (Protocol #1906).

## 3.4. Results

### *3.4.1. Rarefaction analysis*

At the maximum common SH abundance to large, medium, and small stones (i.e., 1310), SH *versatility* significantly differed across stone sizes (i.e., the 95% confidence intervals of the three rarefaction curves did not overlap). Handling small stones was associated with significantly higher SH *versatility* than handling large stones, and handling medium stones was associated with significantly higher SH *versatility* than handling large stones. Specifically, at SH abundance level = 1310, 32 different SH behavioral patterns were exhibited with small stones (95% C. I. 30 – 32), 31 different SH behavioral patterns were exhibited with medium stones (95% C. I. 30 – 31), and 26 different SH behavioral patterns were exhibited with large stones (95% C. I. 26 – 26; Figure 3.1).

**Figure 3.1** - *Rarefaction Curves for Small Stones (Solid Yellow Line), Medium Stones (Solid Blue Line), and Large Stones (Solid Red Line).*




*Note.* The lighter lines with crosses as markers represent the 95% confidence intervals for small stones (yellow line), medium stones (blue line), and large stones (red line). If, at given abundance levels (vertical dotted black lines), rarefaction curves fall outside the 95% confidence intervals, SH *versatility* differs across stone sizes

At the maximum common SH abundance to medium and small stones (i.e., 1371), SH *versatility* did not significantly differ between small stones and medium stones. Handling small stones was associated, on average, with higher SH *versatility* than handling medium stones, but the difference was not statistically significant. Specifically, at SH abundance level = 1371, 32 different SH behavioral patterns were exhibited with small stones (95% C. I. 30 – 32), and 31 different SH behavioral patterns were exhibited with medium stones (95% C. I. 31 – 31; Figure 3.1). Therefore, SH *versatility* was significantly higher for medium and small stones than for large stones; Prediction #1 was partly supported.

### *3.4.2. Duration of SH behavioral patterns*

We found a statistically significant difference in the duration of Pound across stone sizes ($\chi^2$ (2, N = 37) = 16.88, $p < 0.001$). Pound lasted longer when handling medium stones than when handling large stones (z = 0.65, p = 0.005). As expected, Pound lasted on average longer when handling medium stones than when handling small stones, but the difference was not statistically significant (z = 0.00, p = 1.000). Contrary to what we expected, Pound lasted longer when handling small stones than when handling large stones (z = 0.65, p = 0.005). The relative duration of Pound when handling small, medium, and large stones constituted 6.72% (± 10.85), 9.11% (± 14.83), and 1.78% (± 4.03) of the cumulative SH activity, respectively. Prediction #2 was partly supported.

Across stone sizes, we found statistically significant differences in the duration of some SH behavioral patterns. In Table 3.1, we reported the statistics of the Friedman's test and the post-hoc pairwise comparisons of all SH behavioral patterns that comprised 1% or more of the overall sampled SH activity across stone sizes. When handling different stone sizes, durations of SH behavioral patterns differed for Cuddle, Hold, Roll, and Rub. Cuddle lasted longer when handling large stones than when handling small and medium stones.

Hold lasted longer when handling small stones than when handling medium and large stones. Roll lasted longer when handling small stones than when handling medium and large stones. Rub lasted longer when handling medium and large stones than when handling small stones.

**Table 3.1** – *Friedman's Test $\chi^2$ and Dunn's Post Hoc Tests z for Multiple Pairwise Comparisons for the Duration of SH behavioral patterns Across Stone Sizes and P Values, and Average Percentages (± SD) of SH Duration Within the Three Stone Size Categories.*

| SH behavioral pattern | Small vs Medium vs Large | | Small vs Medium | | Small vs Large | | Medium vs Large | |
|---|---|---|---|---|---|---|---|---|
| | χ2 (2, N = 37) | p value α = 0.003 | z | p value α = 0.017 | z | p value α = 0.017 | z | p value α = 0.017 |
| Bite | 0.30 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Carry | 5.31 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Cover | 5.96 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Cuddle | **23.19** | **< 0.001** | -0.08 | n.s. | -0.65 | **0.005** | -0.57 | **0.015** |
| Gather | 6.47 | n.s. | -0.50 | n.s. | -0.51 | n.s. | -0.01 | n.s. |
| Grasp | 6.05 | n.s. | -0.43 | n.s. | -0.54 | n.s. | -0.11 | n.s. |
| Grasp-Walk | 9.84 | n.s. | -0.11 | n.s. | -0.50 | n.s. | -0.39 | n.s. |
| Groom | 1.94 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Hold | **25.81** | **< 0.001** | -0.62 | **0.008** | -1.12 | **< 0.001** | -0.50 | n.s. |
| Pound | **16.88** | **< 0.001** | 0.00 | n.s. | -0.65 | **0.005** | -0.65 | **0.005** |
| Pound-Drag | 3.29 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Roll | **20.72** | **< 0.001** | -0.92 | **< 0.001** | -0.70 | **0.003** | -0.22 | n.s. |
| Roll with Fingers | 6.32 | n.s. | -0.26 | n.s. | -0.43 | n.s. | -0.18 | n.s. |
| Rub | **23.19** | **< 0.001** | -0.92 | **< 0.001** | -0.91 | **< 0.001** | -0.01 | n.s. |
| Scatter | 2.70 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Slap | 2.18 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Tap | 3.43 | n.s. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Wrap | 8.03 | n.s. | -0.34 | n.s. | -0.14 | n.s. | -0.47 | n.s. |

**Table 3.1** (continued)

| SH behavioral pattern | Small | Medium | Large |
|---|---|---|---|
| | **M (± SD)** | **M (± SD)** | **M (± SD)** |
| Bite | 4.99% (± 9.00) | 4.27% (± 9.11) | 2.54% (± 4.17) |
| Carry | 1.29% (± 2.76) | 0.83% (± 1.85) | 2.67% (± 5.89) |
| Cover | 3.03% (± 4.64) | 5.36% (± 5.47) | 4.60% (± 4.39) |
| Cuddle | 0.24% (± 1.44) | 0.43% (± 1.57) | 2.86% (± 5.78) |
| Gather | 6.81% (± 8.12) | 2.52% (± 2.73) | 3.45% (± 3.45) |
| Grasp | 17.47% (± 10.32) | 29.20% (± 19.87) | 33.46% (± 22.74) |
| Grasp-Walk | 2.79% (± 4.68) | 1.72% (± 3.03) | 0.30% (± 1.13) |
| Groom | 2.26% (± 4.94) | 2.29% (± 3.90) | 4.00% (± 7.67) |
| Hold | 8.40% (± 7.88) | 3.60% (± 4.62) | 1.28% (± 2.37) |
| Pound | 6.72% (± 10.85) | 9.11% (± 14.83) | 1.78% (± 4.03) |
| Pound-Drag | 0.40% (± 1.29) | 2.03% (± 7.34) | 1.03% (± 4.76) |
| Roll | 16.79% (± 19.33) | 3.98% (± 8.96) | 4.76% (± 8.58) |
| Roll with Fingers | 2.66% (± 4.16) | 2.13% (± 9.28) | 0.66% (± 2.00) |
| Rub | 5.24% (± 9.24) | 19.47% (± 17.86) | 20.42% (± 21.66) |
| Scatter | 2.68% (± 6.06) | 2.56% (± 5.18) | 2.84% (± 3.36) |
| Slap | 1.06% (± 1.67) | 0.78% (± 1.35) | 1.73% (± 3.45) |
| Tap | 2.62% (± 6.83) | 0.83% (± 1.50) | 5.56% (± 14.14) |
| Wrap | 2.87% (± 5.81) | 3.40% (± 5.13) | 1.43% (± 3.55) |

*Note.* SH = stone handling; α = Bonferroni adjusted-p-value. n.s. = not statistically significant; n.a. = not applicable. Boldface indicates statistically significant results.

### 3.5. Discussion

Our results partly support the two predictions we derived from the Object Affordance hypothesis, whereby the size of the stone handled affects the expression of qualitative aspects of object play in Balinese long-tailed macaques. We found that both small and medium stones were associated with the expression of significantly more SH behavioral patterns (i.e., with a higher SH *versatility*) than large stones, but no significant difference was found in the SH *versatility* associated with small and medium stones (Prediction #1 was partly supported). Additionally, we found that when handling small and medium stones, Pound lasted longer than when handling large stones, but we did not find any statistically significant difference in the duration of Pound when handling medium stones and small stones (Prediction #2 was partly supported). Finally, consistent with previous findings about the different manual grips expressed in the SH repertoire of long-tailed macaques (cf. Pelletier et al., 2017), we found significant differences in the duration of several SH behavioral patterns across stone sizes, suggesting that object size affects the expression of object play actions in this population of long-tailed macaques. Specifically, we found that (1) compared to handling medium and large stones, Hold and Roll with small stones lasted longer, whereas Rub had a shorter duration, and (2) compared to handling small and medium stones, Cuddle with large stones had a longer duration. Taken together, these findings provide some support for the Object Affordance hypothesis, with one of the physical properties of objects (here stone size), significantly influencing the expression of playful stone-directed actions, both at the level of the behavioral repertoire (i.e., SH *versatility*), and at the level of specific stone-play patterns (i.e., Pound and other SH behavioral patterns).

Many studies have suggested that non-instrumental object manipulation, both exploratory and playful, may be a precursor of functional object-assisted actions, through affordance learning (e.g., Bourgeois et al., 2005; Fragaszy & Visalberghi, 1989; Kenward et al., 2006; Lonsdorf, 2005). Following a perception-action perspective, the temporal association between object-directed playful manipulation and instrumental object-mediated actions allow an individual to gradually understand the physical and functional properties of objects through exploratory and pressure-free interactions with its environment (i.e., Affordance Learning theory, E. J. Gibson, 1988; Lockman, 2000). If so, experiencing the physical properties of the object, such as its size, during playful object-directed manipulation may contribute to the motor expression of suitable solutions (1) by allowing individuals to perceive the object's potential for manipulation, and (2) by limiting the array of available actions and improving the performer's sensorimotor coordination, through practice (Lockman, 2000). The behavioral variability associated with object play (Burghardt, 2005; Leca et al., 2010b, 2011) could provide a reservoir of actions directed towards various objects that may be later beneficial for the development, evolution and daily expression of tool use (Cenni & Leca, 2020a; Huffman & Quiatt, 1986; Leca et al., 2012; Lockman, 2000, but see Allison et al., 2020). Through a systematic comparison of qualitative aspects of SH behavior in long-tailed macaques, our results are indicative of a relationship between the size of the stones used and the SH behavioral patterns exhibited.

Our results are in line with Newell's Constraint Model, which emphasizes the role of task constraints, such as the size of the object used, in limiting the expression of available actions (Newell, 1986; Newell et al., 1989). In a study by Cesari and Newell (1999) furthering previous findings from Newell and colleagues (1989), five adult men and five adult women were tested on their ability to grasp a series of cubes differing in sizes, density, and weight, from smaller to larger than the palm of their hands, and from lighter to heavier, in relation to their density (e.g., some cubes were made of cork, others of aluminum). The weight of the cubes started to play a large role in the expression of grip configurations only when it became increasingly large in relation to a participant's hand-weight (which was necessarily associated with an increase in object size; i.e., object size had a greater influence on grip configuration for small and medium weights; Cesari & Newell, 1999). Additionally, several studies have shown how the organization of grip configuration is shaped before the actual contact with the object (e.g., Newell et al., 1993), indicating that visual affordances, and therefore size, play a major role in influencing grasping and consequently object-directed actions (e.g., Sirianni et al., 2018). In our study, small and medium stones were substantially lighter (on average 7.49 ± 4.51 and 36.30 ± 18.54 grams, respectively) than large stones (on average 257.68 ± 176.76 grams), but we do acknowledge that there was a higher variation in the weight of large stones, with five large stones weighing more than 500 grams. Therefore, it is possible that, when handling particularly heavy stones, mass could greatly contribute to explain action expression associated with large (and heavy) stones. Specifically, heavy stones may impede the expression of a range of SH behavioral patterns that require power, precision, and control to be expressed, such as pounding stones on a surface, or that are largely impacted by weight, such as holding stones away from the body or the ground (cf. Nahallage et al., 2016; Pelletier et al., 2017; Pellis et al., 2019).

It is noteworthy that we did not find a statistically significant difference between medium and small stones in the expression of pounding actions, although on average medium stones were associated with longer Pound duration in relation to cumulative SH activity than small stones. In line with Newell's Constraint Model, only a few grip configurations (and therefore, actions) are commonly used towards specific objects differing in sizes, even though theoretically those objects could still be grasped and manipulated via a wider range of grip configurations (cf. Cesari & Newell, 1999; Newell et al., 1989). Thus, actions that generally require specific grip configurations to be expressed, such as Pound, may be performed using behavioral variants that are macro-structurally similar (i.e., the trajectory of the action is maintained, but a different grip configuration is adopted) and therefore qualify as the same SH behavioral pattern; however more data are needed to test this possibility. Furthermore, the potential variability of actions ("motor abundance"; Latash, 2000, 2012) associated with different objects is likely higher in object play than in tool use, which may favor the maintenance of a reservoir of solutions upon which selection can act to shape and refine functional responses to environmental problems (Bateson, 2014; Bruner, 1972). The relaxed selective pressures under which object play is expressed (Burghardt, 2005), together with the anthropogenic influences acting on this population of long-tailed macaques (i.e., food provisioning), may maintain a pool of playful actions directed towards stones of different physical characteristics (i.e., size, weight, texture) that could be co-opted into stone tool use (cf. Huffman & Quiatt, 1986; Leca et al., 2008a,b). In this view, the perception of relevant physical properties of stones by individuals during playful manipulation may later facilitate the functional use of stones during the expression of instrumental object-mediated actions, such as tool-assisted masturbation, a form of stone tool use documented in the long-tailed macaque population living in Ubud (Cenni et al., 2020), but more data are needed to test this prediction.

Contrary to previous reports of SH in some free-ranging groups of Japanese macaques, in which SH activity was mainly observed immediately after feeding on provisioned food (Huffman, 1984, 1996; Leca et al., 2008b; but see Nahallage & Huffman, 2007b), a six-month study conducted in 2016 and based on focal-animal sampling did not show any marked temporal connection between SH and feeding activities in this free-ranging population of long-tailed macaques living in Ubud (unpublished data). However, these data could not be used in the present study because the number and duration of SH bouts were not sufficient to run a rarefaction analysis. As a result, we used behavioral data collected via *ad libitum* sampling. We do acknowledge the limitations inherent to this sampling technique. More specifically, we were unable to assess (1) whether individuals displayed a preference for size-specific stones during the *selection* part of SH activity (i.e., *before* SH started), or (2) whether, at the individual level, SH duration was affected by stone size. Yet, it is noteworthy that these questions were beyond the scope of our study.

Even though we only scored the SH behavioral patterns directed to the selected stone, a subject could use more than one stone, or the stone of interest could be combined with objects other than stones (e.g., locally available hard-shelled nuts, that are commonly manipulated but almost never consumed and usually discarded). When resampling a smaller dataset without the presence of edible objects within SH sequences, our results were qualitatively, and, to large extent, quantitatively similar to the findings of this chapter for Prediction #1 and Prediction #2. Specifically, we found that small and medium stones were significantly associated with the expression of significantly more SH behavioral patterns (i.e., with a higher SH *versatility*) than large stones; we also found that small stones were significantly associated a higher SH *versatility* than medium stones. Additionally, we found that, on average, Pound lasted longer when handling medium stones compared to small and large stones, but the difference was not statistically significant. Finally, we found that Hold with small and medium stones lasted longer compared to handling large stones, Rub with medium stones lasted longer compared to handling small stones, and Cuddle with large stones lasted longer compared to handling small and medium stones.

Future research should investigate the relationships between action expression across stones differing in size and the possible inter-individual SH variability, to understand whether (and if so, how) individual preferences in the expression of SH behavioral patterns covary with the constraints of the stones being manipulated. Specifically, we will test (1) whether individuals have "SH signatures" (i.e., preferences in the expression of a few SH behavioral patterns), and, if so, (2) whether their preference in the expression of SH activity is influenced by a stone's physical characteristics, such as size, or if the preference for SH behavioral patterns performed by an individual overcomes the constraints associated with stones (i.e., action expression is only moderately affected by stone size when an individual's preference is accounted for).

This study has implications for the evolution of human technology and primate intelligence (i.e., Technical Intelligence hypothesis, Cenni & Leca, 2020b). The playful actions afforded by stones of different sizes in the long-tailed macaques living in Ubud leave physical traces (e.g., on surfaces where percussive/rubbing actions occur, on the items flinted/clacked, and on the stones used); these artefacts may contribute to the maintenance of stone play as a behavioral tradition (Leca et al., 2007b; Nahallage et al., 2016; Pelletier et al., 2017), by facilitating the transmission of SH behavior (Leca et al., 2010a) and possibly affording the emergence of stone-tool use (cf. Fragaszy et al., 2013), through stimulus enhancement and indirect forms of social learning. Additionally, the physical traces left after playful object-directed actions can increase the likelihood of social interactions, through the creation of a "lithic niche" that facilitates learning and teaching (cf. Hiscock, 2014). Living in an environment where suitable objects and artifacts for instrumental actions are present may be a necessary step for the emergence of tool-assisted solutions applied to foraging problems (i.e., Ecological Opportunity hypothesis; Fox et al., 1999). Therefore, understanding the interface between the expression of playful and instrumental object-directed actions and the role of affordances mediated by objects in their performance is essential to appreciate the emergence of flexible tool use solutions, lithic culture and primate intelligence.

# CHAPTER 4: EVIDENCE OF STONE-TOOL USE IN THE SEXUAL DOMAIN

This chapter was adapted from the following article: Cenni, C., Casarrubea, M., Gunst, N., Vasey, P., Pellis, S., Wandia N, & Leca, J.-B. (2020). Inferring functional patterns of tool use behavior from the temporal structure of object play sequences in a non-human primate species. *Physiology & Behavior*, *222*, 112938. https://doi.org/10.1016/j.physbeh.2020.112938

At the time of the thesis submission, I have been working on a replication study using a larger sample size. Hence, this chapter uses the results from a larger sample from the manuscript in preparation, titled: "Using the sequential structure of object play behavior to discriminate functional patterns of tool use in long-tailed macaques (*Macaca fascicularis*): A replication study".

The authorship list for the published version is as below. Authors' contribution: C. Cenni: Conceptualization; Methodology; Data collection; Formal Analysis; Writing - Original Draft; M. Casarrubea: Formal Analysis; Writing -Reviewing and Editing; N. Gunst: Supervision; Writing - Reviewing and Editing; P.L. Vasey: Supervision; Writing - Reviewing and Editing; S.M. Pellis: Supervision; Writing - Reviewing and Editing; IN. Wandia: Resources; J.-B. Leca: Supervision; Methodology; Funding acquisition; Writing - Reviewing and Editing.

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## 4.1. Abstract

Inferring functional components of behavioral sequences is a crucial but challenging task. A systematic comparison of their temporal structure is a good starting point, based on the postulate that more functional traits are less structurally variable. We studied stone handling behavior (SH) in Balinese long-tailed macaques, a versatile form of stone-directed play.

We tested the hypothesis that stones are used by male monkeys to stimulate their genitals in a sexual context (i.e., Sex Toy hypothesis). Specifically, two SH actions – the repetitive tapping and rubbing of stones onto the genital area – gained functional properties as self-directed tool-assisted masturbation. Owing to the structural organization of playful activities, we predicted that SH sequences without genital stone-tapping/-rubbing would exhibit higher levels of variability, repeatability, and exaggeration than SH sequences with genital stone-tapping/-rubbing.

To identify and compare recurring series of SH behaviors otherwise undetectable by using conventional quantitative approaches across SH sequences containing genital stone-tapping/-rubbing or not, we used a temporal analysis known as "T-pattern detection and analysis". Our prediction about exaggeration was supported, whereas no differences in variability were found between SH sequences with and without genital stone-tapping/-rubbing. When testing for differences in repeatability, our analyses yielded contrasting results. Overall, the Sex Toy hypothesis was partly supported, and our results suggested that genital stone-tapping and -rubbing are two forms of tool-assisted genital stimulation, possibly derived from the playful handling of stones. These findings are consistent with the view that tool use may evolve in stages from initially non-functional object manipulation, such as object play.

## 4.2. Introduction

Understanding behavior considering its functional characteristics is fundamental to appreciate ecological and evolutionary processes. However, inferring functionality in behavioral research is inherently challenging, for at least two reasons. First, the notion of function has a variety of meanings in the literature, which generates theoretical confusion.

Second, linking function to fitness is a daunting task that highlights methodological limitations. An exemplary case that encompasses these challenges is the study of tool use – the instrumental use of objects, which is typically defined as a functional and possibly fitness-enhancing behavior (e.g., Shumaker et al., 2011; St Amant & Horton, 2008). Yet, to date, there is no reported evidence that instrumental object manipulation improves an individual's survival or reproductive success (cf. Biro et al., 2013). A focus on the proximate factors underlying the expression of tool use (i.e., mechanisms) may inform us about its ultimate causes (i.e., functions).

According to the "design-feature argument", in-depth structural analysis of a given behavioral pattern provides valid information about its hypothesized function (Martin & Caro, 1995; Moran, 1985). The heuristic power of the behavioral structure-function interface is reflected in the following statement by Pellis and Pellis: "Therefore, behavioral description informs functional inference, which in turn, influences further description" (1998, p. 115). Subtle differences in the structural organization of evolutionarily related behaviors are indicative of their respective motivational underpinnings and functional features. This approach has proved particularly useful to compare various types of object manipulation; indeed, it uses structural variables, either based on kinematic or temporal components, to infer underlying psychological mechanisms and explain the actions being performed in terms of relative purpose and utility (e.g., Hughes, 1978, 1979; Pelletier et al., 2017; Pellis et al., 2019).

With regards to kinematic components, Pellis et al. (2019) used a movement notation system to test a series of hypotheses about the motivational processes and functional components pertaining to two object-directed percussive actions performed by free-ranging long-tailed macaques (*Macaca fascicularis*). They systematically compared the type, direction, magnitude, and speed of the movement of specific body segments of the same monkey during the performance of nut-pounding actions (i.e., an unambiguously hunger-motivated and functional foraging behavioral pattern that consists of repeatedly striking a hard-shelled nut onto the ground to crack it open, extract and eat the kernel) and the performance of stone-pounding actions (i.e., a seemingly pleasure-motivated and questionably functional object play behavioral pattern that consists of repeatedly striking a stone of comparable size onto the ground). Even though these two percussive actions look outwardly similar, fine-grained kinematic analysis showed that stone-pounding is not pseudo-foraging, but a distinctly motivated playful action. Moreover, the structural similarities in stone-pounding performed by adult and juvenile monkeys support the view that exaggeration, variability, and incompleteness of body movements are indeed properties of play behavior – whereas their more functional counterpart (i.e., percussive actions performed in a foraging context) are less exaggerated, less variable, and more complete in their kinematic structure.

With regards to temporal components, Hughes (1978, 1979) used a sequential analysis and a hierarchical cluster analysis to explore the amount of stochasticity (i.e., relative predictability or randomness) in the sequence of behavioral patterns expressed by pre-school children engaging in two types of object-directed activities. She systematically compared the range of manipulative actions, the transitional probabilities between these actions, and whether particular subsets of actions were consistently grouped when they were performed during an exploratory context and during a playful context. She found that playful activities were structurally characterized by a higher diversity of actions, a higher level of randomness (or lower level of predictability) in the sequential relationships between actions, and a looser functional grouping of actions than exploratory activities.

Hughes' (1978, 1979) findings support the hypothesis that more functionally constrained object-directed behaviors – like object exploration, which is an object-centered, information-driven, and product-oriented manipulative activity (e.g., "What does this *object* do?"; Hutt, 1966, p. 76) – are more temporally structured than object-directed behaviors that do not appear to be immediately functional – like object play, which is a person-centered, pleasure-driven, and manipulative activity (e.g., "What can *I* do with this object?"; Hutt, 1966, p. 76).

Taken together, these studies indicate that utilitarian motivational processes and functional constraints in object manipulation covary with behavioral structure. When comparing two types of manipulative activities, the more product-oriented one (e.g., object exploration, extractive foraging) show higher levels of kinematic and/or temporal structure than the more process-oriented one (e.g., object play; see also Rasa, 1984). In line with one of the basic tenets of Darwinian evolution, holding that selection strength and phenotypic variability are negatively correlated, more functionally constrained behaviors are subjected to higher selection pressures, which in turn, lead to less structurally variable behaviors. Thus, the behavioral structure of object-directed activities may be used as a proxy to assess their relative functionality. Theoretically, this powerful structure-function interface could be applied to another pair of object-directed activities: object play and tool use. This methodological approach would advance our understanding of the motivational underpinnings and functional features of these two behavioral categories that are often claimed to be associated in the literature. Indeed, following the "play ethos" about the assumed functional importance of play, "[o]ne purported purpose of object play is to allow individuals to discover the affordances of objects, which may facilitate subsequent tool use" (Bjorklund, 2016, p. 8). Therefore, one way to examine the motivational and functional relationships between object play and tool use is to conduct a systematic and comparative structural analysis of these two activities.

This research has implications for the Affordance Learning theory applied to object manipulation (E. J. Gibson, 1988; Lockman, 2000), which generates the following two postulates at two different levels of analysis. First, during an individual's *development*, object play should provide opportunities to explore, and acquire knowledge about, the action-relevant properties of new objects that could enhance the *acquisition* of tool use involving (the same type of) objects (Lockman, 2000). Second, during a species' *evolution*, the object play repertoire should serve as a behavioral reservoir of pre-existing object-directed actions that could be subsequently co-opted (i.e., recycled) for useful purposes in novel problem-solving contexts, thereby facilitating the *emergence* of tool use (S. T. Parker & K. R. Gibson, 1977).

Stone handling (SH), defined as a culturally maintained stone-directed form of object play in several macaque species (Nahallage et al., 2016), is an ideal candidate behavior for testing this hypothesis. Like other types of object play (e.g., Fagen, 1981; Power, 1999), most SH behavioral elements are reminiscent of actions characteristic of foraging activity (e.g., biting, covering, carrying, gathering, pounding, rolling, rubbing, wrapping; Leca et al., 2007a, 2011, 2012; Pelletier et al., 2017); however, compared to their functionally constrained foraging counterpart, SH actions are structurally more variable, more repeated, more exaggerated, and incomplete (e.g., no consummatory phase, because the objects being manipulated are not edible; see Pelletier et al., 2017; Pellis et al., 2019). Even though SH activity as a whole does not seem to serve any immediate instrumental benefits, one of the 45 SH behavioral elements performed by Japanese macaques (*Macaca* *fuscata*) has turned into stone tool use in a social context: unaimed stone-throwing actions can increase the effect of agonistic display (Leca et al., 2008a).

To further explore the view that tool use evolves from less functionally constrained manipulative behaviors, like object play, we examined whether two other SH behavioral elements performed by long-tailed macaques could have given rise to another type of tool use in a sexual context. We focused our analysis on two SH actions performed by males: the repetitive tapping and rubbing of stones onto the genital area (hereafter genital stone-tapping/-rubbing), sometimes accompanied by penile erection (Figure 4.1).

**Figure 4.1** - *Genital Stone-Rubbing Performed by a Male Balinese Long-Tailed Macaque and Associated with Penile Erection.*


We tested the Sex Toy hypothesis, which proposes that genital stone-tapping and -rubbing are two forms of self-directed tool-assisted masturbation. If so, the temporal structure of SH sequences with genital stone-tapping/-rubbing (i.e., utility-driven and instrumental manipulation of stones) should differ from the temporal structure of SH sequences without genital stone-tapping/-rubbing (i.e., playful and seemingly functionless manipulation of stones). More specifically, if genital stone-tapping and -rubbing are two examples of stone tool use in a sexual context, the performance of at least one of these two behavioral elements within SH sequences should make these otherwise playful sequences more functionally constrained than SH sequences without genital stone-tapping/-rubbing.

We generated three predictions grounded in three characteristics of the temporal organization of play behavioral sequences, namely variability, repeatability, and exaggeration (cf. Burghardt, 2005). First, we predicted that SH sequences without genital stone-tapping/-rubbing would be more variable than SH sequences with genital stone-tapping/-rubbing, across repeated analyses (Prediction #1). In other words, a higher number of different SH patterns (recurring series of SH behavioral elements)[1] should be expected in SH sequences without genital stone-tapping/-rubbing compared to SH sequences with genital stone-tapping/-rubbing. Second, we predicted that SH sequences without genital stone-tapping/-rubbing would show a higher degree of repeatability than SH sequences with genital stone-tapping/-rubbing, across repeated analyses (Prediction #2). In other words, more repeated SH patterns should be expected in SH sequences without genital stone-tapping/-rubbing than in SH sequences with genital stone-tapping/-rubbing. Finally, we predicted that SH sequences without genital stone-tapping/-rubbing would be more exaggerated than SH sequences with genital stone-tapping/-rubbing, across repeated analyses (Prediction #3). In other words, longer SH patterns should be expected in SH sequences without genital stone-tapping/-rubbing compared to SH sequences with genital stone-tapping/-rubbing.

[1] In this chapter, a SH behavioral element is defined as a stone-directed action that can be assigned to mutually exclusive behavioral categories defined in the SH repertoire (i.e., what is referred to as a SH behavioral pattern throughout the rest of the thesis and in the SH literature; Huffman, 1984; Leca et al., 2007a,b). In this chapter, a SH pattern is defined as a recurring series of SH behavioral elements, which emerged from T-pattern detection analysis.

## 4.3. Methods

### *4.3.1. Study population and site*

We studied a population of free-ranging, urban-dwelling, habituated and provisioned Balinese long-tailed macaques, living in and around the Sacred Monkey Forest Sanctuary in Ubud, central Bali, Indonesia. This study site, also known as the Ubud Monkey Forest, is a forested area surrounded by human settlements and Hindu temples. The study population totalled approximately 1000 individuals and was comprised of seven neighbouring groups with overlapping home range areas (Giraud, 2021). The monkeys were provisioned at least three times per day with fruits and vegetables by the temple staff.

### *4.3.2. Data collection and study subjects*

Observations were conducted between May and August 2018 and 2019, between 08:00 and 17:00. We do not believe that this season-specific data collection may hinder the generalization of our results to the entire year for following reasons: (1) like many tropical primates, long-tailed macaques living in Indonesia do not show a marked seasonal pattern in their mating/reproductive behaviours, that are expressed throughout the year (van Schaik & van Noordwijk, 1985); (2) SH behaviour is also expressed throughout the year in the study population (Brotcorne, 2014); and (3) none of the data analyses rely on frequency distributions of SH activity or sexual behaviour. SH activity occurred in all seven groups of this primate population, and across both sexes and all age classes (Pelletier et al., 2017). In this study, we sampled 14 individually identified males, 7 juvenile males (aged 2 to 4), 5 subadult males (aged 4 to 6), and 2 adult males (aged 6 or more) from two groups of comparable sizes (i.e., around 100 individuals per group). All the SH sequences used in this study were video-recorded with a digital camera (Sony Full HD Handycam Camcorder). Following *ad libitum* sampling methods (Altmann, 1974), CC and three research assistants collected sequences of SH. During *ad libitum* sampling, the subject was filmed if performing SH. The data used in this study were collected as part of a broader field research season that included a series of field experiments on the same study group aiming to test whether SH activity facilitate the emergence of stone tool use. During daily sessions (mean number = 3 sessions/day, mean duration = 1 hour 30 min/day), we tested and video-recorded the study subjects' ability to solve food-retrieval tasks whose solutions require the functional and action-specific use of stones as tools. The experimental apparatuses consisted of food-baited transparent boxes, each with a different built-in opening mechanism. Each box could be opened by performing either stone-pounding (Box#1) or stone-inserting/dropping actions (Box#2). Five percent of the SH sequences used in this study were recorded during the field experiments. In these cases, the subject was not operating the experimental apparatus, and the spontaneous expression of SH activity occurred within five meters of the experimental task. Because the monkeys were highly habituated to humans, most video-records were collected at close range (3–5m), under good visibility and without disturbing the animals. Whenever possible, the subjects were filmed from the front or side and about two-meter square in-frame.

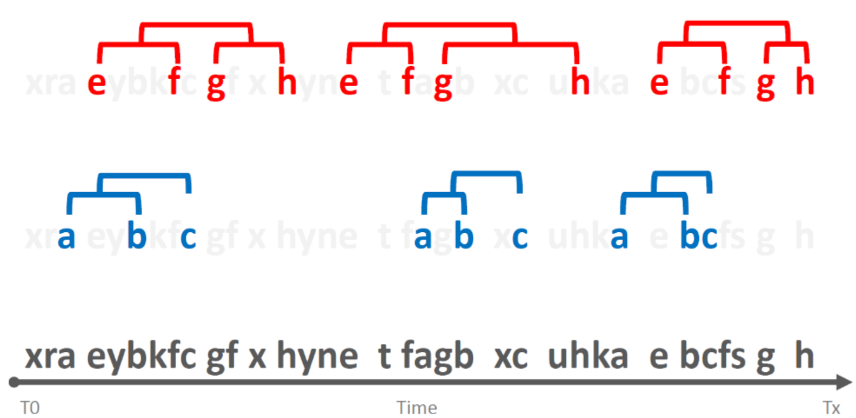
#### *4.3.3. Data analysis*

SH activity was scored using the same SH ethogram as in Pelletier et al. (2017) and Cenni et al. (2021, under review). CC used *The Observer XT 15* (Noldus Information Technology, The Netherlands) to score the video-recorded SH sequences, with a precision to the second, and generate event-log files (i.e., series of consecutive SH behavioral elements) for each subject. We calculated an inter-scorer reliability test after CC and JBL transcribed the same samples of SH video records, involving a total of 12 randomly selected SH sequences (i.e., 21% of the sample; $k$ = 0.92; Martin & Bateson, 1993).

For each subject, we systematically selected two 2-minute sequences of SH with genital stone-tapping/-rubbing and two 2-minute sequences of SH without genital stone-tapping/-rubbing. All SH sequences were truncated from longer SH bouts, and they were independent (i.e., they belonged to SH bouts collected on different days). In SH sequences featuring genital stone-tapping/-rubbing, one of these behavioral elements was performed exactly 60 seconds after the beginning of the sequence (i.e., genital stone-tapping/-rubbing occurred at mid-point within the SH sequence). For SH sequences without genital stone-tapping/-rubbing, the beginning of the truncated SH sequence was randomly selected with the use of a random time generator. SH sequences had to be recorded under optimal visibility conditions, to ensure that all or most of the behavioral elements performed could be reliably identified. During the performance of SH behavior by long-tailed macaques, stones are typically manipulated with leaves, which are used to cover and wrap stones. Additionally, stones are occasionally combined with locally available nuts, twigs or human artifacts (e.g., plastic bottles, plastic bags, cloths). In our sample, SH sequences could feature leaves and human artifacts exclusively used to cover or wrap stones (i.e., plastic bags and toilet paper), but no other objects. When multiple sequences could be selected, selection was made at random.

To systematically compare the temporal structure of SH sequences and detect possible temporal relationships among behavioral elements (i.e., SH behavioral patterns) within and across SH sequences, we took a multivariate approach known as T-pattern detection and analysis (TPA), which requires the use of Theme software (PatternVision Ltd, Iceland). TPA identifies recurring series of behavioral elements (i.e., T-patterns) that would be too difficult to detect from the "background noise" without the use of an algorithm. The essential and most important feature of T-patterns is that recurring series of behavioral elements are detected based on the existence of statistically significant constraints among the interval lengths separating them (Casarrubea et al., 2015; Magnusson et al., 2016). For instance, given a hypothetical sequence of behavioral elements occurring within a $T_0$–$T_x$ period (Figure 4.2, bottom row), an algorithm compares the distributions of each pair of the behavioral elements “a” and “b”, searching for whether “a” is followed by “b” more often than chance expectation within a certain time window. If a statistically significant temporal constraint exists between element “a” and element “b”, they are indicated as (a b), which is a first-level T-pattern. Subsequently, this T-pattern is considered a potential “a” or “b” term in higher-level T-patterns (e.g., ((a b) c)). Importantly, a T-pattern may not be linear, and between the occurrence of some of its constituent behavioral elements, other behavioral elements may occur, which may be involved in additional T-patterns, detected as previously described (e.g., ((e f) (g h)); Figure 4.2, middle and top rows).

**Figure 4.2** - *A Hypothetical T-Pattern with a Stream of Behavioral Elements Occurring Within a T0 – Tx Observation Period is Represented*.




*Note*. Even though there are only two repeated sequences containing three and four behavioral elements, respectively, the detection of these sequences is not an easy task from the bottom row (black bold letters) only. When the “background noise” is removed by the software *Theme*, the two T-patterns ((a b) c) and ((e f)(g h)) become evident.

The analytical power associated with the detection of hidden real-time series of recurring events is an important characteristic of TPA. Once detected, T-patterns have intrinsic qualities, such as *variability*, *repeatability,* and *exaggeration* (Casarrubea et al., 2015). These qualities are meaningful only if relationships among behavioral elements are considered, as they arise from *structural* features of the observed behavior (Casarrubea et al., 2019). This is, by far, the most important benefit of TPA, in comparison with other approaches, such as the calculation of frequencies, durations, and percentage distributions of individual components of a given behavior, disjointed from its comprehensive structure.

SH *variability* is defined as the number of T-patterns of unique composition that are detected across behavioral sequences expressed across subjects. SH *repeatability* is defined as the number of times a given T-pattern is detected across behavioral sequences expressed across subjects. SH *exaggeration* is defined as the number of behavioral elements constituent of a T-pattern detected across behavioral sequences across subjects (i.e., the length of a T-pattern). We performed "concatenated-subject TPA": after concatenating the behavioral data obtained from all the subjects, the analysis sought recurrent T-patterns across sequences and subjects. Without the use of this type of TPA, detecting the relationships among events, based on the statistical significance of their occurrence, first within sequence, and then across sequences and subjects would be extremely difficult. To perform TPA, we used the following parameters:

- minimum sampling parameter = 50%
- significance level = 0.0001
- lumping factor = 0.9

To evaluate whether results were repeatable and representative, we first conducted a TPA on the full dataset containing 14 subjects; second, we conducted a series of 14 additional

TPAs, each containing a different combination of 13 out of the 14 subjects, with each TPA missing a different subject from the original full dataset. These steps were taken to control for the possibility that the SH signature of one or more individuals (Cenni et al., in review) was responsible for the temporal patterns detected in SH sequences with or without genital stone-tapping/-rubbing in the whole sample.

#### *4.3.4. Statistics*

Even though each T-pattern is generally detected with a high level of statistical significance, the theoretically large number of possible temporal relationships among hundreds or even thousands of behavioral elements raises the question of whether T-patterns might be detected only by mere chance. TPA addresses such a critical issue by repeatedly randomizing and re-analyzing the original data set to ensure that a given T-pattern detection is not the result of a random association of behavioral elements. In this study, the mean number of T-patterns (±1 SD) detected in a series of randomized data sets was compared with the actual number of T-patterns detected in the original data set, both in SH sequences with and without genital stone-tapping/-rubbing. Further details about the theories and procedures underlying TPA can be found in the work of Magnusson et al. (2016) and Casarrubea et al. (2015, 2018). We used Student's *t*-tests to compare the number of T-patterns of unique composition (i.e., SH *variability*) in SH sequences with and without genital stone-tapping/-rubbing. To compare the number of times a given T-pattern was detected (i.e., SH *repeatability*), and the length a T-pattern (i.e., SH *exaggeration*) in SH sequences with and without genital stone-tapping/-rubbing, we used Mann-Whitney's U tests because assumptions for conducting parametric tests were violated. To assess whether the results were significantly consistent and replicated across analyses, we used Binomial tests.

### *4.3.5. Ethical statement*

This research was exclusively observational and non-invasive. Our study was conducted in accordance with the Indonesian Ministry of Research and Technology, the Provincial Government of Bali, and the local district authorities and was approved by the institutional Animal Welfare Committee of the University of Lethbridge (Protocol #1906).

## 4.4. Results

As predicted, in the TPA containing the full dataset of 14 subjects, SH sequences without genital stone-tapping/-rubbing exhibited a higher level of variability than SH sequences with genital stone-tapping/-rubbing (i.e., more T-patterns of unique composition; 55 and 25 T-patterns of unique composition, respectively). However, this difference in SH *variability* was not statistically significant ($t_6 = -1.33$, $p = 0.231$). When conducting a series of 14 additional TPAs, each containing a different combination of 13 subjects, SH sequences without genital stone-tapping/-rubbing exhibited a higher level of variability than SH sequences with genital stone-tapping/-rubbing (i.e., more T-patterns of unique composition). However, this difference in SH *variability* was not statistically significant in any of the 14 TPAs (Table 4.1). The proportion of statistically significant results across TPAs (Binomial test: 0.00, $N = 15$, number of significant test $K = 0$, $p < 0.001$) was smaller than the 0.50 level expected by chance. Prediction #1 was not supported.

As predicted, in the TPA containing the full dataset of 14 subjects, SH sequences without genital stone-tapping/-rubbing exhibited a higher level of repeatability than SH sequences with genital stone-tapping/-rubbing (mean number of T-patterns detected: $66.96 \pm 40.56$ and $56.12 \pm 31.01$, respectively). However, this difference in SH *repeatability* was not statistically significant ($U = 806.50$, $p = 0.217$). When conducting a series of 14 additional TPAs, each containing a different combination of 13 subjects, SH sequences without genital stone-tapping/-rubbing exhibited a higher level of repeatability than SH sequences with genital stone-tapping/-rubbing (mean number of T-patterns detected; Table 4.1). However, these differences in SH *repeatability* were statistically significant only in 5 out of 14 TPAs, and the proportion of statistically significant results across TPAs (Binomial test: 0.33, N = 15, K = 5, p = 0.302) was smaller than the 0.50 level expected by chance. Prediction #2 was not supported.

**Table 4.1** – *Number of T-Patterns of Unique Composition (SH Variability), Mean Number of T-Patterns (SH Repeatability), and Mean Length of T-Patterns (SH Exaggeration), Statistical Tests and Associated P-Values.*

| TPA | SH *variability* | | | | SH *repeatability* | | | |
|---|---|---|---|---|---|---|---|---|
| | **TOG/ ROG** | **no TOG/ ROG** | $t_{(df)}$ | **p-value (α = 0.05)** | **TOG/ ROG** | **no TOG/ ROG** | ***U*** | **p-value (α = 0.05)** |
| 14 ids | 25 | 55 | $-1.33_{(6)}$ | 0.231 | 56.12 ± 31.01 | 66.96 ± 40.56 | 806.50 | 0.217 |
| 13 ids - no BASS | 21 | 54 | $-2.44_{(4)}$ | 0.071 | 57.19 ± 28.61 | 61.93 ± 35.30 | 610.50 | 0.608 |
| 13 ids - no C-17 | 26 | 63 | $-1.71_{(6)}$ | 0.137 | 49.00 ± 29.11 | 58.37 ± 36.29 | 970.50 | 0.171 |
| 13 ids - no DOME | 27 | 47 | $-1.07_{(4)}$ | 0.346 | 50.67 ± 27.64 | 63.45 ± 37.73 | 800.00 | 0.063 |
| 13 ids - no GENNARO | 25 | 62 | $-1.55_{(6)}$ | 0.172 | 51.40 ± 30.08 | 61.40 ± 35.95 | 939.50 | 0.123 |
| 13 ids - no IVAN | 23 | 54 | $-1.42_{(6)}$ | 0.204 | 53.96 ± 29.29 | 61.44 ± 36.66 | 698.00 | 0.391 |
| 13 ids - no LOOKOUT | 24 | 52 | $-1.33_{(6)}$ | 0.232 | 52.33 ± 30.04 | 65.58 ± 39.10 | 782.50 | 0.076 |
| 13 ids - no NEWBY | 29 | 57 | $-1.14_{(6)}$ | 0.296 | 48.59 ± 27.89 | 64.54 ± 39.29 | 1060.00 | **0.033** |
| 13 ids - no PAGGIO | 26 | 61 | $-1.43_{(6)}$ | 0.203 | 51.65 ± 28.91 | 60.48 ± 39.14 | 864.00 | 0.510 |
| 13 ids - no PINOCCHIO | 24 | 49 | $-1.46_{(4)}$ | 0.219 | 52.92 ± 30.62 | 67.35 ± 38.22 | 765.00 | **0.038** |
| 13 ids - no SPIKY | 27 | 41 | $-0.89_{(4)}$ | 0.426 | 50.81 ± 28.24 | 71.24 ± 39.86 | 1613.00 | **0.013** |
| 13 ids - no SPLASH | 26 | 48 | $-0.97_{(6)}$ | 0.371 | 53.23 ± 29.93 | 63.35 ± 38.73 | 737.50 | 0.199 |
| 13 ids - no TWEEDLEDUM | 23 | 49 | $-1.61_{(4)}$ | 0.182 | 49.91 ± 29.26 | 66.49 ± 37.93 | 737.50 | **0.036** |
| 13 ids - no VLAD | 23 | 46 | $-1.43_{(4)}$ | 0.227 | 51.39 ± 29.91 | 66.28 ± 37.40 | 690.50 | **0.040** |
| 13 ids - no WATSON | 23 | 55 | $-1.51_{(6)}$ | 0.181 | 55.00 ± 29.48 | 65.56 ± 39.57 | 742.50 | 0.228 |

**Table 4.1** – (continued)

| **TPA** | **SH *exaggeration*** | | | |
|---|---|---|---|---|
| | **TOG/ROG** | **no TOG/ROG** | ***U*** | **p-value (α = 0.05)** |
| 14 ids | 2.36 ± 0.64 | 2.98 ± 0.91 | 956.50 | **0.003** |
| 13 ids - no BASS | 2.38 ± 0.67 | 2.89 ± 0.79 | 770.00 | **0.010** |
| 13 ids - no C-17 | 2.46 ± 0.71 | 3.13 ± 0.94 | 1144.00 | **0.002** |
| 13 ids - no DOME | 2.33 ± 0.62 | 2.81 ± 0.77 | 855.00 | **0.006** |
| 13 ids - no GENNARO | 2.44 ± 0.71 | 2.98 ± 0.88 | 1050.50 | **0.006** |
| 13 ids - no IVAN | 2.35 ± 0.65 | 2.96 ± 0.93 | 856.50 | **0.005** |
| 13 ids - no LOOKOUT | 2.38 ± 0.65 | 2.98 ± 0.94 | 853.00 | **0.006** |
| 13 ids - no NEWBY | 2.38 ± 0.62 | 2.96 ± 0.91 | 1131.00 | **0.003** |
| 13 ids - no PAGGIO | 2.35 ± 0.63 | 3.00 ± 0.89 | 1125.50 | **0.001** |
| 13 ids - no PINOCCHIO | 2.33 ± 0.64 | 2.82 ± 0.78 | 793.00 | **0.008** |
| 13 ids - no SPIKY | 2.44 ± 0.70 | 2.78 ± 0.79 | 685.50 | 0.068 |
| 13 ids - no SPLASH | 2.35 ± 0.63 | 2.92 ± 0.92 | 843.00 | **0.006** |
| 13 ids - no TWEEDLEDUM | 2.35 ± 0.65 | 2.82 ± 0.81 | 746.50 | **0.015** |
| 13 ids - no VLAD | 2.35 ± 0.65 | 2.80 ± 0.81 | 697.00 | **0.018** |
| 13 ids - no WATSON | 2.39 ± 0.66 | 2.98 ± 0.91 | 866.50 | **0.006** |

*Note*. Each TPA contains 14 subjects (i.e., ids) or a different combination of 13 subjects (the missing subject is listed in the TPA's name). TOG/ROG = SH sequences with genital stone-tapping/-rubbing; no TOG/ROG = SH sequences without genital stone-tapping/-rubbing. Boldface indicates statistically significant results.

In the TPA containing the full dataset of 14 subjects, we found a statistically significant difference in SH *exaggeration* between SH sequences without genital stone-tapping/-rubbing and SH sequences with genital stone-tapping/-rubbing (U = 956.50, p = 0.003). SH sequences without genital stone-tapping/-rubbing were characterized by significantly longer T-patterns (i.e., more SH behavioral elements constituent of T-patterns) than SH sequences with genital stone-tapping/-rubbing: 2.98 ± 0.91 and 2.36 ± 0.64 SH behavioral elements, respectively. When conducting a series of 14 additional TPAs, each containing a different combination of 13 subjects, we found a statistically significant difference in SH *exaggeration* between SH sequences with and without genital stone-tapping/-rubbing in 13 out of 14 TPAs (Table 4.1). SH sequences without genital stone-tapping/-rubbing were characterized by significantly longer T-patterns (i.e., more SH behavioral elements constituent of T-patterns) than SH sequences with genital stone-tapping/-rubbing. The proportion of statistically significant results across TPAs (Binomial test: 0.93, N = 15, K = 14, p = 0.001) was higher than the 0.50 level expected by chance. Prediction #3 was supported.

All the descriptive statistics, statistical tests, and associated p-values for the TPA containing 14 subjects, and for the series of 14 additional TPAs, each containing a different combination of 13 subjects, are available in Table 4.1. All the T-patterns detected in the TPAs, and their corresponding contents, occurrence, and length, are available in Supplementary Material S4.1 in Appendix C.

**4.5. Discussion**

Our results provided some support to the Sex Toy hypothesis, which proposes that genital stone-tapping and -rubbing are examples of self-directed stone tool-assisted masturbation in male Balinese long-tailed macaques. The performance of genital stone-tapping and -rubbing, as part of the SH activity in male Balinese long-tailed macaques, is associated with a change in the temporal structure of this form of object manipulation which is indicative of increased functional constraints in these otherwise playful behavioral sequences. In line with the expectation that object play behavior should be more structurally flexible than object-directed activities that are functionally constrained, we found that, *across analyses*, SH sequences without genital stone-tapping/-rubbing (i.e., playful manipulation of stones) were significantly more exaggerated than SH sequences with genital stone-tapping/-rubbing (i.e., instrumental manipulation of stones; Prediction #3 was supported). In line with the expectation that object play behavior should be less temporally structured and more redundant than functionally constrained object-directed activities, SH sequences without genital stone-tapping/-rubbing were, on average, more variable and more repeated than SH sequences with genital stone-tapping/-rubbing. However, *across analyses*, these differences were not statistically significant (Prediction #1 and Prediction #2 were not supported). Taken together, our results are partly consistent with previous findings on a smaller sample of males from the same population (Cenni et al., 2020), and provide converging evidence that in-depth description of temporal structure can be useful to discriminate functional patterns of tool use.

Our results on *exaggeration* suggest that the detection of some functional patterns of tool use, here behavioral optimization, is reliable and could be mostly independent of individual differences in SH behavior. Exaggeration has long been recognized as an identifying feature of play behavior in a variety of taxa (e.g., in birds, Ficken, 1977; in rodents, Pellis & Pellis, 1987; in canids, Bekoff, 1974; in primates, Loizos, 1967). However, this feature is typically not the subject of in-depth qualitative and quantitative analyses, such as that produced by a detailed movement analysis of the actions performed during seemingly playful behavioral sequences (but see Pellis et al., 2019 for a notable exception with a kinematic evaluation of exaggeration in object play). Looking at the temporal structure of play sequences is particularly crucial to detect the *galumphing* organization of actions, as reflected in Miller's words (1973): "play is a way of organizing activity, not a particular set of activities; it is a syntax, not a vocabulary. So whenever the vocabulary happens to be visible and the "this is play" message appears, the syntax still reveals itself" (p. 94). Our study supports this view, suggesting that exaggeration can (a) be detected from the temporal organization of playful sequences, and (b) be used to identify functional attributes of behavioral responses that are outwardly similar.

It is noteworthy that in our work, analyses aiming to test for differences in *repeatability* produced contrasting results, whereas on average, SH sequences without genital stone-tapping/-rubbing were more repeated that SH sequences with genital stone-tapping/-rubbing. Individual differences in the expression of instrumental object-assisted actions are to be expected in forms of flexible tool use (Hunt et al., 2013), because the acquisition of such technical skills takes a considerable amount of time to be mastered over distinct developmental stages, with individual differences in learning trajectories, social influences and experiences. A detailed cross-sectional examination of the behavioral repertoire of 40 subjects detected differences in the overall occurrence, duration, and preference for SH actions (Cenni et al., in review). The lack of consistency found when testing for differences in repeatability could be due to individual idiosyncrasy in the organization of SH behavioral elements, and individuals differing in their organization of SH sequences. However, this possibility remains to be tested. Indeed, to date, no data are available on whether individuals differ in the *sequential* organization of SH actions. Future research should evaluate whether individual differences in the temporal organization of SH sequences predict the expression of tool-assisted actions.

To explain the consistent lack of differences in *variability* between SH sequences with and without genital stone-tapping/-rubbing (which is in line with findings from Cenni et al., 2020), we propose that genital stone-tapping and -rubbing are subject to weaker functional constraints than more (putatively) fitness-enhancing forms of tool use (e.g., object-assisted extractive foraging whose expression covaries with seasonality; cf. Melin et al., 2014). Indeed, genital stone-tapping and -rubbing are hypothetically related to sexual gratification, which is arguably less vital than feeding needs. Furthermore, genital stone-tapping and -rubbing are specific actions integrated within SH sequences that contains several stone-directed movements; indeed, instances of genital stone-tapping and -rubbing have not been recorded outside SH sequences that include other SH behavioral elements. It is possible that these two stone-directed actions are still undergoing some transformational processes involving emancipation from the playful manipulation of stones from which they emerged (cf. Huffman & Quiatt, 1986; Pellis et al., 2019). Thus, the structural variability associated with playful manipulation may still characterize SH sequences with genital stone-tapping and -rubbing.

Many theories on the origins and evolution of instrumental object manipulation hold that object play and tool use are linked at the proximate levels (i.e., in their developmental trajectories and underlying sensorimotor and cognitive mechanisms; see Bjorklund, 2016; Lockman, 2000). Overall, the data-based results actually connecting these two forms of object manipulation have been conflicting, in both human and non-human primates (e.g., Bjorklund & Gardiner, 2011). Empirical and longitudinal research suggested that the relationships between the expression of object play and the development of effective tool use strategies are complex, elusive, and mediated by a number of factors, such as age and sex differences, motivational processes, and task characteristics (e.g., chimpanzees and bonobos, Gruber et al., 2011; Koops et al., 2015a; children, Bock & Johnson, 2004; Vandenberg, 1981, 1990). Taken together, our temporal analyses show that SH sequences with genital stone-tapping and -rubbing have functional patterns that are not detected when these actions are absent, suggesting that SH sequences with and without genital stone-tapping and -rubbing are motivationally and functionally distinct.

This study further indicates that, under relaxed selective pressures on foraging (e.g., food provisioning), SH may allow for the maintenance in some macaque populations of a set of stone-directed behavioral patterns that could transform into stone tool use. Indeed, as these monkeys receive a substantial part of their food requirements from humans, the portion of their activity budget typically devoted to foraging on natural foods decreases (Brotcorne, 2014; Leca et al., 2008b), which automatically creates some spare time that may be invested into less functionally constrained forms of behavior, including object play, like SH (Huffman, 1996; Leca et al., 2008b). In turn, a broader repertoire of stone-directed playful actions probably enhanced the spontaneous innovation and social diffusion of stone tool use in certain groups of Japanese macaques (Leca et al., 2008a). Similarly, we suggest that the regular and culturally maintained practice of SH by the Balinese long-tailed macaques living in Ubud may have facilitated their perception of the affordances of stones as objects with action-relevant properties (Cenni et al., 2021) that can be used as "sex toys" to masturbate (i.e., tools; Cenni et al., 2022). Thus, our research supports the view that tool use may evolve in stages from initially non-functional object manipulation, such as object play, a behavioral category that fits SH activity (cf. Huffman & Quiatt, 1986).

## CHAPTER 5: PHYSIOLOGICAL AND BEHAVIORAL CORRELATES OF STONE-TOOL USE IN THE SEXUAL DOMAIN

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### 5.1. Abstract

Recent reports on tool use in non-foraging contexts have led researchers to reconsider the proximate drivers of instrumental object manipulation. In this study, we explore the physiological and behavioral correlates of two stone-directed and seemingly playful actions, the repetitive tapping and rubbing of stones onto the genital and inguinal area, respectively, that may have been co-opted into self-directed tool-assisted masturbation in long-tailed macaques (i.e., Sex Toy hypothesis). We predicted that genital and inguinal stone-tapping and -rubbing would be more closely temporally associated with physiological responses (e.g., estrus in females, penile erection in males) and behavioral

patterns (e.g., sexual mounts and other mating interactions) that are sexually motivated than other stone-directed play. We also predicted that the stones selected to perform genital and inguinal stone-tapping and -rubbing actions would be less variable in number, size, and texture than the stones typically used during other stone-directed playful actions. Overall, our data partly supported the Sex Toy hypothesis indicating that stone-directed tapping and rubbing onto the genital and inguinal area are sexually motivated behaviors. Our research suggests that instrumental behaviors of questionably adaptive value may be maintained over evolutionary time through pleasurable/self-rewarding mechanisms, such as those underlying playful and sexual activities.

## 5.2. Introduction

The instrumental use of objects (i.e., tool use) in non-human animals has been mostly reported in relation to foraging tasks and subsistence-related activities (Shumaker et al., 2011). As a result, tool use has been primarily discussed from a functional and an adaptive viewpoint (Bentley-Condit & E. O. Smith, 2010; S. T. Parker & K. R. Gibson, 1977). Thus, definitions of tool use pertaining to foraging/subsistence-related activities have focused on the *goal* of actions, describing the functional (both in terms of task-related function and evolutionary function) and possibly fitness-enhancing consequences of object-assisted behaviors (e.g., Shumaker et al., 2011; St Amant & Horton, 2008). However, this functional perspective on tool use comes with at least two caveats. First, unambiguously demonstrating the adaptive value of tool use is challenging; to our knowledge, there is no reported evidence that instrumental object manipulation increases an individual’s survival rate or reproductive success (Biro et al., 2013). Second, this approach may have limited researchers’ attention to object-assisted actions expressed within survival-dependent contexts. Even though reports of instrumental object manipulation outside the foraging domain abound – such as instances of tools used in agonistic displays (e.g., Leca et al., 2008a), courtship interactions (e.g., Falótico & Ottoni, 2013), and self-maintenance behaviors (e.g., Fayet et al., 2020) – their significance for our understanding of the function and evolution of tool use has been underrated. Additionally, identifying the immediate task-related function of such behaviors has been difficult because the end-goal of these object-assisted actions is unclear.

By focusing on the *means* of actions (i.e., on their immediate mechanical consequences), biomechanical definitions of tool use provide an alternative opportunity to explore the processes underlying the development and expression of instrumental object manipulation. According to Fragaszy and Mangalam (2018), tool use is a form of object manipulation that produces a mechanical effect on a target, when the tool is grasped by the user. Through a continuing process of discovering the spatiotemporal relations between objects, mediated by exploratory and non-instrumental interactions with the environment, an individual generates instrumental actions, through affordance learning (Lockman, 2000). Different forms of object manipulation, such as tool use and object play, may be, therefore, inextricably coupled in their developmental trajectories, underlying sensorimotor and cognitive mechanisms, as well as their evolutionary pathways and functional outcomes (Cenni & Leca, 2020a; Lockman, 2000). Stone handling (SH) is a socially learned and culturally maintained form of object play with phylogenetical signals in species of the *Fascicularis* macaque group (Huffman & Hirata, 2003; Nahallage & Huffman, 2008; Nahallage et al., 2016; Pelletier et al., 2017). An individual engaging in SH typically manipulates stones of various sizes (Cenni et al., 2021; Leca et al., 2008b,c) and performs different SH behavioral patterns, such as rubbing stones on a surface, clacking stones together, or repeatedly picking and dropping stones (Huffman, 1984). In macaques, SH behavior is displayed by both sexes and across age classes, throughout an individual's lifespan (Nahallage et al., 2016; Pelletier et al., 2017). SH is an ideal behavioral candidate to explore the relationships between the instrumental and non-instrumental use of objects because (a) the behavioral variability associated with the expression of SH activity may be a good predictor for the emergence of stone-tool use (Cenni et al., in review; Huffman & Quiatt, 1986; Huffman, 1996; Leca & Gunst, accepted; Leca et al., 2011, 2012) and (b) in two species, three SH behavioral patterns may have been co-opted into stone-tool use, in social and sexual contexts (Cenni et al., 2020; Leca et al., 2008a).

First, in Japanese macaques (*Macaca fuscata*), in which SH has been extensively studied for four decades (Leca et al., 2012), one of the 45 SH behavioral patterns, stone throwing, may have been co-opted into stone-tool use in a social context to increase the effect of agonistic displays (Leca et al., 2008a). Quantitative data on the contextual and behavioral correlates of stone throwing across 10 troops of monkeys indicated that (1) individuals were more likely to throw a stone under conditions of disturbance-related vigilance, such as intra-group aggressive interactions, than in playful situations, and (2) the performers displayed behavioral signs of excitement while throwing a stone (Leca et al., 2008a). Additionally, detailed description of stone throwing actions revealed that the behavior was untargeted (i.e., stones were not thrown directionally), and the stones were more likely used to augment the social effect of behavioral displays in agonistic contexts than to hit a conspecific. Even though SH is a behavioral tradition in Japanese macaques (Huffman, 1984; Leca et al., 2007a,b; Nahallage & Huffman, 2007a), the distribution of stone throwing across troops showed that this specific SH behavioral pattern had turned into stone tool use only in the group where stone throwing was commonly performed by several individuals. Longitudinal data showed that stone throwing had increasingly spread over time within the study group and across those individuals with strong social relationships (i.e., they spent more time in physical proximity; Leca et al., 2008a). Thus, quantitative data on the contextual and behavioral correlates of seemingly purposeless object-directed actions may provide insights into the instrumental nature of these actions.

Second, in a free-ranging population of long-tailed macaques (*Macaca fascicularis*) living in Ubud, Bali, Indonesia, where SH was also identified as a behavioral tradition (Pelletier et al., 2017), these monkeys were reported to repeatedly tap and rub one (or more) stone(s) onto their genital area (Cenni et al., 2020; Pelletier et al., 2017). Despite those two stone-directed actions being integrated into SH bouts (i.e., a seemingly playful activity), detailed analysis of the temporal structure of SH sequences with genital stone-tapping or rubbing (also known as "tap on groin" or "rub on groin"; Cenni et al., 2020) performed by males revealed a temporal organization that was less structurally flexible than that in SH sequences without genital stone-tapping or rubbing, suggesting functional attributes of these specific SH behavioral patterns. SH sequences without genital stone-tapping or rubbing were also more exaggerated in their temporal organization (i.e., an intrinsic characteristic of play behavior; cf. Burghardt, 2005) than SH sequences with genital stone-tapping or rubbing (Cenni et al., 2020). Additionally, genital stone-tapping and -rubbing occurred more often and lasted longer in SH sequences in which penile erection – a sexually-motivated physiological response in primates – was observed than in SH sequences in which penile erection was not observed (Cenni et al., 2020). Thus, the performance of genital stone-tapping and genital stone-rubbing by male Balinese long-tailed macaques would be another two examples of SH patterns being co-opted into stone tool use, and this time, in a sexual context (i.e., stone-directed genital tapping and rubbing may be two forms of self-directed tool-assisted masturbation – Sex Toy hypothesis; Cenni et al., 2020). However, a temporal association between genital stone-tapping/-rubbing and penile erection is not sufficient alone to assess the sexual nature of these two SH behavioral patterns; it has not yet been tested whether other SH patterns show a temporal association with sexually underlying physiological responses, such as penile erection. Moreover, penile erection cannot be used to assess the motivational underpinnings of genital stone-tapping and -rubbing in female macaques. To unambiguously determine whether the performance of stone-directed genital tapping and rubbing is a form of solitary tool-assisted masturbation, physiological and behavioral correlates of these two specific SH behavioral patterns should be explored, as a way to test whether their expression is sexually motivated.

Manual masturbation in males has been reported among several primate species (Dixson, 2012; Thomsen et al., 2003). Outside humans, however, manual masturbation seldom leads to ejaculation (Dixson, 2012). According to a study by Thomsen and colleagues (2003), male masturbation was documented in 34 species of non-human primates; however, it led to ejaculation in only 22 of them, and even so, it was occasional. Thus, definitions of manual masturbation in non-human primates do not typically include orgasm, such as ejaculation, as a necessary component of the behavior. Even in primate species in which masturbation leading to ejaculation has been associated with functional consequences, it remains occasional: in most instances, masturbation does not lead to orgasm (e.g., Japanese macaques: Thomsen & Soltis, 2004). Importantly, in non-human primates, functional explanations for masturbation leading to orgasm have never been proposed nor investigated in females, for which masturbation is scarcely documented (but see Allen, 1977 and Temerlin, 1975 for accounts of masturbation leading to orgasm in captive chimpanzees). Additionally, anecdotal evidence suggests that *object-assisted* masturbation is more common in females than in males (e.g., Ford & Beach, 1951; Kollar et al., 1968; Russon et al., 2009; Sinha, 1997). In the Balinese long-tailed macaques living in Ubud, males and females across age classes have been observed engaging in manual masturbation, but in line with findings from other non-human primate species, masturbation leading to orgasm seems to be rare (Cenni, personal observation).

In this study, we reported the distribution of stone-directed genital and inguinal tapping and rubbing (hereafter, genital stone-tapping/-rubbing) within the same free-ranging population of Balinese long-tailed macaques, and we examined the physiological reactions and behavioral responses in which these two stone-directed actions were expressed. In fact, genital stone-tapping/-rubbing has been observed as part of the SH repertoire of both sexes and across age classes (Pelletier et al., 2017), but their performance may be differentially distributed and motivated across age/sex classes. We further tested the Sex Toy hypothesis, which holds that genital stone-tapping/-rubbing is a form of self-directed tool-assisted masturbation (Cenni et al., 2020). Thus, genital stone-tapping/-rubbing should have aspects of both masturbatory behavior and instrumental object-assisted actions. With regards to age/sex classes of the performers, reviews of solitary masturbation across primate species showed that males masturbate more often and for longer periods of time than females (Dixson, 2012). Additionally, a comparison of findings from two studies of masturbation in two free-ranging populations of Japanese macaques suggests that this behavior is particularly frequent in juvenile and subadult males (Inoue, 2012; Thomsen & Soltis, 2004). As for the “tool-assisted” component of some masturbatory behaviors, optimal selection of the most suitable object is expected when performing instrumental actions (e.g., Fragaszy et al., 2010; Gumert & Malaivijitnond, 2013); as a result, there should be higher object selectivity in instrumental forms of object manipulation (e.g., tool use) than in their non-instrumental counterparts (e.g., object play). On the basis of the Sex Toy hypothesis, we generated four predictions.

First, we predicted that penile erection, sexually-underlain physiological response in primates (cf. Nadler & Bartlett, 1997), would be more closely temporally associated with genital stone-tapping/-rubbing than any other SH behavioral patterns performed by juvenile/subadult and adult males (Prediction #1). In other words, the transitional probability from genital stone-tapping/-rubbing to penile erection should be higher than the transitional probability from any other SH behavioral patterns to penile erection. Second, we predicted that, in juvenile/subadult and adult males, the duration of genital stone-tapping/-rubbing would be positively associated with the presence or absence of penile erection (Prediction #2). In other words, genital stone-tapping/-rubbing should last longer in SH sequences featuring penile erection than in SH sequences without penile erection, suggesting a distinct sexual motivation to perform genital stone-tapping/-rubbing, whereas no such differences were expected for other SH behavioral patterns whether penile erection was present or not. Third, we predicted that, in a sexual context and across age/sex classes, genital stone-tapping/-rubbing would be more often expressed than two structurally similar (but arguably not sexually motivated) SH behavioral patterns, namely, the repetitive tapping and rubbing of stones on body parts other than the genital and inguinal regions (Prediction #3). Fourth, we predicted that, across age/sex classes, the number, the relative size, and the texture of stones used to perform genital stone-tapping/-rubbing would be less variable than the stones used to perform tapping/rubbing on other body parts (Prediction #4). Lastly, we reported the distribution of genital stone-tapping/-rubbing across age/sex classes and we discussed these results considering findings pertaining to manual masturbation in other non-primate species.

## 5.3. Methods

### *5.3.1. Study population and site*

We studied a population of free-ranging, urban-dwelling, habituated and provisioned Balinese long-tailed macaques, living within and around the Sacred Monkey Forest Sanctuary in Ubud, central Bali, Indonesia. The area is forested and surrounded by human settlements. Depending on the study period, the study population totalled between 700 and 1000 individuals and was comprised of five to seven neighbouring groups with overlapping home range areas (Giraud et al., 2021; Kluzinski, 2016). The monkeys were provisioned at least three times per day with fruits and vegetables by the temple staff.

### *5.3.2. Data collection and study subjects*

Observations were conducted from May to October 2016, and from May to August 2018 and 2019, between 08:00 and 18:00. SH activity occurred in all groups of this primate population, and across both sexes and all age classes (Pelletier et al., 2017). In this study, from four groups of comparable sizes (i.e., around 100 individuals per group), we sampled a total of 173 individually identified subjects across four predictions, including 63 juvenile/subadult males (aged 2 to 6 years), 37 juvenile/subadult females (aged 2 to 4), 18 adult males (older than 6 years), and 55 adult females (older than 4 years). These groups share large parts of their home ranges; male dispersal into different groups is common and occasionally large groups split into smaller ones (Giraud et al., 2021). All the SH sequences used in this study were video-recorded with a digital camera (Sony Full HD Handycam Camcorder). SH sequences were collected by CC, JBAC, YVdP, and six field research assistants using focal animal sampling and *ad libitum* sampling methods (Altmann, 1974). During focal sampling, the subject was continuously filmed for 15 minutes, independently of its activity. If the focal subject performed SH during the last two minutes of the focal follow, the observation was extended for five minutes, or longer if SH was still in progress (cf. Huffman, 1996). During *ad libitum* sampling, the subject was filmed if performing SH. Because the monkeys were highly habituated to humans, most video-records were collected at close range (3–5m), under good visibility conditions and without disturbing the animals. Whenever possible, the subjects were filmed from the front or side and about two-meter square in-frame.

The data used in this study were collected as part of a broader field season that included a series of field experiments on the same study group aiming to test whether stone tool use is facilitated by SH activity. During daily sessions (mean number = 3 sessions/day, mean duration = 1 hour 30 min/day), we tested and video-recorded the study subjects' ability to solve food-retrieval tasks whose respective solutions require the functional and action-specific use of stones as tools. The experimental devices consisted of food-baited transparent boxes, each with a different built-in opening mechanism. Each box could be opened by performing either stone-pounding (Box#1) or stone-inserting/dropping actions (Box#2). Less than 4% of the SH sequences were recorded during field experiments; in these cases, the subject was not operating the experimental apparatus, and the spontaneous expression of SH activity occurred within five meters of the experimental task. Given that

Prediction #3 specifically tested for the contextual expression of genital stone-tapping/-rubbing, we kept these SH sequences in the dataset.

### *5.3.3. Data analysis*

For all four predictions, SH activity was scored using the same SH ethogram as in Pelletier et al. (2017) and Cenni et al. (2021, in review). During the scoring process, we detected new idiosyncratic variants of stone-assisted actions directed to the genital and inguinal regions, not described by Cenni and colleagues (2020) as genital stone-tapping and -rubbing, which could be due to (a) the current study providing a broader description of the structure of the behavior, and (b) an additional focus on females, not previously included in Cenni et al. (2020). To explore the physiological and behavioral correlates of stone-assisted actions directed to the genital and inguinal regions, we created a merged behavioral category which comprised “Tap on Groin” and “Rub on Groin” (as originally defined in Cenni et al., 2020), and novel behavioral variants directed to the genital and inguinal regions (see Supplementary Material S5.1 to distinguish what was considered genital and inguinal regions in males and females). Thus, the behavioral category *genital stone-tapping/-rubbing* consisted of behaviors under the following operational definitions:

“Tap on groin” = to tap (a) stone(s) in a repeated sweeping gesture using the fingertips onto and around the genital area, including the inguinal region, while the individual is in a sitting posture.

*Comments* = This SH behavioral pattern can be performed in combination with objects and body parts (i.e., to tap a stone against a stone that is in contact with the genital area) or may just involve the genital and inguinal regions. In both males and females, this pattern is performed with one or both hands. When it is expressed with one hand, the other hand is occasionally used to direct the stone(s) to the genital area.

“Rub on groin” = To slide or move (a) stone(s) back and forth onto and around the genital area, including the inguinal region, utilizing a power or precision grip, while the individual is in a sitting posture.

*Comments* = Though this SH behavioral pattern may resemble “Roll,” the hand grip utilized in this activity is different. The stone(s) can slide, move back and forth, or in circular motion, with a power or precision grip. In males, the stone(s) is/are often rubbed with one or both hands on the penis (either erected or held stretched by one hand). In females, the stone(s) is/are often first rubbed on the ground in front of the individual, and then pushed under the lower belly, where the genitals are located.

“Pelvic thrusting” = To slide or move the pelvis back and forth onto a stone, which is stationary on the ground.

*Comments* = This SH behavioral pattern is usually performed with large stones, and stones are generally not held against a body part.

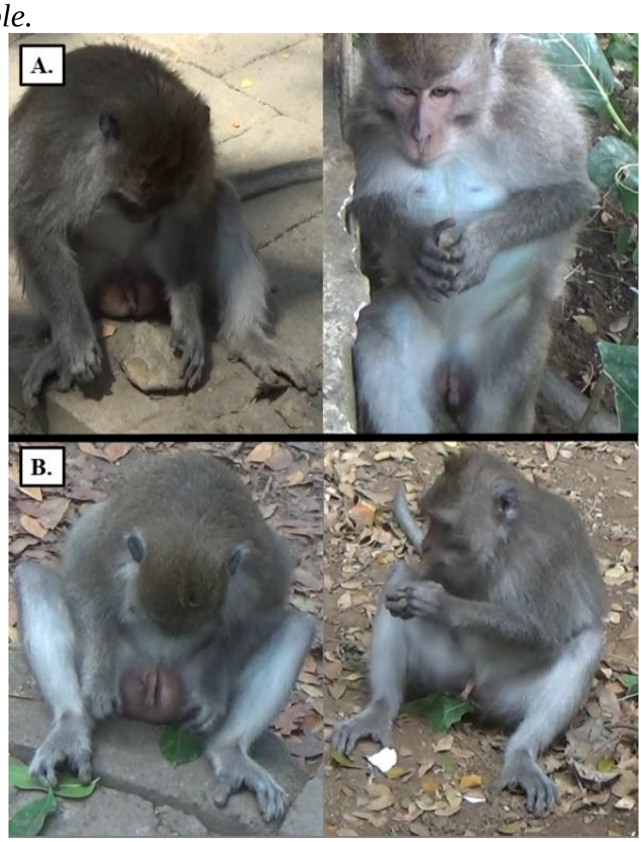
“Roll on groin” = To move (a) stone(s) back and forth onto and around the genital area, including the inguinal region, in a rolling motion, performed with loose grips or open palms.

*Comments* = This SH behavioral pattern resembles “Rub”; however, the hand grip utilized for this activity is different. In males, it is usually expressed with (a) stone(s) being rolled on the penis with both hands and loose grips or open palms.

Video references of genital stone-tapping/-rubbing in males and females can be found in Supplementary Material S5.2. CC used *The Observer XT 15* (Noldus Information Technology, The Netherlands) to score the video-recorded SH sequences, with a precision to the second, and generate event-log files (i.e., series of consecutive SH behavioral patterns) for each subject. To assess reliability of video scoring, we calculated an inter-scorer reliability test for CC and JBL when transcribing the same samples of randomly selected SH video records, involving a total of 1892 SH behavioral patterns (i.e., average Cohen's $k$ across predictions = 0.97; range Cohen's $k$ across predictions = 0.92 – 1; Martin & Bateson, 1993).

To test Prediction #1 (i.e., penile erection should be more closely temporally associated with genital stone-tapping/-rubbing than with any other SH behavioral patterns), for each subject, we selected all available one-minute SH sequences featuring the beginning of a fully rigid penile erection (Figure 5.1B; cf. Hayes et al., 2016) exactly 30 seconds after the beginning of the sequence (i.e., penile erection occurred at mid-point within the SH sequence).

**Figure 5.1** – *Two Categories of Erection Based on Perceived Erection Hardness (cf. Hayes et al., 2016) with (A.) Moderate Increase in Penile Rigidity, but not Completely Hard, with Prepuce Still Visible, and (B.) Completely Hard and Fully Rigid Penile Erection, with Prepuce Fully Visible.*



Since Prediction #1 tested which behavior preceded the expression of penile erection, one-minute intervals provided a physiologically relevant time window. The selected SH sequences were truncated from longer SH sequences, and they were independent (i.e., they belonged to distinct SH sequences collected on different days). To be included in these analyses, penile erection should not have been attributed to external sex-related contextual factors (e.g., sexual inspection, sexual solicitation, sexual mounting behavior). SH sequences had to be recorded under optimal visibility conditions, to ensure that all or most patterns performed were reliably identified. In the end, 38 SH sequences qualified for selection, belonging to 23 subjects (with an average of two sequences per subject), including 20 juvenile/subadult males and 3 adult males.

To evaluate the temporal association between SH behavioral patterns and penile erection, we used a Lag Sequential Analysis (LSA; Bakeman & Gottman, 1997; Bakeman & Quera, 2011). LSA is a technique that captures contingencies among patterns within a sequence, by evaluating the transitions between pairs of behaviors within a certain lag. The term "lag" refers to the position of a target pattern (i.e., the second behavior of the pair) relative to a given criterion pattern (i.e., the first behavior of the pair). For instance, given a hypothetical sequence of patterns occurring within a $T_0$–$T_x$ period (Figure 5.2, top row), a lag +1 sequential analysis determines the probabilistic temporal transition from a criterion pattern to a target pattern occurring immediately after. In an example considering a hypothetical criterion pattern "a", a lag +1 sequential analysis calculates (1) the *frequencies* with which "a" is immediately followed by different hypothetical target patterns, such as "b", "k", "o" (i.e., 5, 2, and 1, respectively; Figure 5.2, bottom row), and (2) the corresponding *transitional probabilities* (i.e., 0.62, 0.25, and 0.12, respectively). We conducted a lag +1 sequential analysis, with all the SH behavioral patterns as criterion behaviors, and "penile erection" as target behavior, using the package "LagSequential" (Draper & O'Connor, 2019) in R 3.6.3 (R Core Team, 2013). The beginning of a fully rigid penile erection at exactly 30 seconds was considered a *point* event (as opposed to SH behavioral patterns, which were considered *state* events). Thus, a lag +1 sequential analysis, with "penile erection" as target behavior tested whether a SH behavioral pattern immediately preceded penile erection.

**Figure 5.2** – *A Hypothetical Sequence of SH Patterns Occurring Within a $T_0$ – $T_x$ Observation Period (Top Row).*


*Note.* A lag +1 sequential analysis detects the temporal transitions from a criterion pattern to a target pattern occurring immediately after (bottom row).

To test Prediction #2 (i.e., genital stone-tapping/-rubbing should last longer in SH sequences featuring penile erection than in SH sequences without penile erection, whereas no such differences were expected for other SH behavioral patterns), for each subject, we selected two three-minute SH sequences, one featuring the beginning of a fully rigid penile erection (Figure 5.1B; cf. Hayes et al., 2016) exactly 90 seconds after the beginning of the sequence (i.e., penile erection occurred at mid-point within the SH sequence), and one without penile erection. Since Prediction #2 tested whether certain SH behavioral patterns lasted longer when the performer was experiencing penile erection, three-minute intervals provided a good trade-off between a physiologically relevant time window and data availability. Occasionally, if penile erection did not reach full rigidity within the observed time period, we included instances of SH sequences featuring the beginning of a moderate increase in penile rigidity (Figure 5.1A; cf. Hayes et al., 2016). The selected SH sequences were truncated from longer SH sequences, and they were independent (i.e., they belonged to distinct SH sequences collected on different days). For one subject, SH sequences with and without penile erection were truncated from the same SH sequence, but they did not overlap in time, being more than 10 minutes apart. For SH sequences featuring penile erection to be included in these analyses, penile erection should not have been attributed to external sex-related contextual factors (e.g., sexual inspection, sexual solicitation, sexual mounting behavior). For SH sequences without penile erection, the beginning of the truncated SH sequence was randomly selected with the use of a random time generator. SH sequences had to be recorded under optimal visibility conditions, to ensure that all or most of the SH behavioral patterns performed were reliably identified. When multiple sequences could be selected, selection was made at random. In the end, we were able to select 18 subjects, including 16 juvenile/subadult males and 2 adult males.

To test Prediction #3 (i.e., genital stone-tapping/-rubbing should be more often expressed in a sexual context than stone-tapping/-rubbing on body parts other than the genital region), for each subject, we selected two one-minute SH sequences, one featuring genital stone-tapping/-rubbing exactly 30 seconds after the beginning of the sequence (i.e., genital stone-tapping/-rubbing occurred at mid-point within the SH sequence), and one featuring either stone-tapping/-rubbing on other body parts, the repetitive tapping and rubbing of stones on body parts other than the genital region, exactly 30 seconds after the beginning of the sequence (i.e., stone-tapping/-rubbing on other body parts occurred at mid-point within the SH sequence). Since Prediction #3 tested for contextual differences between the expression of genital stone-tapping/-rubbing and the expression of stone-tapping/-rubbing on body parts other than the genital region, one-minute intervals provided an environmentally relevant time window. Stone-tapping/-rubbing on other body parts were used as a control to test for the contextual expression (see Table 5.1) of genital stone-tapping/-rubbing, because (a) they are structurally similar to genital stone-tapping/-rubbing, and (b) they also are directed to body parts, but not to the genital and inguinal area. Video references of stone-tapping/-rubbing on other body parts in males and females can be found in Supplementary Material S5.3. To be selected, one-minute SH sequences with genital stone-tapping/-rubbing at mid-point should not include stone-tapping/-rubbing on other body parts and, vice versa, SH sequences with stone-tapping/-rubbing on other body parts at mid-point should not include genital stone-tapping/-rubbing. The selected SH sequences were truncated from longer SH sequences, and whenever possible they belonged to distinct SH sequences collected on different days. When they were truncated from the same SH sequences, they did not overlap in time. In the end, we were able to select 50 subjects, 18 juvenile/subadult males, 9 juvenile/subadult females, 9 adult males, and 14 adult females.

**Table 5.1** – *Contexts and Their Definitions.*

| Context | Definition |
|---|---|
| **Affiliative** | Affiliative situations, involving positive social behaviors performed or received by the subject (i.e., smacking lips, grooming, play mounting, social playing). |
| **Agonistic** | Competitive/conflictual situations, determined by aggressive, submissive, and defensive behaviors, performed or received by the subject (i.e., bared teeth, bite, chase, displace, growl). |
| **Foraging** | Interest in food exhibited by the subject (i.e., visually scan for food, manipulate edible items, eat). |
| **Other SH** | Other individuals performing SH within 5 meters of the subject. |
| **Sexual** | One or a combination of the following situations: the subject or an individual within 5 meters is behaviorally/visually proceptive; the subject or an individual within 5 meters of the subject is experiencing penile erection, or engaging in sexual inspection, sexual solicitation, or sexual mounting behavior. |

To evaluate the context in which genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts were performed, we distinguished five contexts of expression of genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts, namely "affiliative", "agonistic", "foraging", "other SH", and "sexual" context (Table 5.1). Because long-tailed macaques have a moderate degree of reproductive seasonality, a combination of sexual behavior and skin swelling were used to evaluate estrus in females (Engelhardt, 2005). Based on the contextual information derived across an entire 1-minute behavioral sequence, each SH sequence could be assigned to several contexts of expression.

To test Prediction #4 (i.e., the number, the relative size, and the texture of the stones used to perform genital stone-tapping/-rubbing should be less variable compared to the stones used to perform stone-tapping/-rubbing on other body parts), for each subject, we selected all available SH sequences with genital stone-tapping/-rubbing and/or stone-tapping/-rubbing on other body parts. For each sequence, we selected one genital stone-tapping/-rubbing and, if available, one stone-tapping/-rubbing on other body parts; if multiple genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts were available, selection was made at random. To control for any possible bias in stone availability at the study site, we compared stone selectivity between genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts. To test this prediction, only instances of genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts in which individuals manipulated stones with their hands were considered. In other words, no instances of "Pelvic thrusting" were included in this analysis. For each genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts, we recorded the number, size, and texture of the stones used to perform these SH behavioral patterns. Stone size was measured by using a SH performer's hand palm as a standard for relative size (Cenni et al., 2021). A *small* stone was defined as being smaller than the palm of a subject's hand. A *medium* stone was defined as being of similar size to the subject's palm. A *large* stone was defined as being larger than the subject's palm. Two stone textures were distinguished: (1) *angular/rough* stones, defined as stones with sharp edges and/or grainy texture, and (2) *non-angular/smooth* stones, defined as stones with smooth or no edges and honed (i.e., flat and smooth) surface. To compare variability in the stones used to perform genital stone-tapping/-rubbing versus stone-tapping/-rubbing on other body parts, we recorded these characteristics for the stones used in 267 genital stone-tapping/-rubbing and 267 stone-tapping/-rubbing on other body parts. In the end, we were able to select 154 subjects, including 58 juvenile/subadult males, 34 juvenile/subadult females, 13 adult males, and 49 adult females.

To determine whether the stones used in SH sequences with genital stone-tapping/-rubbing were less variable than the stones used in SH sequences with stone-tapping/-rubbing on other body parts, we used the coefficient of unalikeability (*u*; Kader & Perry, 2007). The coefficient *u* ranges from 0 to 1; the higher the value, the more unalike the data set (i.e., the higher the variation in the data).

To explore the distribution of genital stone-tapping/-rubbing across sex/age classes, we randomly selected, by drawing names from an online random generator, 56 subjects, including 14 juvenile/subadult males, 14 juvenile/subadult females, 14 adult males, and 14 adult females (Supplementary Material S5.4). Since (a) genital stone-tapping/-rubbing has never been observed outside SH activity, and (b) SH activity represents a small proportion of the time budget of an individual in Ubud (Leca, unpublished data), we only examined the distribution of genital stone-tapping/-rubbing across sex/age classes within the SH activity. For each of these 56 subjects, CC randomly selected, by drawing sequences from an online random generator, and scored on average 31 minutes of cumulative SH activity across multiple days. Whenever possible, to ensure a more comprehensive representation of an individual's SH activity, no more than 10 minutes of SH activity per day were scored. To do so, SH sequences longer than 10 minutes were randomly truncated with the use of a random time generator.

### *5.3.4. Statistics*

To determine whether criterion behaviors significantly differed in their transitional probabilities to the target behavior (i.e., Prediction #1), we used adjusted residuals and Yule's Q (Bakeman & Gottman, 1997; Bakeman & Quera, 2011). The adjusted residuals indicated whether the transitions between pairs of behaviors differed from chance (with positive values associated with transitions being greater than chance; Bakeman & Quera, 2011). Yule's Q is an index of effect size that varies from –1 to +1, with 0 indicating no effect (Bakeman & Quera, 2011). To determine whether SH sequences with penile erection differed from SH sequences without penile erection in the total duration of any SH patterns expressed in at least 50% of the SH sequences with penile erection (i.e., Prediction #2), we used Wilcoxon signed rank-tests. Due to the small sample size available for adult males to test Predictions #1 and #2, we combined data for juvenile/subadult and adult males when running the analyses. To determine whether the occurrence (i.e., presence or absence) of genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts differed across contexts (i.e., Prediction #3), we used McNemar's tests with separate analyses for each age/sex class. Finally, to test whether the number, size, and texture of the stones used to perform genital stone-tapping/-rubbing differed in their coefficients of unalikeability from stones used to perform stone-tapping/-rubbing on other body parts (i.e., Prediction #4), we used the test statistic *C* (Lehner, 1996), with separate analyses for each age/sex class. To determine whether the duration of genital stone-tapping/-rubbing differed across age/sex classes (i.e., juvenile/subadult males, juvenile/subadult females, adult males, and adult females), we used a Kruskal–Wallis *H*-test with Dunn's post-hoc tests for multiple pairwise comparisons. When conducting multiple identical tests on the same data set, we reported the original p values and used the Bonferroni correction to control for type I errors (i.e., original p values were considered as statistically significant if smaller than Bonferroni's corrected α; Siegel & Castellan, 1988).

### *5.3.5. Ethical statement*

Data used for this research were exclusively observational and non-invasive. 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 #1906).

## 5.4. Results

Among all the SH behavioral patterns performed by juvenile/subadult and adult males, genital stone-tapping/-rubbing was the only criterion behavior that significantly differed in its transitional probability to the target behavior "penile erection" (transitional probability = 0.22, adjusted residuals $z = 7.90$, $p < 0.001$, corrected $\alpha = 0.002$, Yule's $Q = 0.82$). No statistically significant differences were found in the transitional probabilities from other SH behavioral patterns to penile erection (Table 5.2). Prediction #1 was supported.

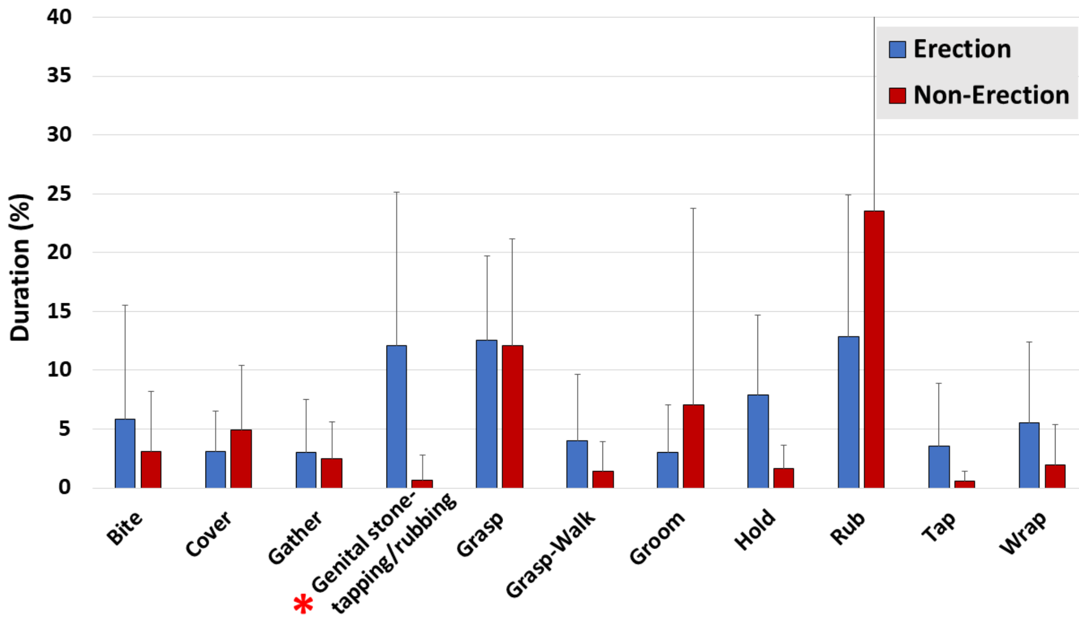
**Table 5.2** – *Transitional Probabilities of Criterion Behaviors to Target Behavior "Penile Erection", and Respective Adjusted Residuals, P-Values and Yule's Q.*

| Criterion | Target: Penile erection | | | |
|---|---|---|---|---|
| | transitional probabilities | adjusted residuals | p-value (α = 0.002) | Yule's Q |
| Bite | 0.04 | -0.25 | 0.81 | -0.13 |
| Clack | 0.00 | -0.52 | 0.60 | -1.00 |
| Cover | 0.03 | -0.70 | 0.48 | -0.34 |
| Cuddle | 0.00 | -1.15 | 0.25 | -1.00 |
| Flint | 0.00 | -0.33 | 0.74 | -1.00 |
| Gather | 0.03 | -0.44 | 0.66 | -0.22 |
| Genital stone-tapping/-rubbing | **0.22** | **7.90** | **< 0.001** | **0.82** |
| Grasp | 0.06 | 0.29 | 0.77 | 0.08 |
| Grasp-Walk | 0.00 | -0.77 | 0.44 | -1.00 |
| Groom | 0.00 | -1.10 | 0.27 | -1.00 |
| Hold | 0.07 | 0.55 | 0.58 | 0.17 |
| Lick | 0.00 | -1.15 | 0.25 | -1.00 |
| Move and Push/Pull | 0.00 | -0.40 | 0.69 | -1.00 |
| Move in Mouth | 0.00 | -0.33 | 0.74 | -1.00 |
| Pick and Drop | 0.14 | 1.12 | 0.26 | 0.52 |
| Pick Up | 0.00 | -0.57 | 0.57 | -1.00 |
| Pound | 0.03 | -0.76 | 0.45 | -0.36 |
| Pound-Drag | 0.00 | -0.87 | 0.38 | -1.00 |
| Roll | 0.07 | 0.68 | 0.50 | 0.21 |
| Roll in Hands | 0.00 | -0.46 | 0.64 | -1.00 |
| Roll with Fingers | 0.00 | -0.70 | 0.49 | -1.00 |
| Rub | 0.02 | -1.17 | 0.24 | -0.39 |
| Rub With Hands | 0.00 | -0.46 | 0.64 | -1.00 |
| Scatter | 0.00 | -0.81 | 0.42 | -1.00 |
| Shift in Hands | 0.00 | -0.57 | 0.57 | -1.00 |
| Slam | 0.00 | -0.33 | 0.74 | -1.00 |
| Slap | 0.00 | -0.96 | 0.34 | -1.00 |
| Sniff | 0.00 | -0.81 | 0.42 | -1.00 |
| Tap | 0.00 | -0.77 | 0.44 | -1.00 |
| Throw | 0.00 | -0.33 | 0.74 | -1.00 |
| Wrap | 0.03 | -0.54 | 0.59 | -0.27 |

*Note.* Boldface indicates statistically significant results.

In juvenile/subadult and adult males, genital stone-tapping/-rubbing lasted significantly longer in SH sequences featuring penile erection than in SH sequences without penile erection (Wilcoxon signed rank-test, z = -3.07, p = 0.002, corrected α = 0.005; 12 ± 13 sec and 1 ± 2 sec, respectively; Figure 5.3), whereas no statistically significant differences were found in the duration of any other SH patterns in the presence or absence of penile erection. Prediction #2 was supported.

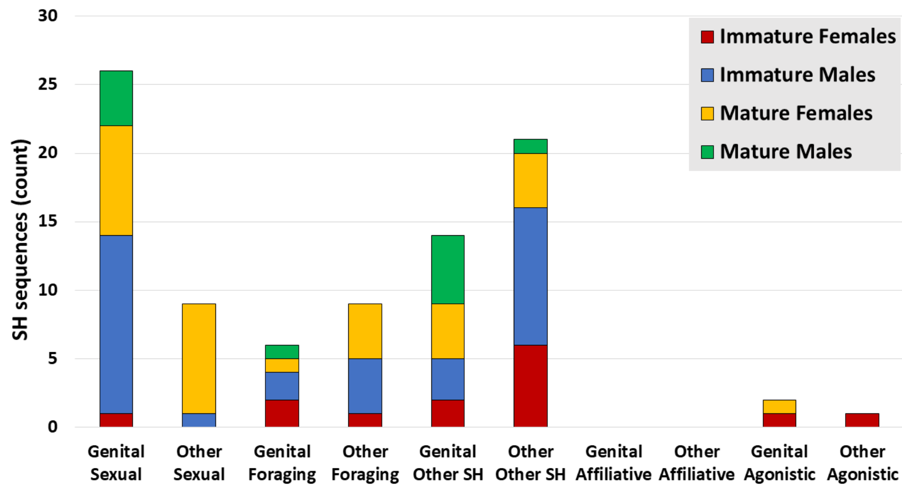
**Figure 5.3** – *Average Percentages of Duration (± SD) of SH Patterns Performed by at Least 50% of the Sample in SH Sequences with Penile Erection (Blue Bars) and in SH Sequences Without Penile Erection (Red Bars).*




*Note.* *: corrected $p < 0.005$.

In juvenile/subadult males, we found that genital stone-tapping/-rubbing was performed significantly more often in a "sexual" context than stone-tapping/-rubbing on other body parts (McNemar's test, $\chi 2$ (1, N = 18) = 10.08, $p < 0.001$, corrected $\alpha = 0.01$; Figure 5.4), whereas no statistically significant differences were found in other contexts. No other statistically significant differences were found between genital stone-tapping/-rubbing and stone-tapping/-rubbing on other body parts in any contexts within age/sex classes. Prediction #3 was partly supported.

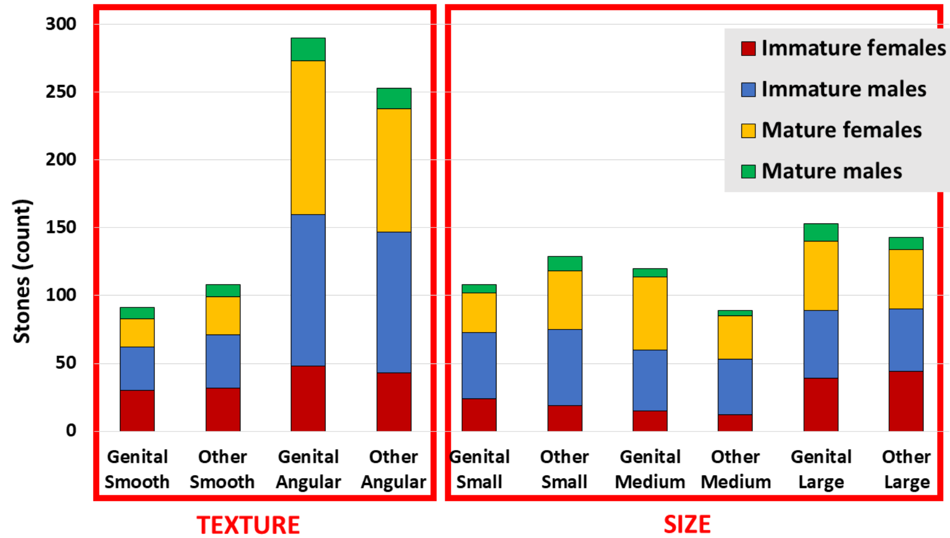
**Figure 5.4** – *Number of SH Sequences with Genital Stone-Tapping/-Rubbing and Stone-Tapping/-Rubbing on Other Body Parts Performed in Different Contexts Across Age/Sex Classes.*




*Note.* Genital = genital stone-tapping/-rubbing. Other = tapping/rubbing on other body parts.

In terms of variability of stones used by different age/sex classes to perform genital stone-tapping/-rubbing and to perform stone-tapping/-rubbing on other body parts, we found that, in adult females, there was significantly less variation in texture in stones used to perform genital stone-tapping/-rubbing than in stones used to perform stone-tapping/-rubbing on other body parts (coefficient of unalikeability, u = 0.26 and u = 0.36, respectively; test statistic C = -3.37, $p < 0.001$, corrected $\alpha = 0.017$; Figure 5.5). When performing genital stone-tapping/-rubbing, adult females used more *angular/rough* stones than *non-angular/smooth* stones (113 and 21, respectively), whereas no statistically significant preference for stone texture was found when performing stone-tapping/-rubbing on other body parts (91 and 28, respectively). No other statistically significant differences were found in other stone characteristics (i.e., number and size) within age/sex classes. Prediction #4 was partly supported.

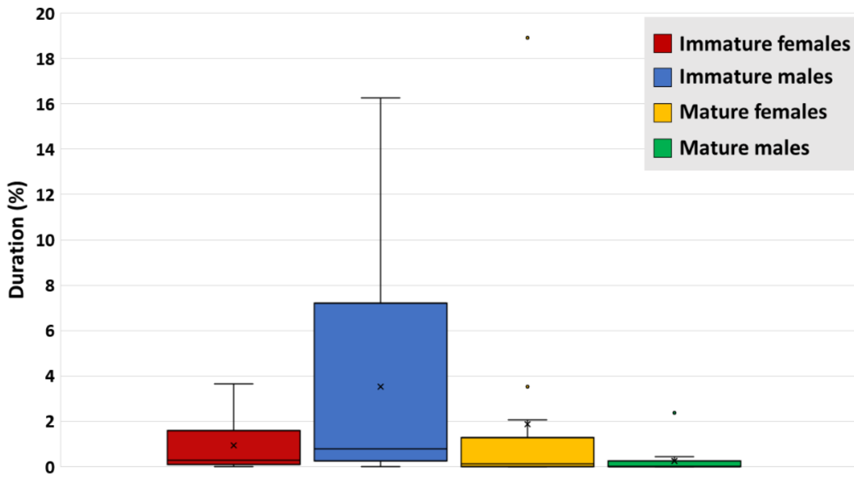
**Figure 5.5** – *Number of Stones, Classified by Texture, and Relative Size, Used to Perform Genital Stone-Tapping/-Rubbing and to Perform Stone-Tapping/-Rubbing on Other Body Parts Across Age/Sex Classes.*




*Note.* Genital = genital stone-tapping/-rubbing. Other = tapping/rubbing on other body parts.

We found a statistically significant difference in the distribution of genital stone-tapping/-rubbing durations across age/sex classes (Kruskal-Wallis' test, $H_3 = 10.35$, $p = 0.016$; Figure 5.6). Dunn's post-hoc tests revealed that juvenile/subadult males spent significantly more time performing genital stone-tapping/-rubbing during their overall SH activity (3.53% ± 5.07) than adult males (0.24% ± 0.63; Dunn's post-hoc test, $z = 18.43$, $p = 0.002$, corrected $\alpha = 0.008$), whereas no statistically significant differences were found between juvenile/subadult males and both, juvenile/subadult females (0.92% ± 1.20; Dunn's post-hoc test, $z = -5.93$, $p = 0.323$, corrected $\alpha = 0.008$) and adult females (1.87% ± 5.01; Dunn's post-hoc test, $z = 11.64$, $p = 0.052$, corrected $\alpha = 0.008$). No other statistically significant differences were found between age/sex classes.

**Figure 5.6** – *Distribution of Percentages of Duration (± SD) of Genital Stone-Tapping/-Rubbing in Relation to Total SH Activity for Each Age/Sex Class.*




## 5.5. Discussion

Our results provide some support to the Sex Toy hypothesis, which holds that genital stone-tapping/-rubbing comprise behavioral variants of self-directed stone tool-assisted masturbation in Balinese long-tailed macaques. Taken together, our results showed that genital stone-tapping/-rubbing (a) immediately preceded the beginning of a fully fledge penile erection, (b) lasted longer when penile erection occurred compared to when penile erection was absent, (c) was expressed within a sexual context in juvenile/subadult males, and (d) bore some degree of selectivity in the stones used by females to perform these actions. Thus, it can be confidently concluded that these actions are not incidental (see also Supplementary Material S5.2, which shows how different variants of the category *genital stone-tapping/-rubbing* are primarily directed towards the genitals, in both males and females). Lastly, we found that young males spent on average more time performing genital stone-tapping/-rubbing than other age/sex classes. However, this difference was significant only when comparing juvenile/subadult males and adult males. Thus, together with previous findings showing a higher temporal organization of SH sequences with genital stone-tapping/-rubbing than that of SH sequences where those two actions were absent (Cenni et al., 2020), our study provides further support to the view that genital stone-tapping/-rubbing comprise behavioral variants of tool-assisted self-directed masturbation in Balinese long-tailed macaques.

In the last two decades, increasing evidence of instrumental object manipulation applied to non-foraging tasks has led researchers to reconsider the proximate drivers of the acquisition and expression of tool use, and whether or not this behavior should be discussed exclusively from a goal-oriented and fitness-enhancing perspective (von Bayern et al., 2020). Tool-assisted masturbatory behavior is an example of a questionably adaptive and functionally opaque form of instrumental object manipulation that is established in the behavioral repertoire of a few primate species (Dixson, 2012). Since orgasm does not represent a necessary end-goal for masturbation in non-human primates, biomechanical definitions of tool use can contribute to detecting instrumental components of object-assisted actions, by investigating the mechanical effect (here, a physiological change measured via penile erection) that the tools have on the target (i.e., the genital and inguinal area). The fact that no other SH behavioral patterns have a temporal association with penile erection suggests that genital stone-tapping/-rubbing is distinctly sexually motivated, compared with other seemingly playful actions.

It is noteworthy that a free-ranging adult female Bonnet macaque (*Macaca radiata*) was reported manufacturing and inserting a twig into her vagina, scraping it vigorously, possibly in response to some irritation (Sinha, 1997), and a similar behavioral pattern was observed in an adult female from the population of long-tailed macaques living in Ubud (Supplementary Material S5.5; Cenni et al., in review). In the long-tailed macaques living in Ubud, pleasurable/self-rewarding mechanisms, such as those underlying both playful and sexual activities (cf. Burghardt, 2005; Georgiadis & Kringelbach, 2012) may have enhanced the motivation to perform genital stone-tapping/-rubbing, thereby facilitating the co-optation and maintenance of these two SH patterns into stone-tool use in a sexual context. Indeed, the pleasurable tactile feedback possibly obtained from the performance of SH activity might be one of the main motivational processes responsible for the maintenance and the transformation over time of this form of object play in macaques (Huffman, 1996). Our results are consistent with a previous study of another SH behavioral pattern (i.e., stone pounding) indicating that the performance of some SH behavioral patterns may be underlain by distinctly playful or pleasure-related motivational processes, even though they *appear* to be structurally similar to some stone tool-assisted extractive foraging behaviors (Pellis et al., 2019). Overall, our findings also support the view that a number of behavioral patterns performed during playful activities (like SH) are shared with (i.e., co-opted from, or exapted into) other behavior systems (e.g., anti-predator behavior, conspecific aggression, sex, foraging; Cenni et al., 2020; Leca et al., 2008a; Pellis et al., 2019).

Several causes have been proposed to explain the proximate and evolutionary significance of masturbatory behavioral patterns (Baker & Bellis, 1993; Dixson & Anderson, 2004; Dubuc et al., 2013; Inoue, 2012; Thomsen & Soltis, 2004; Waterman, 2010). In a questionnaire-based study, Thomsen and colleagues (2003) found a strong association between a primate species' mating system and the occurrence of male masturbation, with masturbation being more often displayed in species living in a multimale/multifemale organizational system, like macaques. In those species, males and females form short-term, and generally non-exclusive, sexual relationships that include courtship behaviors and a single, or a series of, mounting interaction(s) (Dixson, 2012). As a result, multimale/multifemale systems are characterized by high levels of intra-sexual competition, especially among males, for access to, and insemination of, females. Such intra-sexual competition can select for sexual traits in male anatomy, physiology and behaviors (i.e., sperm competition; G. A. Parker, 1970). Males living in these mating systems have relatively large testes, whose numerous Leydig cells produce high levels of testosterone necessary to maintain competitive levels of sexual arousal (Dixson, 2012; Dixson & Anderson, 2004). Therefore, a higher distribution in the performance of male masturbation in species living in multimale/multifemale systems, including macaques, may be proximately (i.e., physiologically) and ultimately (i.e., evolutionarily) explained by higher intra-sexual competition among males. In this regard, the expression of stone tool-assisted masturbation in Balinese long-tailed macaques could be a by-product of sexual arousal and serve as a form of sexual outlet for individuals with limited access to mating opportunities (cf. Sexual Outlet hypothesis; Dixson & Anderson, 2004). However, given that male masturbation events lead to ejaculation in a small proportion of the observed masturbation time, new hypotheses are needed to explain masturbation (Dubuc et al., 2003). The lack of ejaculation after genital stone-tapping/-rubbing and the majority of manual masturbation instances may still be explained from a by-product perspective. The Sexual Pleasure hypothesis is a more holistic approach recently proposed to explain masturbation (Roth et al., 2022). In line with the neurobiology of sexual pleasure, this hypothesis holds that genital self-stimulation (with and without object) is maintained by sexually pleasurable feedback, thereby modulating the individual's emotional state. This could explain our results showing that younger males (which displayed early signs of sexual interest, as demonstrated by the genital inspection of females, mounting attempts directed to females, and self-directed manual masturbation; Cenni, personal observation) spent more time performing genital stone-tapping/-rubbing than older males, who may be more successful in the competition for female mates. However, this hypothesis has not been fully tested yet, and it does not fully account for the time spent by females performing genital stone-tapping/-rubbing in our study population.

Female masturbation in non-human primates has been scarcely documented in the literature, possibly for two reasons. First, inferring masturbatory activities in female non-human primates is not an easy endeavor because genital self-stimulation in females is less conspicuous than in males and usually not accompanied by physiological and behavioral responses specific of sexual arousal, such as penile erection, and sexual facial expressions or vocalizations (Beach, 1976; but see Allen, 1977; Temerlin, 1975). Second, female masturbation is even less frequent than male masturbation (Dixson, 2012). However, anecdotal evidence suggests that *object-assisted* masturbation is more common in females than in males (e.g., Ford & Beach, 1951; Kollar et al., 1968; Russon et al., 2009; Sinha, 1997). There might be two reasons for this sex difference. From an anatomical perspective, because the most erogenous zone of females' genitalia (e.g., clitoris, labia minora) is more internal than its male counterpart in non-human primates, it may be easier to access and stimulate by using objects than fingers (Dixson, 2012; Pavličev & Wagner, 2016). From a psychological perspective, sex differences in tool use found in several primate species are consistent with a female-bias towards object-assisted genital stimulation (Boesch & Boesch, 1984; Gumert et al., 2011; Spagnoletti et al., 2011). Future studies should aim to test whether specific variants of object-assisted genital stone-stimulation (e.g., tapping, rubbing, or rolling) are indicative of sex differences in reaching sexual arousal and pleasure. Indeed, detailed kinematic analyses can help identify individual behavioral styles (cf. Pellis et al., 2019), and could contribute to revealing physiological sexual underpinnings of tool-aided masturbation.

It is important to acknowledge that our study subjects may represent a STRANGE population (as per Webster & Rutz, 2020), in which food provisioning relaxed selective pressures on foraging causing the part of the activity budget typically devoted to looking for natural foods to decrease (Brotcorne, 2014; Leca et al., 2008b). Such anthropogenic influences created spare time for the monkeys that may have been invested into less functionally constrained forms of behavior, including object-assisted masturbation. Indeed, in the *Macaca* genus, SH traditions have only been reported in provisioned groups (Leca et al., 2008b; Pelletier et al., 2017), whereas substance-related tool-assisted behaviors have been primarily reported in populations in which high selective pressure on foraging is high (Gumert et al., 2009). Nonetheless, the phylogenetic closeness among macaque species and populations that handle stones, either playfully or instrumentally, suggests a general tendency to conditionally use stones in some environments, be it functional or non-functional (Tan, 2017).

There are at least two explanations for the modest stone selectivity found in genital stone-tapping/-rubbing. First, the cognitive ability to select stone tools on the basis of their suitable physical characteristics is a crucial component of functionally constrained actions, and it has been demonstrated in several reports of tool use in a foraging context, such as food extractive techniques in non-human primates and corvids (e.g., Fragaszy et al., 2010; St Clair & Rutz, 2013). However, given the questionably adaptive nature of tool-assisted masturbation, the selection of optimal tools may not be decisive for the performers of genital stone-tapping/-rubbing actions to reap potentially pleasurable benefits. If tactile stimulation triggers pleasurable feedback perceived by individuals while performing genital stone-tapping/-rubbing, we could expect stone texture to influence the expression of these SH behavioral patterns. Our results support this idea in mature females, where stones with sharp edges and/or grainy texture were preferentially used to genital stone-tapping/-rubbing. The preference for using angular stones in adult females may be due to anatomical differences between sexes, with genitals being located more posteriorly in females than in males. Second, it is noteworthy that (a) genital stone-tapping/-rubbing are specific actions integrated within longer SH sequences (i.e., more extended and behaviorally diverse bouts of playful object manipulation), and (b) instances of genital stone-tapping/-rubbing have not been recorded separately from other SH behavioral patterns (i.e., we did not observe the performance of genital stone-tapping/-rubbing actions in isolation from other SH behavioral patterns). It is possible that these two stone-directed actions are still undergoing some transformational processes involving emancipation from the playful manipulation of stones from which they emerged (cf. Huffman & Quiatt, 1986; Pellis et al., 2019; but see Cenni et al., 2020).

Taken together, our results support the view that tool use evolves in stages from initially non-functional behaviors, such as object play, through affordance learning (Cenni & Leca, 2020a; Leca, 2020; Leca et al., 2008a, 2011, 2012; Lockman, 2000). The behavioral variability afforded by object play is a relevant source of raw material for, and thus a potential predictor of, the evolutionary origins, the developmental acquisition, and the daily expression of tool use. In the context of SH, behavioral variability provides individuals with a set of stone-directed actions upon which selection can act to refine functional solutions to various environmental problems (Cenni et al., in review; Huffman & Quiatt, 1986; Leca, 2020; Leca et al., 2012). The SH culture in macaques perfectly suits this model because (1) it offers a large repertoire of socially learned SH patterns from which stone tool use can cumulatively emerge over generations of performers, and (2) it is a form of behavioral specialization at the individual level that may contribute to maintaining population-specific behavioral heterogeneity in stone use (Cenni et al., 2020, in review; Leca et al., 2008a, 2012). Moreover, the relaxed selective pressures on foraging, associated with the food provisioning of free-ranging macaque populations, have created favorable environmental conditions under which this form of material culture may allow for the maintenance of a reservoir of stone-directed actions; when opportunities arise, some of this "behavioral junk" may turn them into stone tool use, through spontaneous technical innovations and social diffusion of instrumental object manipulation (Cenni & Leca, 2020b; Leca et al., 2008a,b, 2012, 2016; Leca & Gunst, accepted).

# CHAPTER 6: WHAT IS THE ROLE OF OBJECT PLAY IN THE ACQUISITION OF TOOL USE? ANSWERS VIA FIELD EXPERIMENTS IN BALINESE LONG-TAILED MACAQUES

## 6.1. Abstract

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 with phylogenetic underpinnings, named stone handling, characterized by high inter-individual variation in its behavioral expression, promoted the acquisition of stone-tool use in a non-human primate species.

We conducted a series of field experiments in a free-ranging group of Balinese long-tailed macaques to test whether the stone handling profiles of different individuals would predict their ability to solve a foraging task, whose solution required the functional and action-specific use of stones as tools. Network-based diffusion analysis, multilevel modelling, and description 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 to express 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 behavioral idiosyncrasies associated with stone handling in long-tailed 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 object play in the acquisition of tool use applied to stones.

## 6.2. Introduction

Tools and utilitarian artifacts 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 skillfully manipulate objects in an instrumental way emerges. It has long been suggested that playful manipulation of objects facilitates the development and evolution of tool use (Bruner, 1972; S. T. Parker & K. R. Gibson, 1977). Indeed, children and juveniles (and to a less extent adults) of several species that habitually use tools spend a large amount of time playing with and exploring novel objects (e.g., children, P. K. Smith & Connolly, 1980; chimpanzees, Ramsey & McGrew, 2005; capuchin monkeys, E. J. Jordan et al., 2022; long-tailed macaques, Tan, 2017; New Caledonian crows, Lambert et al., 2017), and the idea that play is a particularly potent experience for the development of tool use is at the core of the Affordance Learning theory (J. J. Gibson 1979; E. J. Gibson, 1982). Following 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 of objects allows them to perceive the objects' potential for actions, including how to use these objects as tools (Lockman, 2000). The Affordance Learning theory has gained a large support in developmental psychology, where experimental evidence from pre-school children showed a facilitatory effect of object play in problem-solving tasks involving tools (e.g., Sylva et al., 1976), and in cognitive psychology, where 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, 1945a). However, the Affordance Learning theory remains loosely and inconsistently tested and empirical evidence connecting these two activities across animal taxa is scant (P. K. Smith, 2010).

In captive non-human animals, several experimental studies have suggested that exploratory, playful and reward-free manipulation favor the acquisition of instrumental knowledge of objects (e.g., Birch, 1945a; E. J. 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 (and reward-free) 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 pre-test exposure. Additionally, when considering the first trial in both conditions (i.e., whether the puzzle box was baited with food or not), apes starting with the food-baited puzzle box took longer to drop a stone inside the tube than apes who started with the non-baited puzzle box; thus, intrinsically motivated object manipulation, such as object play, may provide meaningful information on the action-outcome contingencies of a task. Even though these results provide some support to 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 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, and gorillas, 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 orangutans 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; capuchin monkeys, 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 whether wild populations of non-human 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 non-human animals. However, evidence from innovative problem-solving experiments (involving tools or not) suggests that a higher behavioral flexibility (quantified as the number of different actions expressed during a task) is a key determinant of success (Griffin & Guez, 2014). In two neighboring groups of wild hyenas living in Kenya, the likelihood to solve a novel food-retrieval task was predicted by the degree of behavioral flexibility expressed by individuals on an experimental apparatus (Benson-Amram & Holekamp, 2012). Animals who exhibited a greater diversity of exploratory behaviors in their first trial were significantly more successful than animals with lower exploration diversity (Benson-Amram & Holekamp, 2012). Although this field experimental study did not exclusively focus on *tool*-assisted problem-solving, the positive relationship between behavioral flexibility and motor diversity, that are key to object play behavior, and the acquisition of novel solutions, which tool use may be an example of, suggests that previous playful manipulation may be important for an animal to discover the properties of objects that can be later used as tools. Thus, evaluating the Affordance Learning theory in an ecologically relevant model is a promising and probably necessary step to understand how non-human animals acquire tool use.

Stone handling (SH), a socially learned type of stone-directed play that is part of the cultural repertoire of several macaque species (Huffman & Hirata, 2003; Nahallage & Huffman, 2008; Nahallage et al., 2016), is an ideal candidate to test the ecological validity of the Affordance Learning theory for several reasons. First, given that SH behavior lacks functional constraints typically observed in instrumental actions, the expression of specific SH behavioral patterns is largely arbitrary (i.e., there is no wrong action), and it is performed with stones of different sizes and textures, which afford for a large variety of actions to be expressed (Cenni et al., 2021; Cenni et al., in review). As a result, SH is a versatile form of play, with a vast, complex, although seemingly functionless (but see below) behavioral 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; such a large variety of stone-directed actions may constitute a pool of behavioral alternatives from which tool use can emerge (Cenni et al., 2020; Huffman & Quiatt, 1986; Leca et al., 2008a; Leca & Gunst, accepted). Second, SH behavior 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 concentrated during immature life stages; Huffman, 1996; Leca et al., 2007a; Nahallage & Huffman, 2007a; Pelletier et al., 2017), and it shows a high degree of inter-individual variation, as monkeys of different age/sex classes display individual preference for certain SH actions, that is they have SH profiles (Cenni et al., in review). Third, in at least two instances, in the social and sexual domains, SH behavioral patterns may have been co-opted into stone-tool use: (1) in a group of Japanese macaques, stone-throwing was integrated in agonistic displays in an apparent attempt to augment their effects (Leca et al., 2008b); and (2) in free-ranging Balinese long-tailed macaques, 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 long-tailed macaques, some wild coastal populations living in islands of Thailand customarily use tools to extract seafood from shells, despite not being reported to engage in SH behavior (Gumert et al., 2009, 2011). Hence, (a) populations of long-tailed macaques that do not habitually use stones as tools have the cognitive and physical potential to do so, and (b) testing the link between SH activity and stone tool-assisted actions has ecological relevance. Taken together, these characteristics suggest that SH behavior is amenable for evaluating the 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 and 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*, to play on the experimental apparatus. Second, we explored which individual attributes, both at the asocial and social level, made individuals more likely to solve the Dropping box and the Percussive box. Third, we provided a detailed description of the acquisition curves of individual solvers of different ages and sexes. Following a perception-action approach

(Lockman, 2000), we expected a covariation between an individual's SH profile and the likelihood of that individual to solve the foraging task. Specifically, an individual with a high Dropping SH profile should be more likely to solve the Dropping box than an individual with a low Dropping SH profile (Prediction #1). Additionally, an individual with a high Percussive SH profile should be more likely to solve the Percussive box than individual with a low Percussive SH profile (Prediction #2).

## 6.3. Methods

### *6.3.1. Study population and site*

We studied a population of free-ranging, urban-dwelling, habituated and provisioned Balinese long-tailed 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 comprised of seven neighbouring groups with overlapping home range areas (Giraud et al., 2021). The monkeys were provisioned at least three times per day with fruits and vegetables by the temple staff.

### *6.3.2. Field experiments to induce stone-tool use*

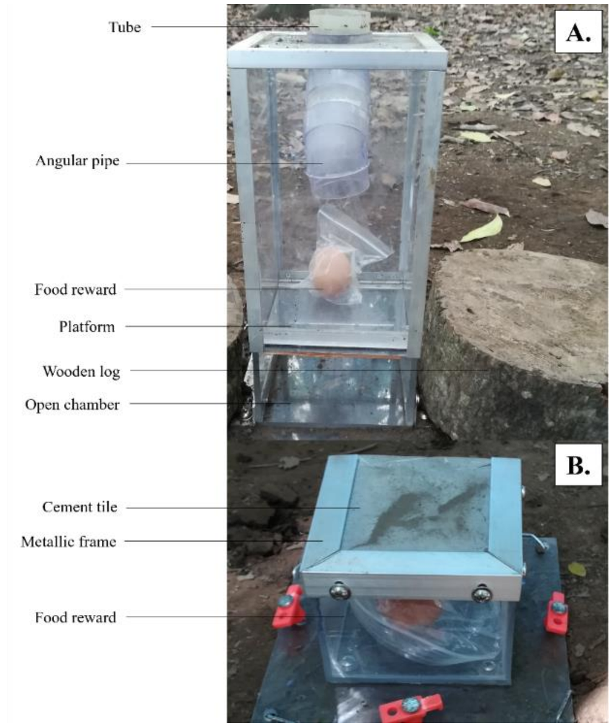
#### *Food-baited boxes*

To test whether the daily practice of SH activity in Balinese long-tailed 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 SH 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 x 20 x 40 cm in 2018, and 15 x 15 x 35 cm in 2019. Each box had an open chamber at the bottom and the open end of a tube attached onto its top (Figure 6.1A). 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). On the upper side of the platform, there was a highly prized food reward (e.g., pieces of fruit, or raw egg), 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, or females) from reaching the food rewards by inserting their arms through the tube. Because macaques are mostly seated when performing spontaneous SH activity (Cenni, personal observation), 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 (Figure 6.1A).

The Percussive Box consisted of a rectangular parallelepiped Lexan transparent box 15 x 15 x 10 cm with a metallic frame on its top part, through which a cement tile 15 x 15 x 1 cm could be inserted to close the box (Figure 6.1B). 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 highly prized food reward (e.g., pieces of fruit, or raw egg), which could be accessed by breaking the tile with the use of stone(s).

**Figure 6.1** – *Dropping Box (A) and Percussive Box (B).*



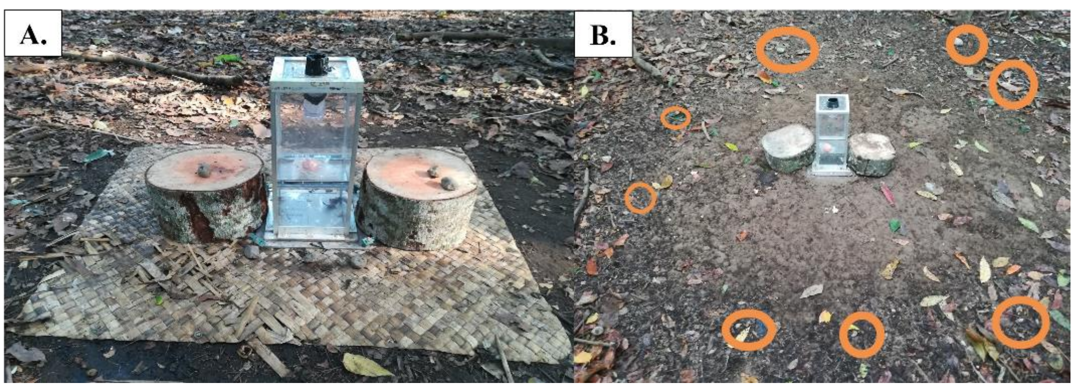

Each box was attached to an aluminum platform 25 x 25 cm (in 2019 the aluminum was replaced with Lexan and the platform measured 20 x 20 cm) and anchored to the ground via long metallic pegs. Each box was tested one at a time over multiple days. During this time, the box remained in the experimental area, emptied of its food reward and covered by a plastic bin anchored to the ground via long metallic pegs, to prevent individuals from accessing the box between experimental events (Figure 6.2). 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 behaviors towards it. In 2019, we removed the mat, because, as interest towards the boxes increased, the monkeys appeared to be more distracted by the mat, often tearing it apart. Thus, to delimit the experimental area, we swept the one-meter area around the box.

**Figure 6.2** – *Plastic Bin (A: 2018; B: 2019) Anchored to the Ground Via Long Metallic Pegs to Prevent Individuals to Access the Puzzle Boxes Between Experimental Events.*


***Stones***

To ensure that stones suitable to open the puzzle boxes would be readily available to the individuals interested in participating in the experiments, we placed 12 stones before the start of an experimental event. 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 (Figure 6.3). To limit potential bias, in 2019, the 12 stones were randomly scattered inconspicuously around two meters from the experimental area (i.e., outside the swept area; Figure 6.3). 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 solved the Dropping box 10 times in a row when used by a human experimenter (CC) because they were easily inserted through the tube and heavy enough to collapse the platform at once. When testing stone suitability, CC released the stones without adding external force to her actions. For the Percussive Box, stone suitability was assessed by selecting stones that could be grasped for pounding or slammed by a monkey (see below), and that could potentially be heavy enough for a monkey to crack the tile (although we could not systematically assess this criterion). Stones selected for the field experiments were preferentially chosen from stones previously manipulated in SH sequences outside experimental events. In addition, suitable stones were also chosen from stones used to perform box-matching SH patterns (i.e., a SH pattern belonging to the Percussive category – see below – for the Percussive Box, and a SH pattern belonging to the Dropping category – see below – for the Dropping Box). If there were no stones available previously used in SH sequences outside field experimental events, we selected stones found in the study area that met the suitability criteria (i.e., easily inserted through the tube and solving the Dropping Box 10 times in a row, as well as graspable or suitable for slamming and heavy enough to crack open the lid of the Percussive Box, when compared to similar stones previously used by monkeys).

**Figure 6.3** – *Experimental Area in 2018 (A.) and 2019 (B.).*




*Note*. In 2019, the stones are less noticeable, and scattered within a two-meter radius around the experimental area. Orange circles identified the scattered stones.

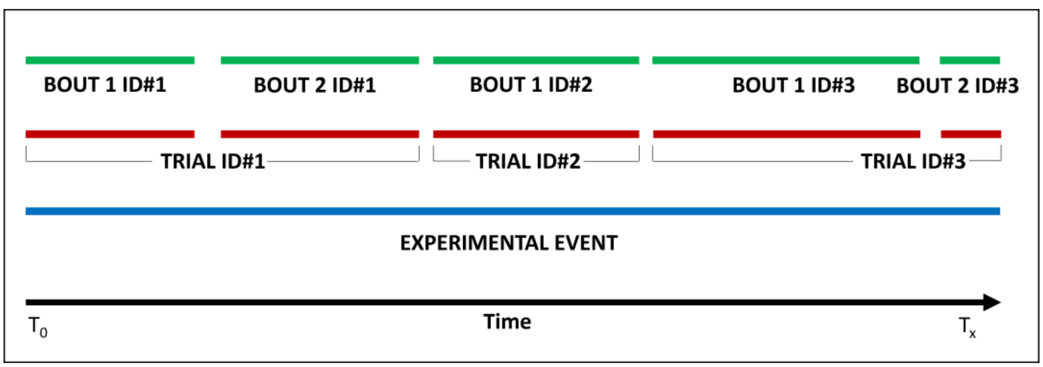
***Procedure***

Experimental events were conducted from June to August 2018 and from May to August 2019, between 08:00 and 17:00, and approximately daily (mean number = 3 sessions/day, mean duration = 1 hour 30 min/day). During an experimental event, only one box was tested. There were two experimenters per experimental event. An experimental event was defined as the time window between the moment the plastic bin covering a puzzle box was lifted by one of the experimenters, with the box baited with a food reward and made accessible to individuals, and the moment when either the food reward was released by an individual, or if nobody accessed the food reward within the experimental event, when the plastic bin covered the box (approximately between 30 minutes to one hour).

Stones were placed before the beginning of an experimental event and were removed after the covering bin has been anchored over the box; in 2019, stones were placed one minute before the beginning of an experimental event, the observer then left the area for one minute, and approached it again with the second observer, to begin the experimental event. Once the plastic bin was lifted, two observers video-recorded an experimental event. One observer was responsible for continuously filming the experimental area, standing between three and five meters from the experimental area. The other observer was moving between three and seven meters from the experimental area and was responsible for recording the identity of the individuals and collecting behavioral data on all the individuals located within five meters of the experimental area. Even after the experimental event was over, we continuously filmed the experimental area until the plastic bin was anchored and the box was once again covered.

Within an experimental event, multiple individuals may be involved in an experimental trial; for each experimental event, a given individual was involved in only one trial (Figure 6.4). An individual trial was defined as the sum of all individual bouts. A bout consisted in an individual touching the box and remaining within the experimental area for at least five seconds. 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 five seconds, 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 (e.g., 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.

**Figure 6.4** – *Visual Representation of a Hypothetical Experimental Event (Blue), Individuals' Trials (Red) and Individuals' Bouts (Green) Through Time for Three Individuals (ID#1, ID#2, and ID#3).*




### *Participants*

Over a 7-month period over both years, 140 individually identified monkeys voluntarily participated in the field experiments: 47 juvenile/subadult males (aged 2 to 6 years), 23 juvenile/subadult females (aged 2 to 4), 19 adult males (older than 6 years) and 51 adult females (older than 4 years; Table 6.1).

**Table 6.1** – *Number of Participants and Trials Across Experimental Apparatuses and Years*.

| Box Type | Year | Number of Participants | Number of Solvers | Number of Successful Trials | Number of Unsuccessful Trials | Total number of 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 | | | |

*Note*. PB = Percussive Box. DB = Dropping Box. In parenthesis, cumulative number of individuals for PB or DB across study periods.

### *6.3.3. SH profiles*

Spontaneous SH activity in the Balinese long-tailed macaques living in Ubud was defined as the (largely) non-instrumental manipulation of locally available stones, sometimes in combination with other objects, such as leaves, twigs, or human artifacts, and outside the context of the experimental trials. No stones were provided to the individuals to measure their spontaneous SH activity. Observations were recorded from May to August 2018 and 2019, between 08:00 and 17:00. SH activity was scored using the same SH ethograms as in Pelletier et al. (2017) and Cenni et al. (2021, in review). All the SH sequences used in this study were video-recorded with a digital camera (Sony Full HD Handycam Camcorder). SH sequences were collected by CC, JBL and three field research assistants using *ad libitum* sampling methods (Altmann, 1974). During *ad libitum* sampling, the individual was filmed if performing SH activity. Because the monkeys were highly habituated to humans, most video-records were collected at close range (3–5m), under good visibility conditions and without disturbing the animals. Whenever possible, the individuals were filmed from the front or side and about two-meter square in-frame.

For each individual, CC randomly selected and scored on average 27 minutes of cumulative SH activity across multiple days. Whenever possible, to ensure a more comprehensive representation of an individual's SH activity, no more than 10 minutes of

SH activity per day were scored. To do so, SH sequences longer than 10 minutes were randomly truncated with the use of a random time generator. Whenever possible, at least 30 minutes of cumulative SH activity were scored. Individuals with less than 5 minutes of cumulative SH activity were discarded from the analyses. Whenever possible, if the same individual participated in the field experiments in 2018 and 2019, two independent SH profiles were scored, one for 2018, and one for 2019. However, if less than 30 minutes of SH activity were available for each year, SH sequences were taken from both years (since we did not find a statistically significant difference in individual SH profiles between 2018 and 2019; Dropping SH profile, Wilcoxon's signed rank test $Z = 49.00$, $N = 18$, $p > 0.05$; Percussive SH profile, Wilcoxon's signed rank test $Z = 63.00$, $N = 18$, $p > 0.05$). After meeting all these selection criteria, we were able to score 127 SH profiles out of 140 individuals that participated in the experimental trials. CC used The Observer XT 15 (Noldus Information Technology, The Netherlands) and BORIS (Friard & Gamba, 2016) to score the video-recorded SH sequences, with a precision to the second, and generate event-log files (i.e., series of consecutive SH patterns). For each individual being involved in each puzzle box (i.e., Dropping box and Percussive box), we extracted its matching SH profile (i.e., a Dropping SH profile and Percussive SH profile).

To determine Dropping SH profiles and Percussive SH profiles, we combined all SH behavioral patterns that belonged to the macro-categories of Dropping and Percussive, respectively. Specifically, a Dropping SH profile combined all the SH behavioral 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 SH profile comprised the following SH behavioral patterns: Pick-and-Drop, Push-Through, Throw, Toss-and-Catch, and Toss-Walk. As previously mentioned, long-tailed macaques in Ubud habitually combine stones with other objects locally available. Specifically, these monkeys have been often observed combining stones with hollow objects, such as empty plastic bottles, water pipes, and spigots (Bunselmeyer, 2022). As part of a Dropping SH 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 SH profile combined all the SH behavioral patterns that required an individual to exert a vertical, forceful, and percussive action onto a surface (including another stone). As a result, a Percussive SH profile comprised the following SH behavioral patterns: Flint, Pound, Pound-Drag, and Slam. Video illustrations of SH behavioral patterns included in Dropping SH profiles and Percussive SH profiles can be found in Supplementary Material S6.1.

### *6.3.4. Data analysis and statistics*

#### *Comparisons between SH profiles and stone-directed actions performed at Dropping box and Percussive box*

To determine whether the action-specific use of stones was instrumental (in other words, whether individuals used stones as tools or as *toys* to play on the Percussive box and Dropping box), we considered only individuals that solved either box more than once. We extracted the relative duration of stone-directed actions, matching the corresponding box type, displayed during the field experiments (e.g., actions belonging to the macro-category Percussive for the Percussive box). We considered stone-directed actions solely directed to the Dropping box or the Percussive box, and we compared the relative duration of box-matching stone-assisted actions (e.g., percussive actions for Percussive box) with an individual’s box-matching SH profile (e.g., Percussive SH profile for Percussive box), using paired-sample t-test (or non-parametric Wilcoxon’s signed-rank test, when assumptions for parametric statistical tests were violated).

### *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). 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), remain the gold standard for distinguishing social from asocial learning in the acquisition of behaviors, those techniques are difficult to implement in wild populations, whereas NBDA infers learning pathways in the spontaneous emergence of behaviors when limited behavior acquisition and production information is available (e.g., when a human observer does not have access to every expression of the behavior, 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 behavioral innovation, while estimating the strength of social learning relative to asocial learning (Hasenhager et al., 2020). In our study, NBDA allowed us to test (a) the likelihood of solving a box via social and asocial contribution, (b) the percentage of first solution events attributable to asocial or social learning, and (c) the contribution of Individual Level Variables (ILVs; i.e., SH 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 transmission effects (e.g., if social transmission had a significant effect on learning and a social contribution of sex was significant for females, then social transmission 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 behavioral solution; hence, observation networks were the most effective way to capture social learning opportunities, as we recorded every individual observing the behavioral solution (see Hobaiter et al., 2014). As the witnessing history of an individual changed over the experimental phase, observation networks were dynamics and updated as new individuals solved the box (i.e., after each acquisition/new production of target behavior; 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 SH behavioral pattern belonging to the Percussive category for the Percussive box and a SH behavioral 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 SH behavioral 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%) where not counted within an observation network, because (a) observation networks tested whether direct observational social learning mechanisms explained the acquisition of the solution to a given puzzle box, and (b) 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 one meter of the box (i.e., within the experimental area) by its latency to solve the task, as any task exposure after this particular individual solving 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 events. 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 fit the models using Order of Acquisition of Diffusion Analysis (OADA; Hasenjager et al., 2020), a NBDA variant that uses the order in which individuals acquired a target behavior (here, puzzle box solution). Separate diffusions were modeled to test the learning pathways for the Dropping box and the Percussive box. Since experimental events were conducted across two study periods, with a nine-month break, 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). Whenever possible, we included, as ILVs, SH profiles, age (as a binary variable, with "juvenile/subadult" and "adult" as attributes), sex, dominance rank (calculated as Elo-Ratings, using the package "EloRating" in R 3.6.3, see Neumann et al., 2011; R Core Team, 2013), exposure to the task, and whether an individual had already solved the other puzzle box (e.g., whether an individual had opened the Percussive box before opening the Dropping box). Since we only had dominance rank values for 2019, rank was not included in 2018. Lastly, 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. In the end, for the model testing for the Dropping box across 2018 and 2019, we included as ILVs: SH profiles, age, sex, exposure to the task, and whether an individual had already solved the other box; for the model testing for the Percussive box in 2019, we included as ILVs: SH profiles, sex, dominance rank, exposure to the task, and whether an individual had already solved the other 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 SH profile could affect asocial learning, but have no explanatory role in social transmission. Akaike Information Criterion (AIC) was used to determine the best model, and model-averaged estimates and Wald's 95% confidence intervals were calculated 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 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 (B. J. T. Morgan, 2010). In one instance (i.e., ILV = "Social Percussive SH profile", in Percussive box 2019), we were unable to calculate confidence intervals. To interpret the contribution of social transmission to explaining learning, we reported 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 behavior. However, it comes with at least two limitations. First, NBDA only provides information on the learning mechanisms for the first occurrence of the target behavior, 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 behavior 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 (a) explore the expression of successful stone-assisted actions at the puzzle box beyond an individual's first production, and (b) 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 multilevel Bernoulli models, 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 modeled whether the following variables affected the likelihood of an individual solving a box using stone-assisted actions:

- Whether an individual had ever been observed manipulating stones outside the experimental sessions (i.e., presence/absence of recorded SH activity for an individual);
- An individual's SH profile, matching the corresponding box type (e.g., Percussive SH profile for Percussive box);
- Age/sex (as a categorical variable, with "juvenile/subadult females", "juvenile/subadult males", "adult females", and "adult males" as attributes);
- Dominance rank;
- Box type (as a binary variable, with Dropping box and Percussive box as attributes);
- Individual's trial number;
- Whether an individual's trial had been interrupted by the occurrence agonistic, affiliative, or sexual interactions (as a binary variable);

- How many times an individual's had previously solved the same box.

Individual's ID, study period, and date were modeled 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 dataset across the two study periods. Then, we constructed another model with all the variables, which only included the 2019 dataset (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 dataset was included in this model. Leave-one out-cross-validation (conceptionally close to an adjusted r-squared measure; Vehtari et al., 2017) was used to estimate the variance explained by the model. Scatterplots of the Markov Chain Monte Carlo draws 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 reported 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 ~ 97.5%, pd ~ 99.5%, and pd ~ 99.95% corresponding to weak, moderate, and strong evidence for an effect, respectively; Henzi et al., 2021; Makowski et al., 2019).

#### *6.3.5. Ethical statement*

This research was non-invasive and participations to the field experiments was voluntary. Balinese long-tailed 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 #1906).

## 6.4. Results

### *6.4.1. Comparisons between SH profiles and stone-directed actions performed at Dropping box and Percussive box*

We conducted 285 experimental events (2018: 96 events; 2019: 189 events). 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 6.1). 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 macro-category Dropping (hereafter, dropping actions) in an individual's SH profile and in the stone-assisted actions performed across trials and directed at the Dropping box (Wilcoxon's signed rank-test, $N = 12$, $Z = 78.00$, $p = 0.002$). Dropping actions directed at the Dropping box lasted significantly longer than during SH activity: 34.9% (± 26.1%) and 1.6% (± 2.5%), respectively.

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 macro-category Percussive (hereafter, percussive actions) in an individual's SH profile and in the stone-assisted actions performed across trials and directed at the Percussive box (paired sample t-test, $N = 7$, $t_6 = -3.45$, $p = 0.014$). Percussive actions directed at the

Percussive box lasted significantly longer than during SH activity: 58.1% (± 38.9%) and 19.5% ± (17.3%), respectively.

### *6.4.2. Information diffusion (i.e., NBDA)*

**Table 6.2** – *Diffusion Through the Observation Network for Dropping Box.*

| Parameter | Model-Averaged Estimate (±95% CIs) | Backtransformed Effect (±95% CIs) | Akaike Weight | Δ AIC |
|---|---|---|---|---|
| Visual Observation Network | 2.546 (0.349, 15.157) | 44.889 (30.550)* | 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 | 0.740 (0.535, 1.412) | x2.096 (x1.707, x4.106)† | 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) | -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 |

*Note*. All variables were scaled to assist with model fit. Grey rows indicate variables that were found in the best model. Age is relative to juveniles/subadults; sex is relative to females. CI = confidence interval. *: 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. †: 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.

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% C.I. = 30.55%) of learning events followed observation network. For the individuals that solved the Dropping box primarily via social learning, there was no effect of SH 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 6.2). 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 SH profile, sex, age, and exposure to the task on asocial learning.

**Table 6.3** – *Diffusion Through the Observation Network per Percussive Box (2019 Only).*

| Parameter | Model-Averaged Estimate (±95% CIs) | Backtransformed Effect (±95% CIs) | Akaike Weight | Δ AIC |
|---|---|---|---|---|
| Visual Observation Network | 0.004 (0.000, 7.997) | | 0.005 | 7.728 |
| **ILVs Asocial Transmission** | | | | |
| Percussive SH profile | 0.481 (0.168, 1.292) | x1.617 (x1.182, x3.639)† | 0.261 | 0.000 |
| Sex (Males) | -0.053 (-1.087, 0.403) | | 0.052 | 3.216 |
| Dominance Rank | 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 | 1.326 (0.830, 1.889) | x3.764 (x2.293, x6.616)† | 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 |

*Note.* All variables were scaled to assist with model fit. Grey rows indicate variables that were found in the best performing model. Sex is relative to males. CI = confidence interval. †: 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.

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 SH profile and exposure to the task (Table 6.3). If an individual had a higher Percussive SH profile, it was 1.6 times more likely to solve the Percussive Box asocially than individuals with lower Percussive SH 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 for both, asocial and social learning, of sex, dominance rank, and of whether an individual had previously solved the Dropping Box.

### *6.4.3. ILVs beyond first production (i.e., Multilevel model)*

**Table 6.4** – *Posterior Estimates of the Likelihood of Solving Either Puzzle Box.*

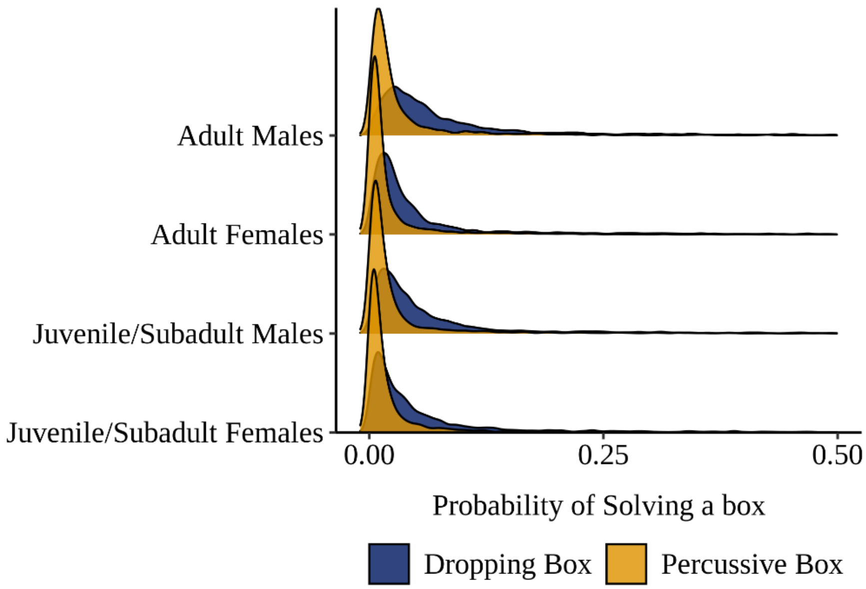
| **Effect** | **Parameter** | **Estimate** | **Est. Error** | **Lower 95% CI** | **Upper 95% CI** | **Pd (%)** |
|---|---|---|---|---|---|---|
| **Population-Level Effects** | Intercept (Adult Males) | -3.10 | 1.69 | -6.20 | 0.65 | 95.10 |
| | Adult Females | -0.67 | 0.58 | -1.81 | 0.47 | 87.60 |
| | 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 |
| | Box 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* | 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 |

Number of observations: 1202; LOO-adjusted $R^2 = 0.59$
*2019 only; number of observations: 742

*Notes.* Population-Level Effects and Group-Level Effects correspond to fixed effect factors and random effect factors, respectively, in frequentist approach. CI = credible interval. Pd = probability of direction. PB = Percussive Box.

The model found variation in group-level variables (which are comparable to random effects in a frequentist approach: Table 6.4). Specifically, there was high variation across individual IDs and study periods, whereas little to no variation was found in date. Overall, individuals were very unlikely to solve the box (Table 6.4). 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%; Figure 6.5). Although there is a level of uncertainty associated with the Dropping box (i.e., as indicated by the spread of the blue curve), 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.

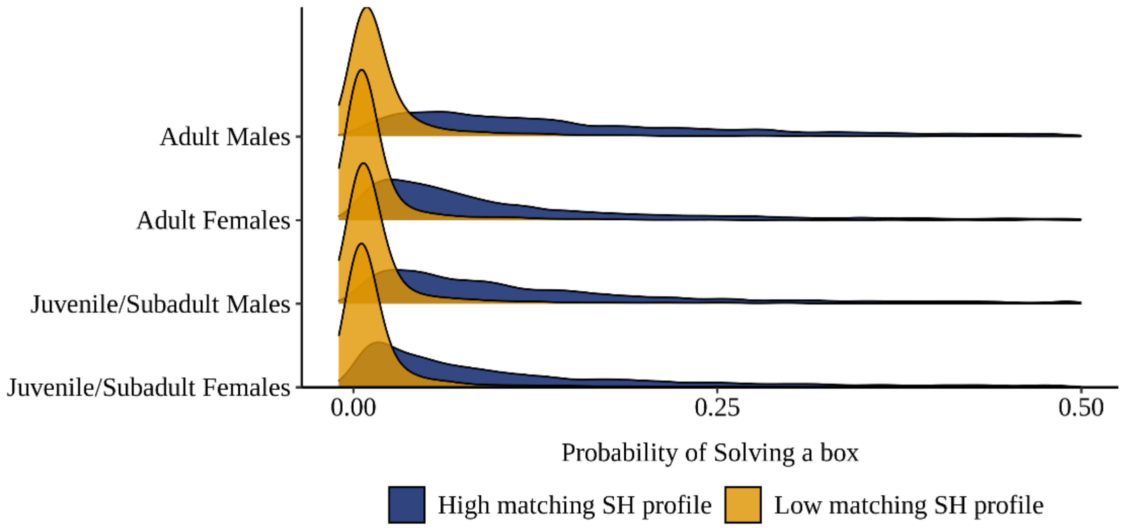
**Figure 6.5** – *Probability of Solving the Dropping Box (Blue) and the Percussive Box (Orange) for Different Age/Sex Classes.*




*Note*. 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 6.4). Probability scale is reduced, and it ranges from 0 to 0.50.

We found no evidence that the presence or absence of SH activity (independently of a SH profile) influenced the likelihood of an individual solving either the Dropping box or the Percussive box (pd = 50.07%; Table 6.4). However, box-matching SH profile (e.g., a Percussive SH profile for the Percussive box) affected the likelihood to solve the box. Specifically, individuals with higher box-matching SH profiles were more likely to solve the box than individuals with lower box-matching SH profiles (pd = 99.80%; Figure 6.6).

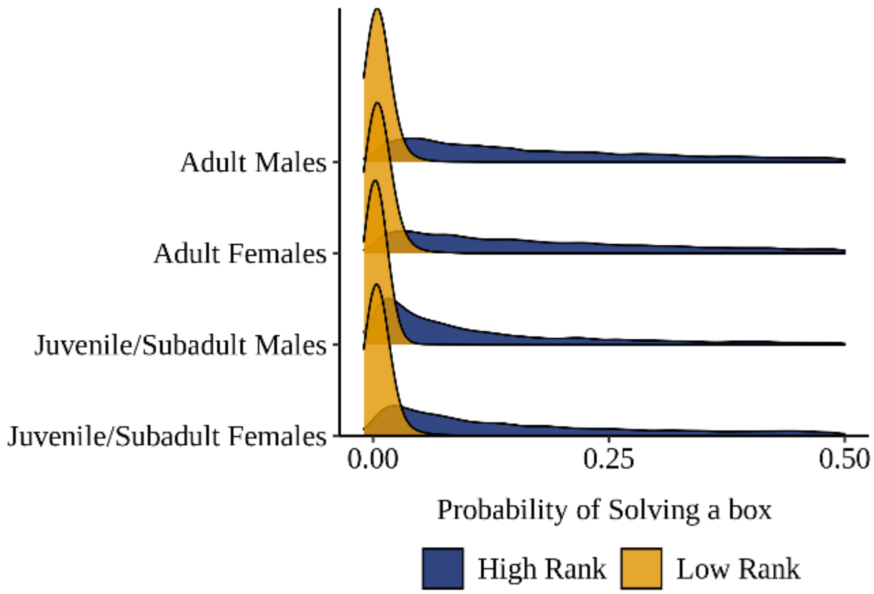
**Figure 6.6** – *Probability of Solving a Puzzle Box by Matching SH Profile (i.e., Dropping SH Profile per Dropping Box and Percussive SH Profile per Percussive Box) for Different Age/Sex Classes.*




*Note*. Density plots per high SH profiles (blue) and low SH profiles (orange) 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 6.4). Probability scale is reduced, and it ranges from 0 to 0.50.

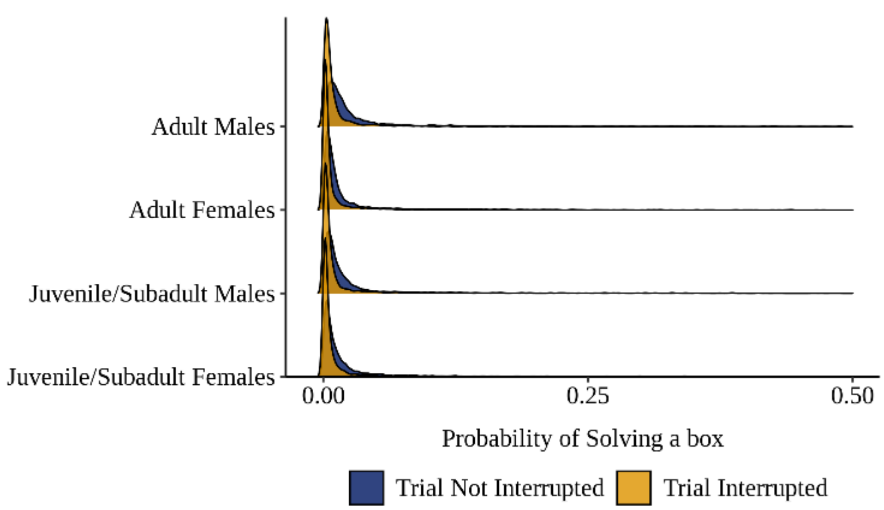
We found weak evidence that an individual's dominance rank influenced the likelihood to solve a puzzle box (pd = 96.50%; Table 6.4; Figure 6.7); specifically, lower-ranking individuals were less likely to solve the puzzle boxes, but there was not enough evidence to suggest that higher-ranking individuals were more likely to solve the puzzle boxes. Additionally, we found strong evidence that an individual's trial number (pd = 99.97%; Table 6.4) and whether they had previously solved the box (pd = 99.93%; Table 6.4) influenced their likelihood to solve a box again. The more trials, and the more times individuals had solved the box, the more likely they would be to solve again. We also found strong evidence that if an individual's trial was interrupted, this would affect its likelihood to solve a box (pd = 100.00%; Figure 6.8); 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 6.4).

**Figure 6.7** – *Probability of Solving a Puzzle Box by Rank for Different Age/Sex Classes.*




*Note*. Density plots per high rank (blue) and low rank (orange) 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 6.4). Probability scale is reduced, and it ranges from 0 to 0.50.

**Figure 6.8** – *Probability of Solving a Puzzle Box by Whether an Individual's Trial Was Interrupted (e.g., Due to Agonistic or Sexual Interactions) for Different Age/Sex Classes.*



*Note*. Density plots per trials not interrupted (blue) and trials interrupted (orange) 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 6.4). Probability scale is reduced, and it ranges from 0 to 0.50.

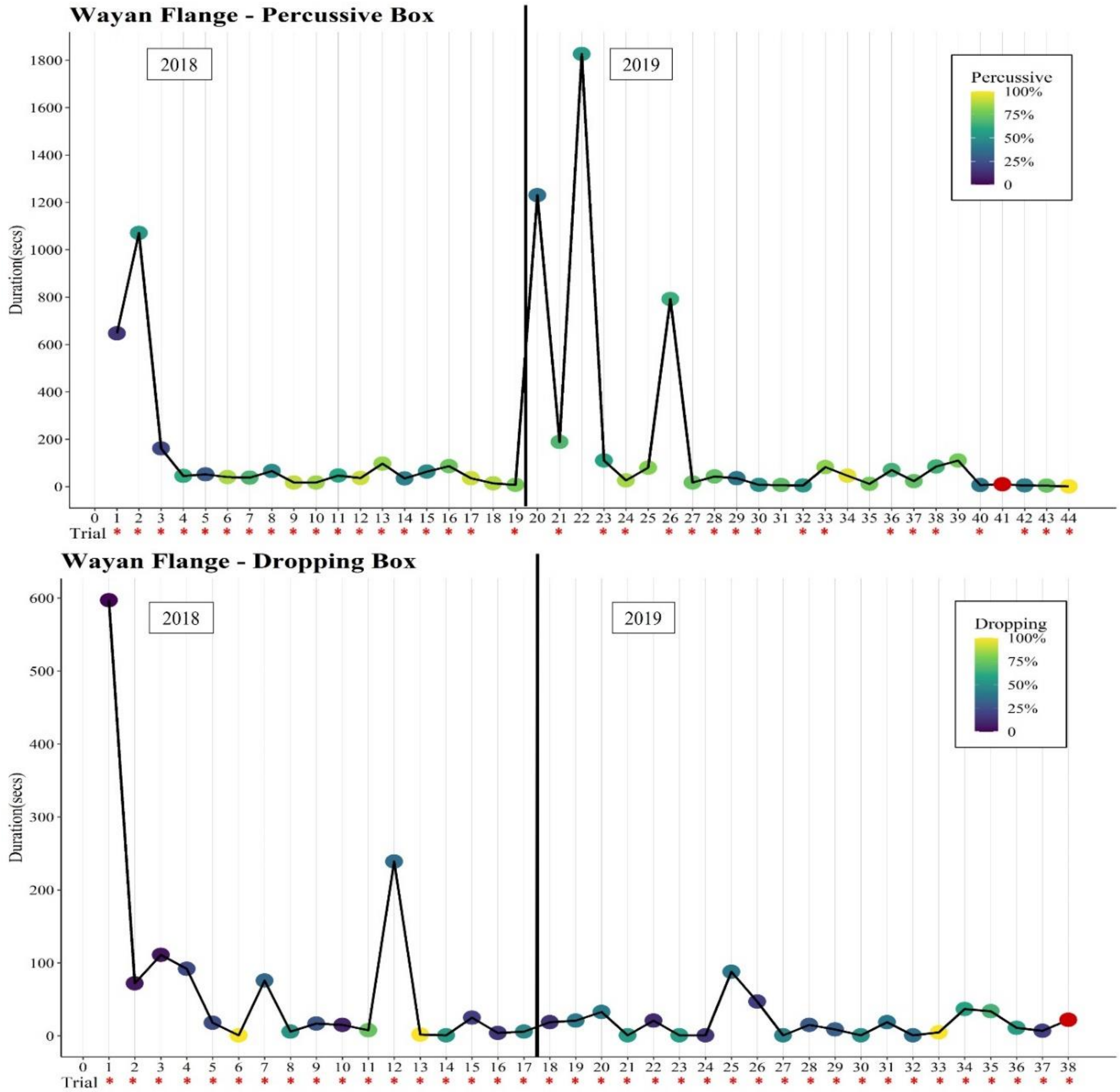
### *6.4.4. Acquisition curves of individuals of different age/sex classes that solved the Dropping box or the Percussive box*

This section describes how several individuals of different age/sex classes acquired the puzzle box solution. Specifically, it provides a 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, which only solved the Dropping box.

#### *First solver for the Dropping box and the Percussive box – Wayan Flange*

Wayan Flange was the first individual to solve both, the Percussive box and the Dropping box; he was a middle-ranking adult male. As shown in Figure 6.9, Wayan Flange solved both, the Percussive box and the Dropping box in his first trial in 2018. For the Percussive box, in his first trial, after extensively manipulating the box with his bare hands, Wayan Flange slammed a large and heavy stone three times on the tile, cracking it, and he used his hands to enlarge the hole and to access the food reward. No other stone-directed actions were performed, other than grasping the stone to inspect the box, and scattering it away at the end to access the food reward.

**Figure 6.9** – *Trial Duration Across Trials for Wayan Flange for Percussive Box and Dropping Box.*




*Note*. Colors represent the relative duration of stone-assisted actions, matching the box type (i.e., Percussive, Dropping; red markers indicate relative duration = 0), within a trial. Vertical black line divides the two study periods, 2018 and 2019. * = successful trial.

For the Dropping box, Wayan Flange had his first trial after solving the Percussive box 15 consecutive times. At first, he reached out for a stone, and he stood in front of the Dropping box, slightly pounding the stone on the side of the box. As the trial proceeded, the pounding actions increased in frequency and duration and became more frantic, interspersed with gathering, rolling, and holding the stone. Eventually, he sat on the top of the box and kept on pounding and pushing stones through the tube. The first stone inserted did not open the box; the second did. He did not realize immediately that the Dropping box was open and eventually got the reward. Because he was the first individual to solve both boxes, there is no evidence for direct observation of the matching action on either puzzle box.

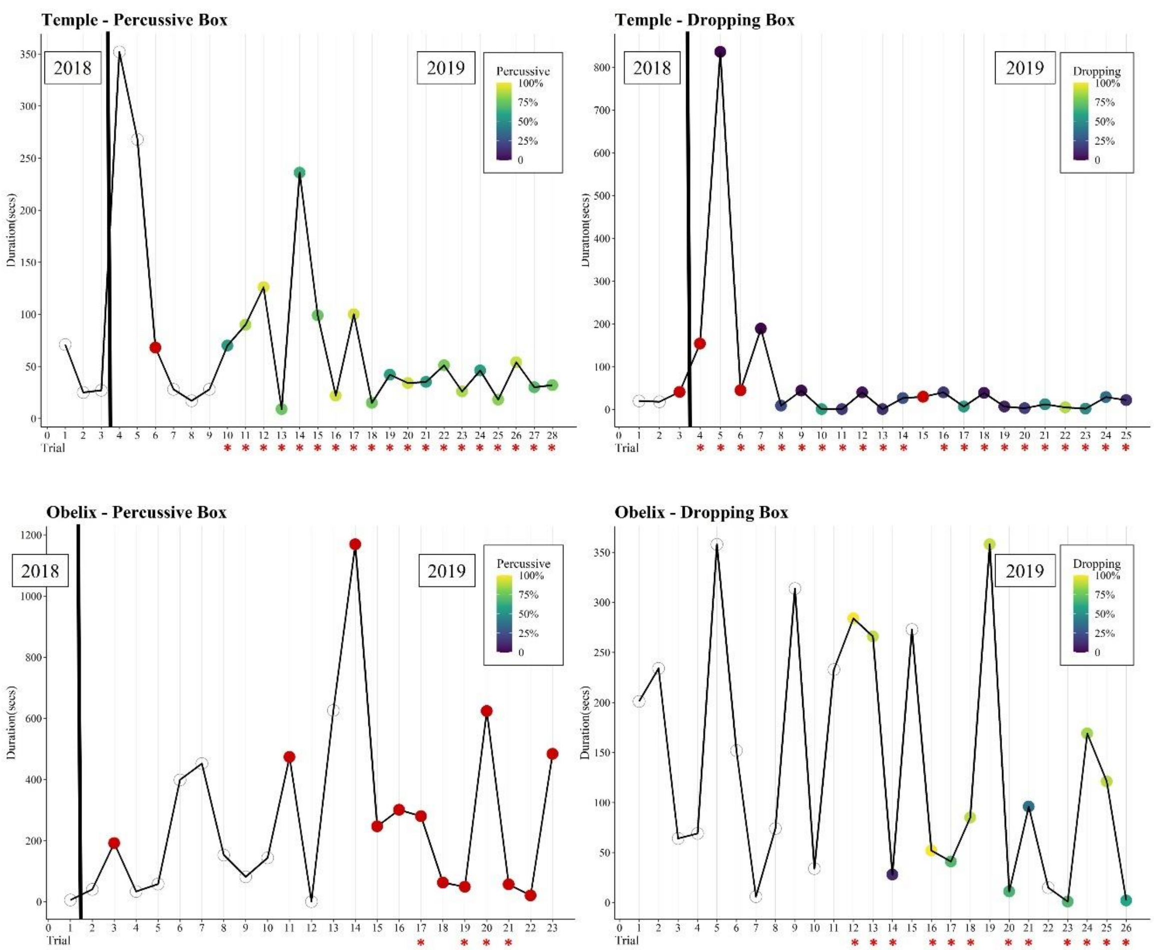
After the first/second trial, Wayan Flange's trial duration dramatically decreased for both, the Percussive box and the Dropping box, and, across subsequent trials, the solution was reached within seconds. Additionally, as the trials proceeded, for the Percussive box, the relative duration of percussive actions increased, with an average of 64.2% (± 22.7%, ranging from 0 to 100%), compared to the 9.0% relative duration of percussive actions observed in Wayan Flange's SH Percussive profile. Similarly, as the trials proceeded, for the Dropping box, the relative duration of dropping actions increased, with an average of 38.1% (± 26.4%, ranging from 0 to 100%), compared to the 0.4% relative duration of dropping actions observed in Wayan Flange's SH Dropping profile. In trial #41 of the Percussive box, Wayan Flange reached out for a stone, but he was shortly after displaced by a more dominant individual that solved the box before him; hence, the relative duration of percussive actions for this trial was 0. A similar explanation applies to all instances in which Wayan Flange did not solve the box.

***Adult males – Temple and Obelix***

Temple and Obelix were two highly dominant adult males; Temple was more dominant than Obelix and he was the beta male of the group. As shown in Figure 6.10, in 2019 Temple and Obelix solved both, the Percussive box and the Dropping box. In 2019, they both started regularly integrating stones after a few trials and shortly after solved the

Percussive box; once they applied stones to the Dropping box, they solved the box within the same trial. After solving both the Percussive box and the Dropping box, Temple's trial duration dramatically decreased, whereas Obelix never reached a plateau in his trial duration. Additionally, the peaks in Obelix's duration were not explained by social constraints (i.e., he was not displaced by more dominant individuals trying to monopolize the box).

**Figure 6.10** – *Trial Duration Across Trials for Temple and Obelix for Percussive Box and Dropping Box.*




*Note*. Colors represent the relative duration of stone-assisted actions, matching the box type (i.e., Percussive, Dropping; red markers indicate relative duration = 0), within a trial. Empty markers indicate trials where no stones were used. Vertical black line divides the two study periods, 2018 and 2019. * = successful trial.

For the Percussive box, Temple never witnessed any individuals solving the box before he solved the first time; a week before solving, Temple witnessed another individual pounding a small pebble and a nut on the tile, but not opening the box. The first time Temple solved the Percussive box, upon arrival there was a large suitable stone on the tile, left by a previous individual, which Temple removed before going to inspect a female. Once back at the box, Temple started manipulating the box with his bare hands; he eventually picked up the same large suitable stone, sniffed it, slammed it on the tile twice, which cracked the tile, rolled it on top, and slammed it again three times, completely cracking the tile and making a hole, before using his hands to lift the broken tile. As the trials proceeded, Temple's pounding actions increased in relative duration, with an average of 73.2% (± 21.8%, ranging from 0 to 95.7%), compared to the 23.3% relative duration of percussive actions observed in Temple's SH Percussive profile.

Similarly, for the Dropping box, Temple never witnessed any individuals solving the box before he first solved it; in 2019, his first trial occurred after he solved the Percussive box eight consecutive times. In 2019, on his first trial (i.e., trial #4), Temple stood in front of the Dropping box, pounding a stone on the floor nearby the box. As the trial proceeded, Temple directed its pounding actions onto the box, which increased in frequency and became more frantic, and he alternated pounding with licking and sniffing the stone, gathering more stones and switching them; he eventually managed to open the Dropping box by pounding, releasing the magnet and collapsing the platform. As the trials proceeded, the relative duration of dropping actions increased, with an average of 20.9% (± 24.2%, ranging from 0 to 88.4%), compared to the 0.8% relative duration of dropping actions observed for Temple's SH Dropping profile. In trial #15, Temple reached out for a stone, but another individual swiftly solved the box; hence, he did not solve the Dropping box.

For the Percussive box, Obelix witnessed other individuals solving the box using percussive actions a few times; however, he never solved the box using percussive actions. His preferred way of solving the Percussive box was by using dropping actions, which he had never witnessed performed by other individuals on the Percussive box. In trials #6, 8, 11, and 12, he managed to open the box using solely his teeth and hands, because the tile was already cracked by other individuals. Eventually, in trial #16, after solving the Dropping box three consecutive times, Obelix solved the Percussive box by dropping. In his previous trial (i.e., trial 15), the day before, he had cracked the tile by dropping a stone, but he was not able to open the box, as he was displaced by Temple. In trial #17, Obelix first gathered stones and dropped them in the experimental area. Eventually, he applied a small stone to the box, and he alternated dropping and rolling actions, before losing interest and leaving the box to inspect a female. Once back at the box, he gathered different stones and repeatedly dropped them on the tile, which eventually cracked the tile; he opened the box by pulling up the tile with his hands. Since his preferred technique was dropping, the relative duration of percussive actions remained 0 for the entirety of trials, compared to the 8.5% relative duration of percussive actions observed for Obelix's SH Percussive profile. When considering dropping actions, the relative duration of dropping actions increased, with an average of 39.4% (± 28.2%, ranging from 0 to 76.1%), compared to the 0.8% relative duration of dropping actions observed for Obelix's SH Dropping profile.

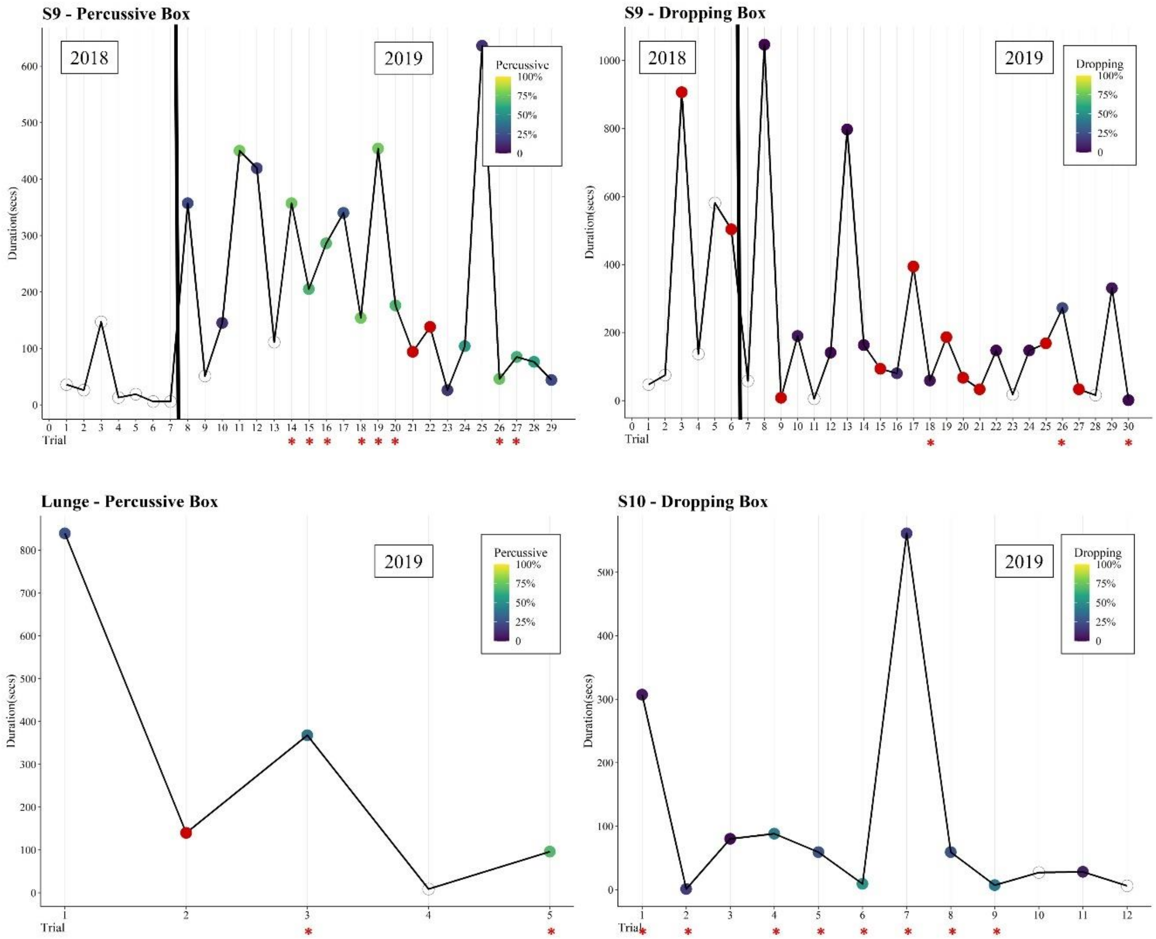
For the Dropping box, Obelix witnessed another individual solving the puzzle box by dropping stones twice. After witnessing the solution, Obelix had several trials at the

Dropping box, and he managed to solve the puzzle box after a month from witnessing. In trial #12, the first time Obelix solved the Dropping box, he manipulated the box with his hands, then losing interest and leaving the box to inspect females nearby several times throughout the entire trial. Eventually, a more subordinate adult male started to repeatedly drop a stone in front of the box and on the side (but never on the top of the box or near the tube). When Obelix came back to the box, he picked up the stone left by the previous individual, placed it on top of the box, and pushed it through the tube; he opened the Dropping box but he did not immediately realize it; he eventually got the food reward. As the trials proceeded, the relative duration of dropping actions increased, with an average of 73.6% (± 26.1%, ranging from 10.8% to 100%), compared to the 0.8% of dropping actions observed in Obelix's SH Dropping profile. In trials #15, 19, and 22 of the Dropping box, Obelix touched the puzzle box but either (a) he did not combine stones with the box or (b) he did not persist long enough to open it (e.g., on one occasion, he inserted a stone by dropping, but the Dropping box did not open and he did not repeat the action with another stone), and eventually he lost interest in the box, leaving to inspect nearby females.

***Adult females – Lunge, S9 and S10***

Lunge, S9, and S10 were three adult females. As shown in Figure 6.11, in 2019 S9 solved both the Percussive box and the Dropping box, whereas Lunge and S10 only solved one box, the Percussive box and the Dropping box, respectively. They all started regularly applying stones to the box after a few trials, but their trial durations greatly differed.

**Figure 6.11** – *Trial Duration Across Trials for Lunge, S9, and S10 for Percussive Box (Lunge and S9) and Dropping Box (S9 and S10).*




*Note*. Colors represent the relative duration of stone-assisted actions, matching the box type (i.e., Percussive, Dropping; red markers indicate relative duration = 0), within a trial. Empty markers indicate trials where no stones were used. Vertical black line divides the two study periods, 2018 and 2019. * = successful trial.

Lunge only had five trials for the Percussive box. She never witnessed any individuals solving the box before her; however, when she first solved it, another individual had been pounding on the Percussive box before she could access the box. She waited in the experimental area for more than 20 minutes, and her trial was interrupted several times due to agonistic and sexual interactions; she then started manipulating a large and suitable stone within the experimental area. When the individual previously monopolizing the box was displaced by a more dominant male, she repeatedly pounded a large stone on the box, she cracked the tile and made a hole. Despite having opened the box by pounding, she was then immediately displaced by a dominant male, who pulled up the tile with his bare hands. As the trials proceeded, the duration of her trials started to decrease and the relative duration of her percussive actions increased, with an average of 33.1% (± 28.6%, ranging from 0 to 68.9%), compared to the 49.8% relative duration of percussive actions observed in Lunge's SH Percussive profile.

For the Percussive box, S9 witnessed individuals solving the box several times, and she then had many trials at the box before she solved for the first time. In trial #14, the first time S9 solved the Percussive box, she extensively manipulated the box with her bare hands; she eventually picked up a large suitable stone, repeatedly pounded it on the tile, which cracked; she then used her hands and teeth to remove the tile, but she was displaced by a higher-ranking male, who accessed the food reward. As trials proceeded, for the Percussive box, the relative duration of her trials, as well as the duration of percussive actions, varied greatly, with an average of 44.4% (±29.0%, ranging from 0 to 77.2%) percussive actions, compared to the 34.1% of percussive actions observed in S9's SH Percussive profile.

Similarly, for the Dropping box, S9 witnessed many individuals solving the box several times, and she then had many trials at the box before she solved the Dropping box for the first time. In trial #18, the first time S9 solved the Dropping box, she displaced a lower-ranking female and started manipulating the box with her bare hands. Eventually she picked up a stone and started pounding on the side of the box; she jumped on top of the box and inserted the stone on the tube, opening the box. As the trials proceeded, the relative duration of her trials varied greatly, and the relative duration of S9's dropping actions always remained low, with an average of 2.6% (± 5.3%, ranging from 0 to 22.9%) dropping actions, compared to the 0.6% relative duration of dropping actions observed in S9's SH Dropping profile.

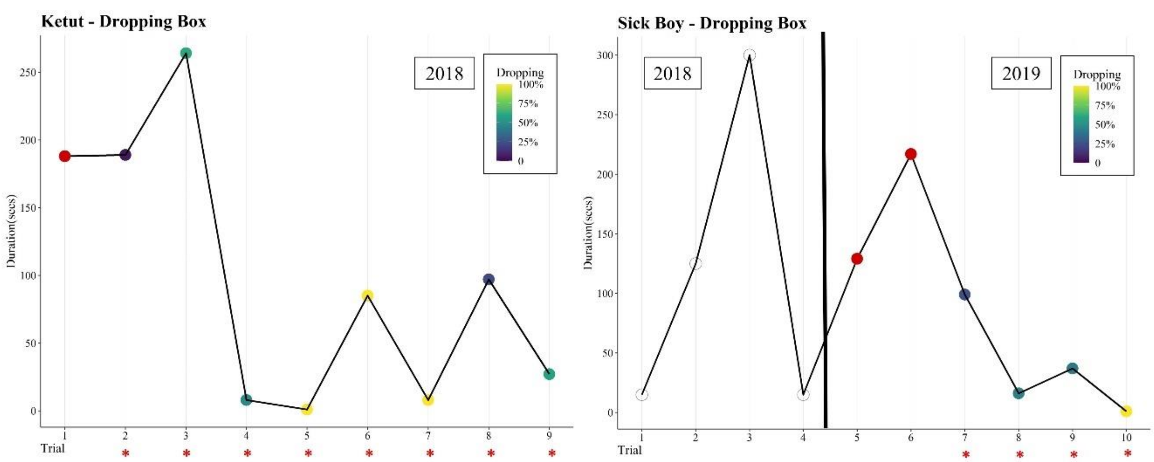
S9 did not consistently solved either the Percussive box or the Dropping box. Failure to solve the Percussive box in trials #17 and 21-25 was due to social constraints, with males or higher-ranking individuals preventing S9 from accessing and thus possibly solving the box, despite her showing sustained interest for the Percussive box. For the Dropping box, on several occasions (e.g., trial #19), S9 could access the box but she failed to solve it because she did not perform a suitable action, and repeatedly pounded the side of the box with a stone. She maintained sustained interest for the box, unless being displaced by other individuals.

S10 witnessed another individual solving the Dropping box four days before her first trial, during which she solved the box. At first, S10 stood in front of the box, sniffing and visually inspecting the box. Then, she reached out for two stones and started manipulating them within the experimental area, alternating pounding, rolling, sniffing and covering actions. She then applied the stone to the Dropping box, alternating pounding, sniffing, and dropping actions onto the box. S10 dropped two stones inside the box and opened the box with the second one; however, she was displaced by a higher-ranking male individual, and she could not access the food reward. The relative duration of her dropping actions fluctuated, with an average of 23.6% (± 17.0%, ranging from 1.7 to 52.2%), compared to the 2.0% relative duration of dropping actions observed in S10's SH Dropping profile. Overall, the relative duration of her trials decreased, with the exception of trial #7, in which she dropped one stone as she arrived at the Dropping box, but the puzzle box did not open, and she was then constrained by the presence of another higher-ranking individual sitting within the experimental area and regularly threatening her as she would get close to the box. Similarly, in trials #3, and 10-12 other individuals, males or higher-ranking ones, monopolized access to the box.

***Juvenile/subadult males – Ketut and Sick Boy***

Ketut and Sick Boy were two juvenile/subadult males, ranking lower than several older males and females. As shown in Figure 6.12, Ketut and Sick Boy solved only the Dropping box. They both immediately integrated stones during their first trial and solved the box within one or few trials; their trial duration decreased after first/second solution.

**Figure 6.12** – *Trial Duration Across Trials for Ketut and Sick Boy for the Dropping Box.*




*Note*. Colors represent the relative duration of stone-assisted actions, matching the box type (i.e., Dropping; red markers indicate relative duration = 0), within a trial. Vertical black line divides the two study periods, 2018 and 2019. * = successful trial.

Ketut never witnessed any individuals solving the box before he solved the first time. The first time Ketut solved the Dropping box, he started handling stones in the experimental area shortly after arriving, rolling and tapping stones on the floor. Eventually, he applied one stone to the box, rolling it up the top and pushing it inside the tube, which opened the box. As the trials proceeded, the relative duration of its dropping actions increased, with an average of 55.0% (± 39.9%, ranging from 0 to 100%), compared to the 5.0% relative duration of dropping actions observed in Ketut's SH Dropping profile.

Sick Boy witnessed individuals solving the Dropping box several times, and he then had a few trials at the box before solving for the first time; the day before solving it, he witnessed another individual solving the box. In trial #7, when Sick Boy solved the Dropping box, he started by manipulating the box solely with his hands; later he combined a stone with the box, attempting to push a large unsuitable stone through the tube. He switched to a smaller stone and after manipulating it on the floor, he switched to two additional stones that he inserted into the tube, opening the box and readily accessing the food reward. As the trials proceeded, the relative duration of its dropping actions increased, with an average of 35.0% (± 37.1%, ranging from 0 to 100%), compared to the absence of dropping actions observed in Sick Boy's SH Dropping profile. Despite their age and their position in the group hierarchy, they were able to consistently solve the box after their first solution, because their trials were not interrupted by the presence of higher-ranking individuals.

## 6.5. Discussion

In this study, we used a combination of descriptive, frequentist, and Bayesian statistics. Despite methodological differences, the convergent evidence from these three different approaches provides a compelling case for the role of SH 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 SH activity (i.e., playful manipulation). 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 SH profile would predict, to some extent, the likelihood to open a puzzle box with stone-directed actions. Specifically, we found that a higher Percussive SH profile predicted an individual's first solution at the Percussive box (Prediction #2 was supported). However, we found that a higher Dropping SH 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 the first time), an individual with a higher box-matching SH profile (i.e., a Dropping SH profile for the Dropping box and a Percussive SH 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 ILVs in generating the solution to the puzzle boxes. In the following sections, we are going to discuss each variable/mechanism separately; lastly, we provide a general discussion of the main findings of this study.

### *6.5.1. The role of SH activity and individuals' SH profiles in the acquisition of stone-tool use*

The key aim of the current study was to evaluate the contribution of the daily expression of SH activity in the performance of a foraging task, whose solution required the use of stones as tools. In line with a perception-action approach (i.e., that spontaneous manipulation of objects provides opportunities for individuals to familiarize 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 SH profile contributed to predicting (a) the first solution to the Percussive box, and (b) the overall solutions to both the Dropping box and the Percussive box. Specifically, an individual with a higher box-matching SH profile (e.g., a Percussive SH profile for the Percussive box) was more likely to solve the corresponding box, compared to an individual with a lower box-matching SH 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 SH 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 SH 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., SH profiles) may contribute to the emergence of tool use. A recent conceptual analysis by Leca and Gunst (accepted) offers a compelling hypothesis for how SH activity holds an exaptive potential for 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 SH behavioral repertoire of the population we studied may have been co-opted into tool use in a sexual domain (Cenni et al., 2020, 2022). In line with the exaptive potential of SH activity, the stone-directed actions directed at the puzzle box to release the food reward may constitute another example of SH actions co-opted into tool use, this time in a foraging domain.

As previously mentioned in 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. This is in line with the view that behavioral innovation, like some forms of tool use, may emerge from accidental circumstances, provided the rightful conditions (*context*, *coincidence*, *consequence*, Wasserman, 2021). For instance, in Japanese macaques, an adult female was repeatedly observed flossing her teeth with hair, and although this tool-assisted behavior 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., 2010c). In our case, object play (and SH activity more specifically) may provide a large pool of behavioral 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 behavioral 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 behavior. Indeed, stone-directed actions by juvenile/subadult males seemed less frantic, less focused on 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 behaviors 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 (Cenni, personal observation; see Supplementary Material S6.2). 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 SH profile in comparison to the Dropping SH profile in predicting the likelihood of solving a puzzle box with stones. 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 SH behavior. SH behavioral patterns that comprise the behavioral macro-category Dropping have been documented in the daily practice of the SH repertoire of Balinese long-tailed macaques living in Ubud (Bunselmeyer, 2022; Pelletier et al., 2017). However, when looking at the distribution of dropping actions across individuals, these actions were much less frequent than other behavioral macro-categories, such as percussive actions (i.e., Dropping SH profile 2018: 1.1% ± 2.4%, Dropping SH profile 2019: 0.9% ± 2.1%, Percussive SH profile 2018: 7.4 % ± 10.3%, Dropping SH profile 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 SH 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 SH behavioral patterns and SH behavioral patterns that constitute a larger proportion of individuals' SH repertoire, such as "tapping". However, possible ceiling effects should be avoided by not choosing SH behavioral patterns that are frequently expressed by most individuals and for which there would be little or no variance.

### *6.5.2. 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 (a) individuals 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 (b) persistent behavior, 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 percussing the Percussive box with a stone to open it). Indeed, we found that when an individual lost interest in the puzzle box (e.g., inspected or mounted nearby females), its likelihood to solve the box decreased. For instance, as shown in Figure 6.10, 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 other individuals' that habitually solved the box is

Obelix's frequent loss of interest for the puzzle box, mainly to inspect nearby females, and the 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 behaviors 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) behavior (Yerkes, 1907). As a result, much attention has been given to the motivators associated to the task. 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 behaviors (Sol et al., 2011). Specifically, previous studies have shown that behavioral 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 SH activity and the high degree of inter-individual variation and (to some extent) intra-individual consistency found in the expression of SH activity in this population (Cenni et al., in review). Object play is by definition intrinsically motivated and varying levels of predisposition to engage in SH behavior 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).

### *6.5.3. Social influences and social learning*

To our knowledge, this is the first experimental study to assess the validity of the Affordance Learning theory in an ecologically relevant model. We investigated the non-mutually exclusive contribution of social influences in the acquisition of task solutions. 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 for 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 percuss a stone onto the cement tile, and several actions might be needed to crack the tile and access the food reward. As an individual is percussing the tile, other witnesses might lose interest and disengage visual attention with 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, there is a minimum physical strength required to access the Percussive box (see section "6.5.4. Physical and social constraints"). This may explain why no juvenile/subadult individuals solved the Percussive box. Additionally, a minimum duration is needed to access the food reward in the Percussive box because an individual (often) has to repeatedly percuss a stone on the tile to crack it. Each action produces a loud sound that is likely to attract more dominant 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). It is thus likely that social influences mediated the acquisition of the solutions to the Dropping box and the Percussive box.

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), the majority of monkeys saw direct solutions to both puzzle boxes, but even when given the opportunity (i.e., when having a 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. Thus, social influences alone do not explain success at the puzzle boxes. Additionally, 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.

Keas (*Nestor notabilis*) are endemic parrots of New Zealand renowned for their playfulness and problem-solving abilities but not known to habitually use tools in the wild (but see Goodman et al., 2018 for an example of tool use in a wild population of keas). In a study by Gajdon and colleagues (2011), keas were tested on their social learning abilities in a tool use task. In comparison with keas that did not have access to a skilled conspecific demonstrator, keas that observed another skilled conspecific were faster at solving the box. However, after initially relying on social information, keas' overt exploration led animals to vary their behavior in favor of individual solutions (Gajdon et al., 2011). In another study on the same group of keas, previous playful insertion of objects into an empty tube predicted later insertion of objects into the tube when a food reward was added, suggesting that their intrinsic propensity to play with objects may have led the birds to use these objects as tools (Gajdon et al., 2014).

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 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.

#### *6.5.4. 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 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. It is likely that to open the Percussive box, sufficient strength and motor coordination are required; similar developmental pathways are observed in the acquisition of instrumental object manipulation in habitually tool-using species. In the case of nut-cracking behavior performed by capuchin monkeys, it takes more than two years to gain the necessary motor coordination and physical strength required to master the behavior (de 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. Although a higher dominance rank was not associated with a higher likelihood to solve the box, we found little 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 in 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 behavioral 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.

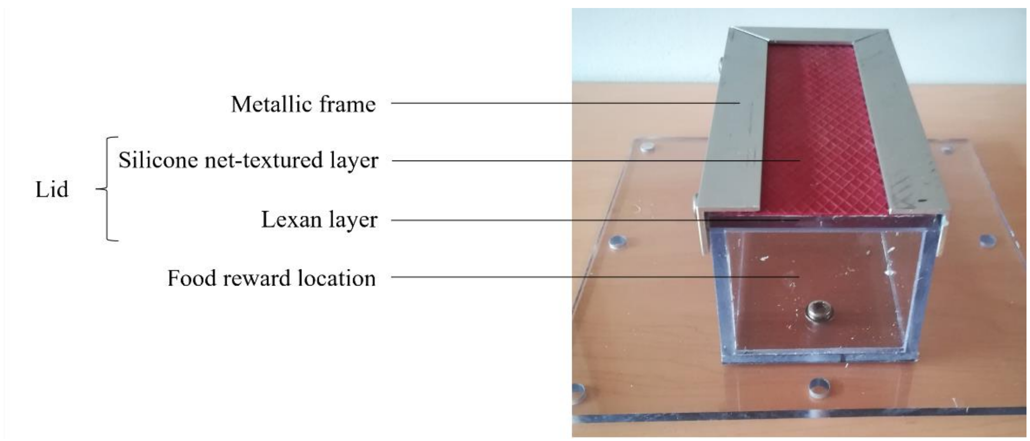
In conclusion, because of the shorter time required to open the Dropping box (i.e., in most cases one suitable stone would open the box in a single insertion), and the looser constraints associated with the physical requirements to solve the Dropping box, it is not surprising that more individuals solved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

### *6.5.5. General discussion*

Taken together, our results highlight the complex interplay between many ILVs in the acquisition of stone-tool use in this population of long-tailed macaques. The interaction of several ILVs may explain why only 15% of individuals that participated in the field experiments solved the puzzle boxes using stones. Nonetheless, our study provides some support for the Affordance Learning theory, suggesting that qualitative and quantitative differences in SH activity affect the expression of tool use. In our investigation, we considered SH profiles as continuous variables, rather than identifying a threshold for a *high* SH profile for a specific macro-category (e.g., a high Percussive SH profile). We believe this approach is a powerful way to circumvent the differential expression of SH behavioral actions across individuals. Indeed, some SH behavioral actions (e.g., “Clack”) are rare across individuals, and when they are expressed regularly, they still constitute a small proportion of SH actions in an individual’s repertoire compared to other SH behavioral patterns (Cenni et al., in review). In line with the Affordance Learning theory, future studies should examine whether an individual’s SH *versatility* (Cenni et al., 2021; Cenni et al., in review) predicts the expression of stone-tool use, and whether differences in SH *versatility* reflect the performance of groups that habitually perform SH behavior, and groups in which SH is absent, or expressed to a lower extent (in terms of frequency and complexity).

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 x 15 x 10 cm with a metallic frame on its top part, through which a lid was inserted to close the box (Figure 6.13). The lid consisted of a Lexan layer of 30 x 15 x 1 cm, on top of which a thin net-textured silicone layer was glued. Inside the box, there was a highly prized food reward (e.g., pieces of fruit, or raw egg), which could be accessed by sliding the lid through the metallic frame with the use of stone(s) rubbed against the lid. Due to the net texture, the friction generated by rubbing actions with suitable stones (i.e., stones with a grainy texture) would facilitate the opening of the box with stones.

**Figure 6.13** – *Rubbing Box.*




However, during experimental events with the Rubbing box, we repeatedly encountered several problems associated with the malfunctioning of the Rubbing box (e.g., dirt gathered by individuals while manipulating the Rubbing box would jam the sliding mechanism, repetitive pounding actions on the metallic frame would press and block the sliding lid). Thus, we excluded the Rubbing box from this study. We acknowledge the possibility that during experimental events with the Rubbing box, individuals may have acquired information from (a) the manipulation of this puzzle box and (b) the witnessing of other individuals solving this puzzle box, which may have contributed to explaining the solving of other puzzle boxes. More attention will be given in future attempts to designing experimental apparatuses with less chances of malfunctioning.

Lastly, another avenue to explore how stone-assisted actions differ across contexts (specifically, between the expression of SH activity and 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., Chappel & Kacelnik, 2002; Visalberghi et al., 2009). We have previously mentioned that the expression of specific SH behavioral patterns is likely to be arbitrary, and monkeys use stones of different sizes and textures to perform SH behavior (Cenni et al., 2021). However, during the instrumental expression of stone-assisted self-directed genital tapping and rubbing, adult females of this population 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, Cenni et al., 2022).

# CHAPTER 7: GENERAL DISCUSSION

This chapter contains excerpts from the following article: Cenni, C., & Leca, J.-B. (2020). Technical intelligence hypothesis. In J. Vonk, & T. K. Shackelford (Eds.), *Encyclopedia of Animal Cognition and Behavior*. Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_103-1. Authors' contribution: C. Cenni: Conceptualization; Writing - Original Draft; J.-B. Leca: Supervision; Writing - Reviewing and Editing.

"It would be perverse to argue that nothing was learnt in play, since inevitably play brings […] experience with objects, and peers, the main sources of developmental experience. However, play is not the only way of getting experience with objects and peers, unless we define play so broadly that the concept becomes meaningless."

P. K. Smith (1988, p. 223)

In this thesis, I investigated the proximate underpinnings of different forms of object manipulation in the context of the SH behavioral tradition in a population of free-ranging provisioned Balinese long-tailed macaques. This concluding chapter provides an opportunity to review the main findings of this thesis in light of their broader implications for our understanding of the proximate (and ultimate) links between object play and tool use. In the last section, I reflect on some of the limitations of this project, and how they can inform future research.

## 7.1. What is the role of object play in the *expression* of tool use?

Even though the "play ethos" has imbued many theories on the origins and evolution of tool use, empirical findings have often failed to validate these views (cf. Smith, 2010). In children, lure-retrieval tasks, in which out-of-reach objects can be recovered with the use of tools (i.e., sticks and clamps) have been primarily used to experimentally test the putative facilitatory role of object play in the expression of innovative problem solving with objects (i.e., tool use; P. K. Smith, 2010). After acknowledging potential methodological confounders, including experimenter biases, selective interpretation of results, and inadequate control conditions (see Lillard et al., 2015; P. K. Smith, 1988), studies that initially found support for the role of previous playful manipulation in the instrumental use of objects in subsequent testing (e.g., P. K. Smith & Dutton, 1979; Sylva et al., 1976) could not be replicated (e.g., Simon & P. K. Smith, 1983; P. K. Smith et al., 1985). Correlational studies aiming to adopt a more naturalistic and ecologically relevant approach found that in children observed over an entire school year, preschoolers that spent more time in free construction activities were better at solving lure-retrieval tasks (Pellegrini & Gustafson, 2005). Hence, a more adequate methodological design might unravel the facilitatory effects of object play, if any, in the expression of tool use.

Allison and colleagues (2020) investigated the relationships between object play and innovative problem-solving in two otter species. Specifically, they tested whether rock-juggling behavior, a form of SH 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 (a) Asian small-clawed otters, a species that habitually use stones as tools to forage on crabs and shellfish (Kruuk, 2006), and (b) smoothed-coated otters, for which stone-tool use is not documented (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 (which solution 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). Taken together, these results suggest that the relationship (if any) between object play and tool use is not straightforward and is mediated by several factors, and thus, "that the theoretical framework behind the 'play ethos' is, in part at least, incorrect" (P. K. Smith, 1988, p. 221).

In line with the results of this thesis, 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 *variety* of and *preference* for certain actions expressed. Specifically, in Chapter 2, I found that the expression of SH behavior differs across individuals in qualitative and quantitative features, and that these differences are, to some extent, repeated over time in Balinese long-tailed macaques. Interestingly, differences in individual SH repertoires are largely independent of age and sex, which indicates that SH behavior in long-tailed macaques may have an individual signature (i.e., individuals have a unique SH profile). In Chapter 6, I used this inter-individual variation in the expression of SH to test whether qualitative and quantitative aspects of an individual's SH profile would predict the instrumental use of stones to open novel food-baited puzzle boxes. Additionally, I explored which individual attributes, other than SH profile, both at the asocial and social levels, contributed to inter-individual differences in the ability to solve the puzzle boxes. Lastly, I described the acquisition curves of individual solvers of different ages and sexes. I found that, although the solution of the puzzle boxes was overall unlikely – with only 15% of the individuals solving the puzzle boxes with stones – the solvers' stone-assisted actions directed at the box were instrumental, and, to some extent, a solver's box-matching SH profile was correlated with the likelihood of opening the puzzle box.

Additionally, social influences, motivational processes, as well as physical and social constraints affected the likelihood of solving a puzzle box. Taken together, these results suggest that there is a proximate relationship between object play and tool use, but that (a) there is substantial inter-individual variation in how object play and tool use may be connected, and (b) the links between these two activities are mediated by a number of confounding factors (see also Bjorklund & Gardiner, 2011; Vandenberg, 1981). Specifically, the behavioral flexibility associated with play and the affordance learning process arising from the action-outcome contingencies of specific behavioral patterns applied to certain objects may explain the relationships between these two activities.

In experimentally-induced innovative problem-solving situations, which tool use may be an example of, behavioral flexibility is consistently found to be a key predictor of an individual's success (Griffin & Guez, 2014). Interestingly, behavioral flexibility in the context of innovative problem-solving experiments is usually claimed to be indicative of trial-and-error learning (e.g., Sol et al., 2012). For instance, in a study aimed to investigate innovative problem-solving in wild hyenas, Benson-Amram and Holekamp (2012) compared the shape of the learning curves across individuals to infer task acquisition via trial-and-error, as the curves smoothly lowered over time, suggesting that individuals gradually figured out the box solution across multiple trials. However, in the context of tool use, behavioral flexibility associated with object play may constitute the raw material that facilitates the expression of tool use via affordance learning. To assess whether this is the case, we can look at the shape of individuals' learning curves: "[i]f the curve was steep and smooth, this might suggest the occurrence of insight learning" (Benson-Amram & Holekamp, 2012, p. 4092).

Insight learning is defined as a sudden *understanding* of a problem manifested by its solution (Köhler, 1925). A textbook example of insight learning was proposed by Köhler (1925) who observed captive chimpanzees solving novel problems (e.g., using objects as tools to access out-of-reach food) and attributed this solution to an individual's causal understanding of the problem. However, since then, results from experimental studies aiming to explain insight learning have challenged this view (e.g., Neilands et al., 2011), under the argument that "once we begin exploring the actual mechanisms that animals use to negotiate their worlds, it becomes very hard to decide where "perception" ends and "cognition" starts" (Barrett, 2011, pp. 55-56). In other words, the apparently sudden appreciation of a problem may be largely explained by affordance learning, with an individual's previous experience and familiarization with (some of) the properties of (part of) the problem playing a crucial role in how that individual responds to novel problems. Thus, the behavioral flexibility associated with (object) play (Burghardt, 2005), together with the individual preference for specific actions, could serve as a pool of raw behavioral materials for exaptive solutions to emerge (i.e., stone-tool use; Leca & Gunst, accepted).

Taken together, the results of this thesis provide some support for this view. First, in Chapter 2, I found that behavioral flexibility, expressed as SH *versatility* (i.e., the total number of different SH behavioral patterns expressed by a given individual) showed substantial inter-individual variation. This suggests that the behavioral flexibility associated with object play is individual-specific. Thus, individual differences in how variable SH is may contribute to explaining the differential acquisition of stone-tool use. Second, social influences (through direct observation or stimulus enhancement) only partly predicted the solution of the puzzle boxes, whereas an individual's SH profile, which could be regarded as a behavioral proxy for the degree of familiarity with specific stone-directed actions that are relevant to open the puzzle boxes, was likely to explain the likelihood of solving the puzzle boxes (Chapter 6). Third, once individuals incorporated stones into their box-directed actions, the solution was reached within a few trials, with only a few types of stone-assisted actions directed at the puzzle boxes (Chapter 6). Thus, the apparent *insight* associated with the solution to the puzzle boxes (as shown by the learning curve of the individual named "Wayan Flange") may be a result of an affordance learning process, gained through the appreciation of the properties of stones after being routinely used by specific individuals in arbitrary and sometimes in idiosyncratic ways.

At this stage, more analyses are needed to fully assess the validity of this interpretation. In a systematic attempt to test whether affordance learning explains the acquisition of stone tool use as part of the solution to these puzzle boxes, future studies should explore the specific role of behavioral flexibility, measured by SH *versatility*, in the expression of stone tool-assisted actions, by examining whether (a) an individual's SH *versatility* in the context of SH behavior and (b) SH *versatility* associated with an individual's first combination of stones with the puzzle boxes correlate with the opening of the puzzle boxes with stones. Due to the complex interplay among individual attributes in predicting the likelihood of solving the puzzle boxes (Chapter 6), and the high inter-individual variation in SH behavior (Chapter 2), future studies should carefully analyze the learning curves of individuals separately, rather than as an average (cf. Benson-Amram & Holekamp, 2012). Indeed, different learning strategies are likely to be adopted depending on individual characteristics, such as age, sex, and dominance status (see Slater, 1981).

## 7.2. What is the role of object play in the *evolution* of tool use?

Among the many explanations proposed to justify the increased relative brain size and intelligence across various animal taxa, the Technical Intelligence hypothesis holds that material innovations and object-oriented behavioral skills (e.g., caching and recovering non-perishable food, detecting and extracting encased food, making and using tools, building shelters) constitute major driving forces for the selection of cognitive features that sustain such complex and flexible technical proficiency (R. W. Byrne, 1997). The Technical Intelligence hypothesis aims to provide a mechanistic and functional explanation for the evolution of intelligence in humans and non-human animals. Technical innovations, based on the ability to combine and use inanimate objects sequentially and instrumentally to solve a variety of problems in the physical domain, may have created higher cognitive demands that favored an increase in the encephalization quotient (i.e., brain-to-body weight ratio after controlling for allometric effects as well as the size and organization of specific brain components, such as the neocortex, which are broadly considered neural proxies for intelligence; R. W. Byrne, 1997).

In support of the Technical Intelligence hypothesis, cross-species comparative analyses showed a strong positive correlation between relative brain size of birds and primates and their ability to use different objects in novel, instrumental, and flexible ways (Overington et al., 2009; Reader & Laland, 2002). More encephalized primate species (i.e., those with a bigger "executive brain," including larger neocortex and striatum) exhibited more tool use in a foraging context than less encephalized ones (Lefebvre, 2012). In primates, nontechnical innovations also showed positive correlations with relative and absolute brain size, but those relationships were not direct; they were mediated by additional factors, such as social learning, diet, and life-history variables (Navarrete et al., 2016). For instance, dietary generalism (i.e., a broad selectivity for different food resources) predicted enhanced encephalization, suggesting that the ability to exploit novel food sources may have led to an increase in brain size.

In cognitive tasks testing for physical cognition, causal reasoning, working memory and self-control, tool-using bird species generally outperform closely related non-tool-using species, with some exceptions (Teschke et al., 2013). Advanced forms of sensorimotor intelligence have also been found in non-tool-using animal species that show flexible extractive foraging techniques (e.g., keas, a New Zealand parrot species, exhibit outstanding performance in several physico-cognitive tasks, suggesting good understanding of the physical properties of objects; Huber & Gajdon, 2006). Indeed, it is not the *fact* that animals use tools, but the *way* they use them (i.e., in a hierarchically organized sequence of actions) that may shed light on the sophisticated cognitive abilities underlying complex extractive foraging strategies (R. W. Byrne, 1997). Recent findings from phylogenetic neuroanatomical studies challenge the relationship between tool use and relative brain size in birds, suggesting that many of the tool-using species tested also engage in various forms of play, and that play behavior (mainly social play, but to a significant extent non-social play, to which object play belongs), and not tool use, may be driving increased cognitive capacity (Kaplan, 2020). Specifically, when controlling for play behavior, there is no relationship between the presence of tool use and larger relative brain size in birds, but larger relative brain size is associated with the presence of play behavior (including object play; Kaplan, 2020).

In a wide range of animal taxa, functional/“serious” technical innovations (e.g., tool use) and purposeless/“playful” object-oriented actions covary in their frequencies and share broad structural similarities. For example, object play behavioral patterns and tool use actions are significantly more frequent, diverse, and complex in chimpanzees than in their sister species, bonobos, even in similar natural habitats (Koops et al., 2015a,b). Likewise, within the corvid taxon, there is a high degree of cross-species covariation between material neophilia (i.e., object-directed explorative tendencies and the propensity to engage in versatile and complex object play) and physico-cognitive abilities (i.e., mechanical problem-solving strategies, extractive foraging techniques, and tool use proficiency; Huber & Gajdon, 2006). However, the nature of the evolutionary links between various object-directed activities is far from being unravelled.

On the one hand, object play behavior may have driven the selection for the functional manipulation of objects by providing pre-existing schemata transferable to instrumental contexts (S. T. Parker & K. R. Gibson, 1977). Non-instrumental exposure to, and handling experience with, objects provide opportunities to learn about the properties and affordances of these objects, and help refine sensori-motor coordination, through the acquisition and practice of manipulative dexterity (Lockman, 2000). In the Sonso chimpanzee community in Uganda, a gradual decrease in interest in, and limited spontaneous manipulation of, sticks may explain the lack of stick-assisted tool use; individuals preferentially explored other objects that were later used as tools, such as leaves, vine, sapling, and branch (Lamon et al. 2018). Similarly, Kenward and colleagues (2011) compared the development of non-instrumental object manipulation (i.e., object handling that is not immediately functional) in New Caledonian crows, a tool-using species, and in common ravens, a species that does not seem to use tools in the wild. They found no significant difference in the rates of noncombinatorial object manipulation, which probably results from a general and inherited manipulative tendency in all corvids. However, plastic object-directed playful sequences involving object combinations (e.g., object positioning, inserting, or rubbing in relation to other objects or a substrate) that are considered behavioral precursors of later functional manipulation (e.g., tool use) became significantly more frequent in New Caledonian crows than in common ravens during critical stages of development (Kenward et al. 2011).

On the other hand, the intrinsic propensity to manipulate objects could facilitate the emergence of technical innovations by maintaining high levels of sustained interest in, and attention to, objects. Intrinsic motivation for object manipulation may promote the integration and functional use of objects in various behavioral technical domains. In primates, tool use acquisition is a lengthy process, in which learners only start reaping extrinsic rewards for their actions after years of unsuccessful practice (e.g., stone tool-assisted nut-cracking behavior in chimpanzees and capuchin monkeys; Fragaszy et al., 2013; Lonsdorf, 2006). In the meantime, the intrinsically rewarding nature of non-instrumental object manipulation, including object play, characteristic of immature individuals, may serve the function of maintaining high levels of motivation in unskilled learners. For example, the playful manipulation of lithic material by juvenile monkeys precedes the acquisition of stone tool-assisted shellfish foraging in a free-ranging and coastal population of Burmese long-tailed macaques in Thailand (Tan, 2017).

As opposed to instrumental object manipulation which is *product-oriented*, object play is a *process-oriented* activity during which the performer acquires information about how a specific action can be performed and what object(s) can be involved in the expression of this action. It is acknowledged that problem-solving performance depends on an individual's motivational state, with low levels of extrinsic motivation being generally associated with poor performance. However, high levels of extrinsic motivation may also reduce an individual's technical performance, by narrowing its attention towards the product, target, or goal, rather than the process to achieve them. A comparative experimental study in great apes showed that learning about action–outcome contingencies preferentially happened during free exploration, whereas the presence of a food reward during the baited-condition distracted the subjects and delayed the acquisition of the solution to the problem (Ebel & Call, 2018).

In the case of SH expression, pleasurable or other self-rewarding mechanisms, such as those underlying playful activities (cf. Burghardt, 2005), may enhance the motivation to engage in SH activity, through the pleasurable tactile feedback possibly obtained from the performance of this form of object play. These proximate factors may be part of the main motivational processes responsible for the maintenance and the transformation over time of this behavioral tradition in macaques (Huffman, 1996). Additionally, these features may have enhanced the motivation to perform genital stone-tapping/-rubbing, thereby facilitating the co-optation of these two SH behavioral patterns into stone-tool use in a sexual context in Balinese long-tailed macaques. The results from Chapter 4 and 5 support this view. Specifically, in Chapter 4, I found that, when performed by males, SH sequences with genital stone-tapping and -rubbing were structurally different from SH sequences without these actions. SH sequences without genital stone-tapping and -rubbing were more exaggerated and, to some degrees, more repeated than SH sequences in which these actions were present, with exaggeration and repeatability being intrinsic characteristics of play behavior (cf. Burghardt, 2005). In Chapter 5, I found that genital stone-tapping and genital stone-rubbing actions are distinctly motivated from other SH behavioral patterns, in the sense that the former are sexually motivated. Genital stone-tapping and -rubbing immediately preceded the beginning of a fully-fledged penile erection, lasted longer in the presence of penile erection, and were expressed within a sexual context in juvenile/subadult males. Additionally, there was some degree of selectivity in the stones used by adult females to perform these actions. Taken together, the results from these two chapters provide strong evidence that in Balinese long-tailed macaques, at least two stone-directed actions, namely the repetitive tapping and rubbing of stones onto the genital area, have been co-opted into stone-tool use within the sexual domain, and can be construed as a form of self-directed tool-assisted masturbation. Overall, these findings support the view that a number of behavioral patterns performed during playful activities (like SH) are shared with (i.e., co-opted from, or exapted into) other behavior systems (e.g., sex, conspecific aggression, foraging; Cenni et al., 2020, 2022; Leca et al., 2008a; Pelletier et al., 2017; Pellis et al., 2019).

Given the cultural nature of SH behavior and its phylogenetic distribution in the *Fascicularis* group (Leca et al., 2007a; Nahallage et al., 2016), SH is an ideal behavioral candidate to test the Technical Intelligence hypothesis. Future comparative research should replicate this study design in other populations of Balinese long-tailed macaques living under similar ecological conditions (i.e., relaxed selective pressures on foraging; Leca et al., 2008b, cf. Leca et al., 2007a). Such an endeavor may allow researchers to assess (1) whether experimentally-induced stone-tool use can spontaneously emerge in these groups, independently of their SH status (presence or absence of SH, and group-specific SH form), (2) whether the expression of instrumental object manipulation (i.e., stone-tool use) covaries with the presence or absence of SH activity, as well with quantitative and qualitative features of SH or (3) whether stone-tool use is primarily explained by a species' cognitive repertoire in the physical domain (Tennie et al., 2009).

## 7.3. What is the role of *objects* in the expression and evolution of object play and of tool use?

In Chapter 3, I investigated how a specific property of the object being manipulated (i.e., stone size) affects the expression of stone-directed actions across individuals of different age and sex classes. The results from this investigation showed that, despite the intrinsic arbitrariness often associated with the expression of playful actions (Leca et al., 2011; Leca, 2015), stone size affects the variety and duration of certain SH behavioral patterns performed by a given individual. Interestingly, there were no significant differences between small and medium stones in terms of SH *versatility* and duration of the action "Pound"; this result is in line with the view that playful manipulation has an intrinsic motor abundance in its expression, meaning that the sensori-motor constraints underlying the performance of playful actions are, to some degree, looser than those underlying the performance of instrumental actions (cf. Burghardt, 2005; Latash, 2000). Overall, the expression of SH behavior in Balinese long-tailed macaques is mediated by intrinsic and extrinsic factors, such as individual preference for the expression of certain SH behavioral patterns and the physical properties associated with the stones used to engage in this form of object play.

These findings are important to understand the ecological underpinnings of population-specific SH traditions. The affordances associated with particular objects (here stones) may provide opportunities (or lack thereof) for action, which may contribute to maintaining the expression of specific stone-directed actions in certain populations of macaques (J. J. Gibson, 1979; cf. Cenni et al., 2021). Even though stone availability or the relative exposure to them before acquisition per se is not a sufficient condition for SH behavior to emerge (Nahallage & Huffman, 2007a; Leca et al., 2008c), the performance of certain SH behavioral patterns, particularly stone-assisted percussive/rubbing actions, can leave physical traces on the surfaces, stones, and other objects involved in SH activity, which contribute to creating a lithic landscape that may facilitate the cross-generational transmission and transformation of the SH tradition (Huffman & Quiatt, 1986; Leca et al., 2007b; 2010a, 2012; Nahallage et al., 2016; Pelletier et al., 2017). Future research should further explore the role of object affordances in the expression and maintenance of object play and tool use. First, it should be assessed whether (and if so, how) individual preferences in the expression of SH behavioral patterns covary with the constraints associated with the stones being manipulated. Specifically, it is important to consider whether an individual's preference in the expression of playful object-directed manipulation is influenced by the physical characteristics of the objects, or if the preference for certain object-assisted actions performed by an individual overcomes the affordances and constraints associated with the objects (i.e., action expression is only moderately affected by the object when an individual's preference is accounted for). Second, object selectivity is a crucial component of instrumental object manipulation, and optimal selection of the most suitable object is expected when performing instrumental actions (e.g., Fragaszy et al., 2010; Gumert & Malaivijitnond, 2013). Thus, future analyses should investigate whether during field experiments aiming to induce stone-tool use (like the ones conducted in Chapter 6), individuals (a) selected suitable stones more than non-suitable stones (while controlling for confounding factors, such as familiarity with stones and proximity), and (b) whether the selected stones affected the types of actions performed on the puzzle boxes. In Chapter 5, we found moderate degrees of stone selectivity in stone-tool use within the sexual domain in adult females, which preferentially performed genital stone-tapping and -rubbing with angular and sharp stones. Given the questionably adaptive nature of genital stone-tapping and -rubbing as a form of self-directed tool-assisted masturbation, a higher degree of selectivity is expected in subsistence-related behaviors, such as those performed in the foraging domain.

### 7.4. Limitations

This thesis combines findings from observational and experimental studies conducted in free-ranging Balinese long-tailed macaques; as a result, the relatively high ecological validity of this research (compared to studies conducted in laboratory settings) was constrained by a number of challenges inherent to field studies (see Morand-Ferron et al., 2016). One of the crucial limitations of several analyses presented in this thesis was the absence of a *true* baseline of SH behavior across individuals. Due to the time constraints associated with the data collection, individual SH profiles were collected throughout the entire study period (i.e., across two years). Similarly, field experiments aiming to test whether stone-tool use would emerge in the foraging domain were conducted during the same period and overlapped in time with the data collection of individual SH profiles. Therefore, we have no information on whether the field experiments involving food-baited puzzle boxes whose solution required stones to be used as tools affected an individual's expression of SH behavior during the period of data collection. However, this limitation is mitigated by two pieces of argument. First our results showed that individuals are, to some degree, consistent in their own SH repertoire (i.e., in terms of SH *versatility*, SH *evenness*, and SH *preference*; Chapter 2) and SH profiles did not differ between 2018 and 2019 (Chapter 6). Second, SH behavior is a well-established and relatively stable cultural practice in the Balinese long-tailed macaques living in Ubud (Pelletier et al., 2017). Thus, we suggest that the presence of the puzzle boxes did not (or only minimally) affect an individual's SH repertoire. However, future investigations in other macaque populations should strive to collect individual SH profiles before starting the field experimental phase.

Moreover, the collection of observational data was largely opportunistic. Unlike SH in many free-ranging populations of Japanese macaques, in which this behavior is strongly associated with food provisioning, making the expression of SH activity relatively predictable (Leca et al., 2008b), SH activity in the Balinese long-tailed macaques living at Ubud was distributed throughout the day, regardless of food provisioning times; we have no evidence of obvious temporal association between food-related/foraging activity and SH that would make the occurrence of this behavior predictable (Pelletier et al., 2017). Additionally, as SH activity represents a small proportion of the time budget of an individual in Ubud (Leca, unpublished data), focal animal sampling methods are impractical to gather sufficient data to investigate the research questions pertaining to this thesis (Altmann, 1974). As such, in this thesis we have not used frequencies and absolute durations of SH behavioral patterns, but relative frequencies and durations within an individual's overall SH activity.

## 7.5. Conclusions

The unquestioned support advocated by the proponents of the “play ethos” for object play facilitating tool use (P. K. Smith, 2010) must be fully scrutinized. After building a strong case for why SH behavior is an ideal candidate to evaluate the Affordance Learning theory in Balinese long-tailed macaques, I tested whether an individual’s SH profile would predict the expression of stone-tool use in a foraging domain. The results from this work suggest that, to some extent, object play and tool use are linked at the proximate level in Balinese long-tailed macaques, but that several factors mediate this relationship. Specifically, qualitative and quantitative aspects of SH behavior may correlate with the expression of tool use, but the interplay of additional attributes contributes to the emergence of instrumental object-assisted actions. Although specific features of object play covary with tool use, at this stage we cannot clearly conclude that object play is *essential* for tool use to emerge; however, this dissertation provides strong evidence that object play alone is clearly not sufficient for tool use to emerge. The findings obtained in this thesis highlight the need for systematic comparative analyses across taxa focusing on the structural components that characterize object play and tool use. Evidence from a structural perspective will shed light on whether, through spontaneous and playful manipulation, individuals become familiar with the opportunity for action associated with objects and can later use this practice and knowledge in new contexts and novel problems.

## REFERENCES


Albanese, V., Berardi, R., Llorente, M., Huffman, M. A., & Leca, J.-B. (2022). Mechanisms of expression of object play: A comparative study of stone handling in two captive groups of long-tailed macaques (*Macaca fascicularis fascicularis*). *Behavioural Processes*, 104774. https://doi.org/10.1016/j.beproc.2022.104774

Alcock, J. (1972). The evolution of the use of tools by feeding animals. *Evolution*, *26*, 464-473. https://doi.org/10.2307/2407020

Allen, M. L. (1977). *Sexual response and orgasm in the female chimpanzee (Pan troglodytes)*. [Doctoral thesis, University of Oklahoma].

Allison, M. L., Reed, R., Michels, E., & Boogert, N. J. (2020). The drivers and functions of rock juggling in otters. *Royal Society Open Science*, *7*, 200141. https://doi.org/10.1098/rsos.200141

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227-267. https://doi.org/10.1163/156853974x00534

Amodio, P., Jelbert, S. A., & Clayton, N. S. (2018). The interplay between psychological predispositions and skill learning in the evolution of tool use. *Current Opinion in Behavioral Sciences*, *20*, 130-137. https://doi.org/10.1016/j.cobeha.2018.01.002

Auersperg, A. M., von Bayern, A. M., 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*, e20231. https://doi.org/10.1371/journal.pone.0020231

Auersperg, A. M., von Bayern, A. M., Weber, S., Szabadvari, A., Bugnyar, T., & Kacelnik, A. (2014). Social transmission of tool use and tool manufacture in Goffin cockatoos (*Cacatua goffini*). *Proceedings of the Royal Society B*, *281*, 20140972. https://doi.org/10.1098/rspb.2014.0972

Bakeman, R., & Gottman, J. M. (1997). *Observing interaction: An introduction to sequential analysis*. Cambridge University Press. https://doi.org/10.1017/cbo9780511527685

Bakeman, R., & Quera, V. (2011). *Sequential analysis and observational methods for the behavioral sciences*. Cambridge University Press. https://doi.org/10.1017/cbo9781139017343

Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: ejaculate adjustment by males and the function of masturbation. *Animal Behaviour*, *46*, 861-885. https://doi.org/10.1006/anbe.1993.1271

Bandini, E., & Tennie, C. (2020). Exploring the role of individual learning in animal tool-use. *PeerJ*, *8*, e9877. https://doi.org/10.7717/peerj.9877

Bandini, E., Bandini, M., & Tennie, C. (2021). A short report on the extent of stone handling behavior across otter species. *Animal Behavior and Cognition*, *8*, 15-22. https://doi.org/10.26451/abc.08.01.02.2021

Barcell, M., Benítez, J. R., Solera, F., Román, B., & Donázar, J. A. (2015). Egyptian vulture (*Neophron percnopterus*) uses stone-throwing to break into a griffon vulture (*Gyps fulvus*) egg. *Journal of Raptor Research*, *49*, 521-523. https://doi.org/10.3356/rapt-49-04-521-522.1

Bardo, A., Cornette, R., Borel, A., & Pouydebat, E. (2017). Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology*, *164*, 821-836. https://doi.org/10.1002/ajpa.23323

Barrett, L. (2011). *Beyond the brain.* Princeton University Press.

Bateson, P. (2014). Play, playfulness, creativity and innovation. *Animal Behavior and Cognition*, *1*, 99-112. https://doi.org/10.12966/abc.05.02.2014

Bateson, P. (2015). Why are individuals so different from each other? *Heredity*, *115*, 285-292. https://doi.org/10.1038/hdy.2014.103

Beach, F. A. (1976). Cross-species comparisons and the human heritage. *Archives of Sexual Behavior*, *5*, 469-485. https://doi.org/10.1007/bf01541337

Beck, B. B. (1980). *Animal tool behavior: The use and manufacture of tools by animals*. Garland STPM Press.

Bekoff, M. (1974). Social play in coyotes, wolves, and dogs. *Bioscience*, *24*, 225-230. https://doi.org/10.2307/1296803

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

Bentley-Condit, V., & Smith, E. O. (2010). Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour*, *147*, 185-221. https://doi.org/10.1163/000579509x12512865686555

Bernardi, G. (2012). The use of tools by wrasses (*Labridae*). *Coral Reefs*, *31*, 31-39. https://doi.org/10.1007/s00338-011-0823-6

Bernstein, N. A. (1996). *Dexterity and its development*. Psychology Press. https://doi.org/10.4324/9781410603357

Birch, H. G. (1945a). The relation of previous experience to insightful problem-solving. *Journal of Comparative and Physiological Psychology*, *38*, 367–383. https://doi.org/10.1037/h0056104

Birch, H. G. (1945b). The role of motivational factors in insightful problem-solving. *Journal of Comparative Psychology*, *38*, 295-317. https://doi.org/10.1037/h0059937

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

Biro, D., Haslam, M., & Rutz, C. (2013). Tool use as adaptation. *Philosophical Transactions of the Royal Society B*, *368*, 20120408. https://doi.org/10.1098/rstb.2012.0408

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity?. *Trends in Ecology & Evolution*, *23*, 361-368. https://doi.org/10.1016/j.tree.2008.04.003

Bjorklund, D. F. (2016). Incorporating development into evolutionary psychology: Evolved probabilistic cognitive mechanisms. *Evolutionary Psychology*, *14*, 1-14. https://doi.org/10.1177/1474704916670166

Bjorklund, D. F., & Gardiner, A. K. (2011). Object play and tool use: Developmental and evolutionary perspectives. In A. D. Pellegrini (Ed.), *The Oxford handbook of the development of play* (pp. 153-171). Oxford Psychology Library. https://doi.org/10.1093%2Foxfordhb%2F9780195393002.013.0013

Bock, J., & Johnson, S. E. (2004). Subsistence ecology and play among the Okavango Delta peoples of Botswana. *Human Nature*, *15*, 63-81. https://doi.org/10.1007/s12110-004-1004-x

Boesch, C. (1996). The emergence of cultures among wild chimpanzees. *Proceedings of the British Academy*, *88*, 251-268.

Boesch, C. (2013). Ecology and cognition of tool use in chimpanzees. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 21-47). Cambridge University Press. https://doi.org/10.1017/cbo9780511894800.003

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, *13*, 415-440. https://doi.org/10.1016/s0047-2484(84)80055-x

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioral ecology and evolution*. Oxford University Press.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, *161*, 1-28. https://doi.org/10.1086/343878

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

Boose, K. J., White, F. J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American Journal of Primatology*, *75*, 917-926. https://doi.org/10.1002/ajp.22155

Bourgeois, K. S., Khawar, A. W., Neal, A. S., & Lockman, J. J. (2005). Infant manual exploration of objects, surfaces, and their interrelations. *Infancy*, *8*, 233–252. https://doi.org/10.1207/s15327078in0803_3

Brockmann, H. J. (1985). Tool use in digger wasps (Hymenoptera: *Sphecinae*). *Psyche*, *92*, 309-329. https://doi.org/10.1155/1985/73184

Bronson, F. H. (1989). *Mammalian reproductive biology*. University of Chicago Press.

Brotcorne, F. (2014). Behavioral ecology of commensal long-tailed macaque (*Macaca fascicularis*) populations in Bali, Indonesia: Impact of anthropic factors. [Doctoral thesis, University of Liège].

Brotcorne, F., Fuentes, A., Wandia, I. N., Beudels-Jamar, R. C., & Huynen, M. C. (2015). Changes in activity patterns and intergroup relationships after a significant mortality event in commensal long-tailed macaques (*Macaca fascicularis*) in Bali, Indonesia. *International Journal of Primatology, 36*, 548-566. https://doi.org/10.1007/s10764-015-9841-5

Bruner, J. (1972). Nature and uses of immaturity. *American Psychologist*, *27*, 687–708. https://doi.org/10.1037/h0033144

Brunon, A., Bovet, D., Bourgeois, A., & Pouydebat, E. (2014). Motivation and manipulation capacities of the blue and yellow macaw and the tufted capuchin: A comparative approach. *Behavioural Processes*, *107*, 1-14. https://doi.org/10.1016/j.beproc.2014.06.006

Bunselmeyer, C. (2022, March 25th). *Novel object manipulation in Balinese long-tailed macaques* [podium presentation]. Meeting of the Minds 2022, Lethbridge.

Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. MIT Press. https://doi.org/10.7551%2Fmitpress%2F3229.001.0001

Burghardt, G. M. (2007). Critical anthropomorphism, uncritical anthropocentrism, and naïve nominalism. *Comparative Cognition & Behavior Reviews*, *2*, 136-138. https://doi.org/10.3819/ccbr.2008.20009

Bürkner, P.-C. (2017). Advanced Bayesian multilevel modeling with the R package brms. *arXiv*, *1705*, 11123. https://doi.org/10.48550/arXiv.1705.11123

Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *The American Naturalist*, *146*, 25-40. https://doi.org/10.1086/285785

Byrne, G., & Suomi, S. J. (1996). Individual differences in object manipulation in a colony of tufted capuchins. *Journal of Human Evolution*, *31*, 259-267. https://doi.org/10.1006/jhev.1996.0060

Byrne, R. W. (1997). The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In A. Whiten, & R. W. Byrne (Eds.), *Machiavellian intelligence. vol II: Extensions and evaluations* (pp 289-211). Cambridge University Press. https://doi.org/10.1017/cbo9780511525636.012

Byrne, R. W. (2015). The what as well as the why of animal fun. *Current Biology*, *25*, R2-R4. https://doi.org/10.1016/j.cub.2014.09.008

Call, J. (2013). Three ingredients for becoming a creative tool user. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 21-47). Cambridge University Press. https://doi.org/10.1017/cbo9780511894800.002

Cangiano, M., & Palagi, E. (2020). First evidence of stone handling in geladas: From simple to more complex forms of object play. *Behavioural Processes*, *180*, 104253. https://doi.org/10.1016/j.beproc.2020.104253

Casarrubea, M., Aiello, S., Di Giovanni, G., Santangelo, A., Palacino, M., Crescimanno, G. (2019). Combining quantitative and qualitative data in the study of feeding behavior in male Wistar rats. *Frontiers in Psychology*, *10*, 881. https://doi.org/10.3389/fpsyg.2019.00881

Casarrubea, M., Jonsson, G. K., Faulisi, F., Sorbera, F., Di Giovanni, G., Benigno, A., ... & Magnusson, M. S. (2015). T-pattern analysis for the study of temporal structure of animal and human behavior: a comprehensive review. *Journal of Neuroscience Methods*, *239*, 34-46. https://doi.org/10.1016%2Fj.jneumeth.2014.09.024

Casarrubea, M., Magnusson, M. S., Anguera, M. T., Jonsson, G. K., Castañer, M., Santangelo, A., ... & Puigarnau, S. (2018). T-pattern detection and analysis for the discovery of hidden features of behaviour. *Journal of Neuroscience Methods*, *310*, 24-32. https://doi.org/10.1016%2Fj.jneumeth.2018.06.013

Cenni, C., & Leca, J.-B. (2020a). Tool use. In J. Vonk, & T. K. Shackelford (Eds.), *Encyclopedia of Animal Cognition and Behavior*. Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_1541-1

Cenni, C., & Leca, J.-B. (2020b). Technical intelligence hypothesis. In J. Vonk, & T. K. Shackelford (Eds.), *Encyclopedia of Animal Cognition and Behavior*. Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_103-1

Cenni, C., Casarrubea, M., Gunst, N., Vasey, P. L., Pellis, S. M., Wandia, I. N., & Leca, J.-B. (2020). Inferring tool use behavior patterns from the temporal structure of object play sequences in a non-human primate species. *Physiology & Behavior, 222*, 112938. https://doi.org/10.1016/j.physbeh.2020.112938

Cenni, C., Christie, J. B. A., Van der Pant, Y., Gunst, N., Vasey, P. L., Wandia, I N., & Leca, J.-B. (2022). Do monkeys use sex toys? Evidence of stone tool-assisted masturbation in free-ranging long-tailed macaques. *Ethology*, *128*, 632–646. *https://doi.org/10.1111/eth.13324*

Cenni, C., Christie, J. B. A., Van der Pant, Y., Wright, C. I., Gunst, N., Pellis, S. M., Wandia, I N., & Leca, J.-B. (in review). Does object play have an individual signature in long-tailed macaques (*Macaca fascicularis*)? Inter-individual variation in stone handling behavior. *Animal Cognition*.

Cenni, C., Pellis, S. M., Wandia, I N., Leca, J.-B. (2021) Stone affordances as potential for action expression in object play in long-tailed macaques (*Macaca fascicularis*). *Journal of Comparative Psychology*, *135*, 430-438. https://doi.org/10.1037/com0000283

Cenni, C., Wandia, I N., & Leca, J.-B. (in review). Twig-assisted masturbation in Balinese long-tailed macaques. *Behaviour*.

Cesari, P., & Newell, K. M. (1999). The scaling of human grip configurations. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 927-935. https://doi.org/10.1037/0096-1523.25.4.927

Chapman, C. A., & Rothman, J. M. (2009). Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates*, *50*, 12-22. https://doi.org/10.1007/s10329-008-0123-0

Chappell, J., & Kacelnik, A. (2002). Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, *5*, 71-78. https://doi.org/10.1007/s10071-002-0130-2

Chertoff, S. (2021). *Do monkeys fidget? Using movement analysis to understand the role of gaze direction on non-instrumental object manipulation: stone handling in Balinese long-tailed macaques*. [MSc thesis, University of Lethbridge].

Chevalier-Skolnikoff, S. (1989). Spontaneous tool use and sensorimotor intelligence in *Cebus* compared with other monkeys and apes. *Behavioral and Brain Sciences*, *12*, 561-588. https://doi.org/10.1017/s0140525x00057678

Colwell, R. K. (2013). EstimateS: statistical estimation of species richness and shared species from samples. Version 9. http://purl.oclc.org/estimates

Colwell, R. K., & Elsensohn, J. E. (2014). EstimateS turns 20: statistical estimation of species richness and shared species from samples, with non-parametric extrapolation. *Ecography*, *37*, 609-613. https://doi.org/10.1111/ecog.00814

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*, 1441-1453. https://doi.org/10.1016/0003-3472(95)80001-8

Crain, B. J., Giray, T., & Abramson, C. I. (2013). A tool for every job: assessing the need for a universal definition of tool use. *International Journal of Comparative Psychology*, *26*, 281-303. https://doi.org/10.46867/ijcp.2013.26.04.03

Dawkins, M. S. (1986). *Unravelling animal behavior*. Longman Scientific & Technical.

de Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nutcracking in young tufted capuchin monkeys (*Cebus apella*): A perception–action perspective. *Developmental Science*, *11*, 828-840. https://doi.org/10.1111/j.1467-7687.2008.00731.x

Dixson, A. (2012). *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and humans*. Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199544646.001.0001

Dixson, A. F., & Anderson, M. J. (2004). Sexual behavior, reproductive physiology and sperm competition in male mammals. *Physiology & Behavior*, *83*, 361-371. https://doi.org/10.1016/j.physbeh.2004.08.022

Draper, Z. A., & O'Connor, B. P. (2019). Package 'LagSequential'. Retrieved from https://cran.r-project.org/web/packages/LagSequential/LagSequential.pdf

Dubuc, C., Coyne, S. P., & Maestripieri, D. (2013). Effect of mating activity and dominance rank on male masturbation among free-ranging male rhesus macaques. *Ethology*, *119*, 1006-1013. https://doi.org/10.1111/eth.12146

Duckworth, R. A. (2009). The role of behavior in evolution: a search for mechanism. *Evolutionary Ecology*, *23*, 513-531. https://doi.org/10.1007/s10682-008-9252-6

Ebel, S. J., & Call, J. (2018). The interplay of prior experience and motivation in great ape problem-solving (*Gorilla gorilla, Pan paniscus, Pan troglodytes, and Pongo abelii*). *Journal of Comparative Psychology*, *132*, 294-305. https://doi.org/10.1037/com0000117

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, *306,* 1903-1907. https://doi.org/10.1126/science.1098410

Emery, N. J., & Clayton, N. S. (2009). Tool use and physical cognition in birds and mammals. *Current Opinion in Neurobiology*, *19,* 27-33. https://doi.org/10.1016/j.conb.2009.02.003

Engelhardt, A., Hodges, J. K., Niemitz, C., & Heistermann, M. (2005). Female sexual behavior, but not sex skin swelling, reliably indicates the timing of the fertile phase in wild long-tailed macaques (*Macaca fascicularis*). *Hormones and Behavior*, *47*, 195-204. https://doi.org/10.1016/j.yhbeh.2004.09.007

Eshchar, Y., Izar, P., Visalberghi, E., de Resende, B. D., & Fragaszy, D. M. (2016). When and where to practice: social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Animal Cognition*, *19*, 605-618. https://doi.org/10.1007/s10071-016-0965-6

Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango

National Park, Gabon: Techniques and individual differences. *American Journal of Primatology*, *79*, e22672. https://doi.org/10.1002/ajp.22672

Evans, T. A., & Westergaard, G. C. (2006). Self-control and tool use in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *120*, 163-166. https://doi.org/10.1037/0735-7036.120.2.163

Fagen, R. (1981). *Animal play behavior*. Oxford University Press.

Falótico, T. (2022). Robust capuchin tool use cognition in the wild. *Current Opinion in Behavioral Sciences*, 46, 101170. https://doi.org/10.31234/osf.io/tgc7q

Falótico, T., & Ottoni, E. B. (2013). Stone throwing as a sexual display in wild female bearded capuchin monkeys, *Sapajus libidinosus*. *PLoS One*, *8*, e79535. https://doi.org/10.1371/journal.pone.0079535

Fayet, A. L., Hansen, E. S., & Biro, D. (2020). Evidence of tool use in a seabird. *Proceedings of the National Academy of Sciences*, *117*, 1277-1279. https://doi.org/10.1073/pnas.1918060117

Fentress, J. C. (1983). A view of ontogeny. *Advances in the Study of Mammalian Behavior*, *7*, 24-64.

Ficken, M. S. (1977). Avian play. *The Auk*, *94*, 573-582. https://doi.org/10.1093/auk/94.3.573

Finn, J. K., Tregenza, T., & Norman, M. D. (2009). Defensive tool use in a coconut-carrying octopus. *Current Biology*, *19*, R1069-R1070. https://doi.org/10.1016/j.cub.2009.10.052

Fontanelle, S. A., Kahrs, B. A., Neal, S. A., Newton, A. T., & Lockman, J. J. (2007). Infant manual exploration of composite substrates. *Journal of Experimental Child Psychology*, *98*, 153-167. https://doi.org/10.1016/j.jecp.2007.07.001

Ford, C. S., & Beach, F. A. (1951). *Patterns of sexual behavior*. Harper & Brothers, Publishers.

Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The mentality of gorillas and orangutans* (pp. 99–116). Cambridge University Press. https://doi.org/10.1017/cbo9780511542305.005

Fox, E. A., van Schaik, C. P., Sitompul, A., & Wright, D. N. (2004). Intra-and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology*, *125*, 162-174. https://doi.org/10.1002/ajpa.10386

Fragaszy, D. M., & Mangalam, M. (2018). Tooling. *Advances in the Study of Behavior, 50*, 177–241. https://doi.org/10.1016/bs.asb.2018.01.001

Fragaszy, D. M., & Visalberghi, E. (1989). Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *103*, 159–170. https://doi.org/10.1037/0735-7036.103.2.159

Fragaszy, D. M., & Visalberghi, E. (1990). Social processes affecting the appearance of innovative behaviors in capuchin monkeys. *Folia Primatologica, 54***,** 155-165. https://doi.org/10.1159/000156439

Fragaszy, D. M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Visalberghi, E. (2013). The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society B, 368*, 20120410. https://doi.org/10.1098/rstb.2012.0410

Fragaszy, D. M., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P., & Liu, Q. (2010). How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour, 80*, 205-214. https://doi:10.1016/j.anbehav.2010.04.018

Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E. B., & de Oliveira, M. G. (2004a). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, *64*, 359-366. https://doi.org/10.1002/ajp.20085

Fragaszy, D. M., Pickering, T., Liu, Q., Izar, P., Ottoni, E., & Visalberghi, E. (2010). Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Animal Behaviour*, *79*, 321-332. https://doi.org/10.1016/j.anbehav.2009.11.004

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004b). *The complete capuchin: The biology of the genus Cebus*. Cambridge University Press.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*, 1325-1330. https://doi.org/10.1111/2041-210x.12584

Fuentes, A. (1992) Object rubbing in Balinese macaques (*Macaca fascicularis*). *Laboratory Primate Newsletter*, *31*, 14-15

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society*, *182*, 389-402. https://doi.org/10.1111/rssa.12378

Gajdon, G. K., Amann, L., & Huber, L. (2011). Keas rely on social information in a tool use task but abandon it in favour of overt exploration. *Interaction Studies*, *12*, 304-323. https://doi.org/10.1075/is.12.2.06gaj

Gajdon, G. K., Lichtnegger, M., & Huber, L. (2014). What a parrot's mind adds to play: the urge to produce novelty fosters tool use acquisition in kea. *Open Journal of Animal Sciences*, *4*, 51-58. https://doi.org/10.4236/ojas.2014.42008

Georgiadis, J. R., & Kringelbach, M. L. (2012). The human sexual response cycle: brain imaging evidence linking sex to other pleasures. *Progress in Neurobiology*, 98, 49-81. https://doi.org/10.1016/j.pneurobio.2012.05.004

Gibson, E. J. (1982) The concept of affordances in development: The renascence of functionalism. In W.A. Collins (Ed.), *The concept of development: The Minnesota symposia on child psychology, Vol. 15*, (pp. 55–81). Lawrence Erlbaum Associates.

Gibson, E. J. (1988). Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. *Annual Review of Psychology*, *39*, 1-42. https://doi.org/10.1146/annurev.ps.39.020188.000245

Gibson, E. J., & Walker, A. S. (1984). Development of knowledge of visual-tactual affordances of substance. *Child Development*, *55*, 453-460. https://doi.org/10.2307/1129956

Gibson, J. J. (1979). *The ecological approach to visual perception*. Houghton Mifflin. https://doi.org/10.4324/9780203767764

Giraud, G., Sosa, S., Hambuckers, A., Deleuze, S., Wandia, I N., Huynen, M. -C., Poncin, P., & Brotcorne, F. (2021). Effect of infant presence on social networks of sterilized and intact wild female Balinese macaques (*Macaca fascicularis*). *Animals*, *11*, 2538. https://doi.org/10.3390/ani11092538

Goodman, M., Hayward, T., & Hunt, G. R. (2018). Habitual tool use innovated by free-living New Zealand kea. *Scientific Reports*, *8*, 1-12. https://doi.org/10.1038/s41598-018-32363-9

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology*, *4*, 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Gotelli, N. J., & Entsminger, G. L. (2001). EcoSim: Null models software for ecology. Version 7.0. *Acquired Intelligence Inc. & Kesey-Bear*.

Greer, T., & Lockman, J. J. (1998). Using writing instruments: Invariances in young children and adults. *Child Development*, *69*, 888-902. https://doi.org/10.1111/j.1467-8624.1998.tb06150.x

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

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the Pan lineage. *Animal Behaviour*, *80*, 1023-1033. https://doi.org/10.1016/j.anbehav.2010.09.005

Gruber, T., Muller, M. N., Reynolds, V., Wrangham, R. W., & Zuberbühler, K. (2011). Community-specific evaluation of tool affordances in wild chimpanzees. *Scientific Reports*, *1*, 128. https://doi.org/10.1038/srep00128

Guillette, L. M, Hollis, K. L., & Markarian, A. (2009). Learning in a sedentary insect predator: antlions (Neuroptera: *Myrmeleontidae*) anticipate a long wait. *Behavioural Processes*, *80*, 224-232. https://doi.org/10.1016/j.beproc.2008.12.015

Gumert, M. D., & Malaivijitnond, S. (2013). Long-tailed macaques select mass of stone tools according to food type. *Philosophical Transactions of the Royal Society B, 368*, 20120413. https://doi.org/10.1098/rstb.2012.0413

Gumert, M. D., Hoong, L. K., & Malaivijitnond, S. (2011). Sex differences in the stone tool-use behavior of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). *American Journal of Primatology*, *73*, 1239-1249. https://doi.org/10.1002/ajp.20996

Gumert, M. D., Kluck, M., & Malaivijitnond, S. (2009). The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. *American Journal of Primatology*, *71*, 594-608. https://doi.org/10.1002/ajp.20694

Haidle, M. N. (2010). Working-memory capacity and the evolution of modern cognitive potential. *Current Anthropology*, *51*, S149–S166. https://doi.org/10.1086/650295

Hall, K., & Schaller, G. (1964). Tool-using behavior of the California sea otter. *Journal of Mammalogy*, *45*, 287-299. https://doi.org/10.2307/1376994

Hasenjager, M. J., Leadbeater, E., & Hoppitt, W. (2020). Detecting and quantifying social transmission using network-based diffusion analysis. *Journal of Animal Ecology, 90*, 8-26. https://doi.org/10.1111/1365-2656.13307

Haslam, M. (2013). "Captivity bias" in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B, 368*, 20120421. https://doi.org/10.1098/rstb.2012.0421

Hayes, J., Powell, N., Lathrop, G., Heneine, W., & Dobard, C. W. (2016). Assessment of penile erection methods in rhesus macaques to model pharmacokinetics of antiretroviral drugs and penile infection with simian immunodeficiency virus. *Journal of Medical Primatology*, *45*, 34-41. https://doi.org/10.1111/jmp.12207

Heldstab, S. A., Kosonen, Z. K., Koski, S. E., Burkart, J. M., van Schaik, C. P., & Karin Isler, K. (2016). Manipulation complexity in primates coevolved with brain size and terrestriality. *Scientific Reports*, *6*, 24528. https://doi.org/10.1038/srep24528

Henzi, S. P., Bonnell, T., Pasternak, G. M., Freeman, N. J., Dostie, M. J., Kienzle, S., ... & Barrett, L. (2021). Keep calm and carry on: reactive indifference to predator encounters by a gregarious prey species. *Animal Behaviour*, *181*, 1-11. https://doi.org/10.1016/j.anbehav.2021.08.024

Hihara, S., Notoya, T., Tanaka, M., Ichinose, S., Ojima, H., Obayashi, S., . . . & Iriki, A. (2006). Extension of corticocortical afferents into the anterior bank of the intraparietal sulcus by tool-use training in adult monkeys. *Neuropsychologia*, *44*, 2636–2646. https://doi.org/10.1016/j.neuropsychologia.2005.11.020

Hiscock, P. (2014). Learning in lithic landscapes: a reconsideration of the hominid “toolmaking” niche. *Biological Theory*, *9*, 27-41. https://doi.org/10.1007/s13752-013-0158-3

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology*, *12*, e1001960. https://doi.org/10.1371/journal.pbio.1001960

Holzhaider, J.C., Hunt, G.R., & Gray, R.D. (2010). Social learning in new Caledonian crows. *Learning & Behavior*, *38*, 206–219. https://doi.org/10.3758/LB.38.3.206

Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, *73*, 1021-1032. https://doi.org/10.1016/j.anbehav.2006.07.016

Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods and models.* Princeton University Press. https://doi.org/10.23943/princeton/9780691150703.001.0001

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). *Methods in Ecology and Evolution*, *7*, 1451-1456. https://doi.org/10.1111/2041-210x.12613

Huber, L., & Gajdon, G. K. (2006). Technical intelligence in animals: the kea model. *Animal Cognition*, *9*, 295-305. https://doi.org/10.1007/s10071-006-0033-8

Huffman, M. A. (1984). Stone-play of Macaca fuscata in Arashiyama B troop: transmission of a non-adaptive behavior. *Journal of Human Evolution*, *13*, 725-735. https://doi.org/10.1016/s0047-2484(84)80022-6

Huffman, M. A. (1996). Acquisition of innovative cultural behaviors in non-human primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques. In Jr. G. Galef & C. Heyes (Eds.), *Social learning in animals: The roots of culture*. (pp. 267-289). Academic Press. https://doi.org/10.1016/b978-012273965-1/50014-5

Huffman, M. A., & Hirata, S. (2003). Biological and ecological foundations of primate behavioral tradition. In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence*, (pp. 267-296). Cambridge University Press. https://doi.org/10.1017/cbo9780511584022.011

Huffman, M., A., & Quiatt, D. (1986). Stone handling by Japanese macaques (*Macaca fuscata*): Implications for tool use of stone. *Primates*, *27*, 413-423. https://doi.org/10.1007/bf02381887

Hughes, M. M. (1978). Sequential analysis of exploration and play. *International Journal of Behavioral Development*, *1*, 83-97. https://doi.org/10.1177%2F016502547800100106

Hughes, M. M. (1979). Exploration and play re-visited: A hierarchical analysis. *International Journal of Behavioral Development*, *2*, 215-224. https://doi.org/10.1177%2F016502547900200301

Humle, T., Snowdon, C. T., & Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, *12*, 37-48. https://doi.org/10.1007/s10071-009-0272-6

Hunt, G. R., Gray, R. D., & Taylor, A. H. (2013). Why is tool use rare in animals? In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 89–118). Cambridge University Press. https://doi.org/10.1017/cbo9780511894800.007

Hurlbert, S. H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, *52*, 577-586. https://doi.org/10.2307/1934145

Hutt, C. (1966). Exploration and play in children. *Symposia of the Zoological Society of London*, *18*, 61-81.

Inoue, E. (2012). Male masturbation behavior if Japanese macaques in the Arashiyama E troop. In J.-B. Leca, M. A. Huffman, & P. L. Vasey (Eds.), *The monkeys of stormy* *mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (pp. 204-219). Cambridge University Press. https://doi.org/10.1017/cbo9781139019415.018

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*, 159-173. https://doi.org/10.1037/0735-7036.111.2.159

Izar, P., Peternelli-dos-Santos, L., Rothman, J. M., Raubenheimer, D., Presotto, A., Gort, G., ... & Fragaszy, D. M. (in press). Stone tools improve diet quality in wild monkeys. *Current Biology*. https://doi.org/10.1016/j.cub.2022.07.056

Jalles-Filho, E. (1995). Manipulative propensity and tool use in capuchin monkeys. *Current Anthropology*, *36*, 664-667. https://doi.org/10.1086/204414

Johnson-Frey, S. H. (2003). What's so special about human tool use? *Neuron*, *39*, 201-204. https://doi.org/10.1016/s0896-6273(03)00424-0

Jordan, C. (1982). Object manipulation and tool-use in captive pygmy chimpanzees (*Pan paniscus*). *Journal of Human Evolution*, *11*, 35-39. https://doi.org/10.1016/s0047-2484(82)80029-8

Jordan, E. J., Townrow, L. A. J., Wright, C. I., & Seed, A. M. (2020). Understanding solidity: investigating knowledge of a functional object property in brown capuchin monkeys (*Sapajus apella*) and common squirrel monkeys (*Saimiri sciureus*). *Animal Behavior and Cognition*, *7*, 365-391. https://doi.org/10.26451/abc.07.03.07.2020

Jordan, E. J., Völter, C. J., & Seed, A. M. (2022). Do capuchin monkeys (*Sapajus apella*) use exploration to form intuitions about physical properties?. *Cognitive Neuropsychology*, 1-13. https://doi.org/10.1080/02643294.2022.2088273

Kacelnik, A. (2009). Tools for thought or thoughts for tools? *Proceedings of the National Academy of Sciences*, *106*, 10071-10072. https://doi.org/10.1073/pnas.0904735106

Kader, G. D., & Perry, M. (2007). Variability for categorical variables. *Journal of Statistics Education*, *15*, 1-16. https://doi.org/10.1080/10691898.2007.11889465

Kahrs, B. A., Jung, W. P., & Lockman, J. J. (2012). What is the role of infant banging in the development of tool use? *Experimental Brain Research*, *218*, 315-320. https://doi.org/10.1007/s00221-012-3062-3

Kahrs, B. A., Jung, W. P., & Lockman, J. J. (2013). Motor origins of tool use. *Child Development*, *84*, 810-816. https://doi.org/10.1111/cdev.12000

Kaplan, G. (2020). Play behaviour, not tool using, relates to brain mass in a sample of birds. *Scientific Reports*, *10*, 1-15. https://doi.org/10.1038/s41598-020-76572-7

Kappeler, P., & Kraus, C. (2010). Levels and mechanisms of behavioral variability. In P. Kappeler (Ed.), *Animal behavior: Evolution and mechanisms* (pp. 655-684). Springer, Berlin. https://doi.org/10.1007/978-3-642-02624-9_21

Kenward, B., Rutz, C., Weir, A. A. S., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour*, *72*, 1329–1343. https://doi.org/10.1016/j.anbehav.2006.04.007

Kenward, B., Schloegl, C., Rutz, C., Weir, A. A., Bugnyar, T., & Kacelnik, A. (2011). On the evolutionary and ontogenetic origins of tool-oriented behavior in New Caledonian crows (*Corvus moneduloides*). *Biological Journal of the Linnean Society*, *102*, 870-877. https://doi.org/10.1111/j.1095-8312.2011.01613.x

Kluiver, C. E., de Jong, J. A., Massen, J. J., & Bhattacharjee, D. (2022). Personality as a predictor of time-activity budget in lion-tailed macaques (*Macaca silenus*). *Animals*, *12*, 1495. https://doi.org/10.3390/ani12121495

Kluzinski, A. (2016) Démographie et impact des stratégies d'approvisionnement alimentaire dans un contexte de gestion d'une population de macaques commensaux (*Macaca fascicularis*) à Bali (Indonésie), [MSc Dissertation – in French, Université de Liège].

Köhler, W. (1925). *The mentality of apes*. Routledge. https://doi.org/10.4324/9781351294966

Kollar, E. J., Beckwith, W. C., & Edgerton, R. B. (1968). Sexual behavior of the ARL colony chimpanzees. *The Journal of Nervous and Mental Disease*, *147*, 444-459. https://doi.org/10.1097/00005053-196811000-00002

Koops, K., Furuichi, T., & Hashimoto, C. (2015a). Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Scientific Reports*, *5*, 11356. https://doi.org/10.1038/srep11356

Koops, K., Furuichi, T., Hashimoto, C., & van Schaik, C. P. (2015b). Sex differences in object manipulation in wild immature chimpanzees (*Pan troglodytes schweinfurthii*) and bonobos (*Pan paniscus*): Preparation for tool use? *PloS One*, *10*, e0139909. https://doi.org/10.7287/peerj.preprints.1815v1

Kruuk H. (2006). *Otters: ecology, behaviour and conservation.* Oxford University Press.

Kühl, H. S., Kalan, A. K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., ... & Ton, E. (2016). Chimpanzee accumulative stone throwing. *Scientific Reports*, *6*, 22219. https://doi.org/10.1038/srep22219

Laland, K. N., & Reader, S. M. (1999). Foraging innovation in the guppy. *Animal Behaviour*, *57*, 331-340. https://doi.org/10.1006/anbe.1998.0967

Lambert, M. L., Schiestl, M., Schwing, R., Taylor, A. H., Gajdon, G. K., Slocombe, K. E., & Seed, A. M. (2017). Function and flexibility of object exploration in kea and New Caledonian crows. *Royal Society Open Science*, *4*, 170652. https://doi.org/10.1098/rsos.170652

Lamon, N., Neumann, C., & Zuberbühler, K. (2018). Development of object manipulation in wild chimpanzees. *Animal Behaviour*, *135*, 121-130. https://doi.org/10.1016/j.anbehav.2017.11.003

Latash, M L. (2000). There is no motor redundancy in human movements. There is motor abundance. *Motor Control*, *4*, 259-261. https://doi.org/10.1123/mcj.4.3.259

Latash, M. L. (2012). The bliss (not the problem) of motor abundance (not redundancy). *Experimental Brain Research*, *217*, 1-5. https://doi.org/10.1007/s00221-012-3000-4

Laumer, I. B., Auersperg, A. M., Bugnyar, T., & Call, J. (2019). Orangutans (*Pongo abelii*) make flexible decisions relative to reward quality and tool functionality in a multi-dimensional tool-use task. *PloS One*, *14*, e0211031. https://doi.org/10.1371/journal.pone.0211031

Leca J.-B. (2015). Arbitrary cultural behavior patterns are not unique to humans. *Current Anthropology*, *56*, 112-113.

Leca, J.-B. (2020). By-products of adaptations. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer International Publishing. https://doi.org/10.1007/978-3-319-19650-3_599

Leca, J.-B., & Gunst, N. (accepted). The exaptive potential of (object) play behavior. *International Journal of Play*.

Leca, J.-B., Gunst, N., & Huffman, M. (2011). Complexity in object manipulation by Japanese macaques (*Macaca fuscata*): A cross-sectional analysis of manual coordination in stone handling patterns. *Journal of Comparative Psychology*, *125*, 61-71. https://doi.org/10.1037/a0020868

Leca, J.-B., Gunst, N., & Huffman, M. A. (2007a). Japanese macaque cultures: inter-and intra-troop behavioural variability of stone handling patterns across 10 troops. *Behaviour*, *144*, 251-281. https://doi.org/10.1163/156853907780425712

Leca, J.-B., Gunst, N., & Huffman, M. A. (2007b). Age-related differences in the performance, diffusion, and maintenance of stone handling, a behavioral tradition in Japanese macaques. *Journal of Human Evolution*, *53*, 691-708. https://doi.org/10.1016/j.jhevol.2007.05.009

Leca, J.-B., Gunst, N., & Huffman, M. A. (2008b). Food provisioning and stone handling tradition in Japanese macaques: a comparative study of ten troops. *American Journal of Primatology*, *70*, 803-813. https://doi.org/10.1002/ajp.20551

Leca, J.-B., Gunst, N., & Huffman, M. A. (2008c). Of stones and monkeys: Testing ecological constraints on stone handling, a behavioral tradition in Japanese macaques. *American Journal of Physical Anthropology*, *135*, 233-244. https://doi.org/10.1002/ajpa.20726

Leca, J.-B., Gunst, N., & Huffman, M. A. (2010a). Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*. *Animal Behaviour*, *79*, 117-126. https://doi.org/10.1016/j.anbehav.2009.09.035

Leca, J.-B., Gunst, N., & Huffman, M. A. (2010b). Principles and levels of laterality in unimanual and bimanual stone handling patterns by Japanese macaques. *Journal of Human Evolution*, *58*, 155-165. https://doi.org/10.1016/j.jhevol.2009.09.005

Leca, J.-B., Gunst, N., & Huffman, M. A. (2010c). The first case of dental flossing by a Japanese macaque (*Macaca fuscata*): implications for the determinants of behavioral innovation and the constraints on social transmission. *Primates*, *51*, 13–22. https://doi.org/10.1007/s10329-009-0159-9

Leca, J.-B., Gunst, N., & Huffman, M. A. (2011). Complexity in object manipulation by Japanese macaques (*Macaca fuscata*): A cross-sectional analysis of manual coordination in stone handling patterns. *Journal of Comparative Psychology*, *125*, 61-71. https://doi.org/10.1037/a0020868

Leca, J.-B., Gunst, N., & Huffman, M. A. (2012). Thirty years of stone handling tradition in Arashiyama-Kyoto macaques: Implications for cumulative culture and tool use in non-human primates. In J.-B. Leca, M. A. Huffman, & P. L. Vasey (Eds.), *The monkeys of stormy mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (pp. 223-257). Cambridge University Press. https://doi.org/10.1017%2Fcbo9781139019415.020

Leca, J.-B., Gunst, N., & Vasey, P. L. (2014). Male homosexual behavior in a free-ranging all-male group of Japanese macaques at Minoo, Japan. *Archives of Sexual Behavior*, *43*, 853-861. https://doi.org/10.1007/s10508-014-0310-6

Leca, J.-B., Gunst, N., Pelletier, A. N., Vasey, P. L., Nahallage, C. A. D., Watanabe, K., Huffman, M. A. (2016). A multidisciplinary view on cultural primatology: Behavioral innovations and traditions in Japanese macaques. *Primates*, *57*, 333-338. https://doi.org/10.1007/s10329-016-0518-2

Leca, J.-B., Nahallage, C. A. D., Gunst, N., Huffman, M. A. (2008a). Stone-throwing by Japanese macaques: Form and functional aspects of a group-specific behavioral tradition. *Journal of Human Evolution*, *55*, 989-998. https://doi.org/10.1016%2Fj.jhevol.2008.06.004

Lee, M. D., & Vanpaemel, W. (2018). Determining informative priors for cognitive models. *Psychonomic Bulletin & Review*, *25*, 114-127. https://doi.org/10.3758/s13423-017-1238-3

Lefebvre, L. (2012). Primate encephalization. In M. A. Hofman & D. Falk (Eds), *Progress in Brain Research* (vol. 195, pp. 393-412). Elsevier. https://doi.org/10.1016/b978-0-444-53860-4.00019-2

Lefebvre, L., Boire, D., & Nicolakakis, N. (2002). Tools and brains in birds. *Behaviour*, *139*, 939-973. https://doi.org/10.1163/156853902320387918

Lefebvre, L., Whittle, P.W., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour*, *53*, 549-560. https://doi.org/10.1006/anbe.1996.0330

Lehner, P. N. (1996). *Handbook of ethological methods*. Cambridge University Press.

Lillard, A. S., Dore, R. A., Hopkins, E. J., & Smith, E. D. (2015). Challenges to Research on Play. In J. E. Johnson, S. G. Eberle, T. S. Henricks & D. Kuschner (Eds.), *The handbook of the study of play*, (vol. 2, pp. 445-452). Rowman & Littlefield.

Limongelli, L., Visalberghi, E., & Boyzen, S. T. (1995). The comprehension of cause–effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *109*, 18-26. https://doi.org/10.1037/0735-7036.109.1.18

Lockman, J. (2000). A perception-action perspective on tool use development. *Child Development*, *71*, 137-144. https://doi.org/10.1111%2F1467-8624.00127

Lockman, J. J., Tamis-LeMonda, C. S., & Adolph, K. E. (2020). Missing in action: Tool use is action based. *Behavioral and Brain Sciences*, *43*, e170. https://doi.org/10.1017/s0140525x20000138

Loizos, C. (1967). Play behavior in higher primates: a review. In: D. Morris (Ed.), *Primate Ethology* (pp. 226-282). Aldine Publishing Co. https://doi.org/10.4324/9781315127392-5

Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*, 673–683. https://doi.org/10.1016/j.anbehav.2004.12.014

Lonsdorf, E. V. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, *9*, 36-46. https://doi.org/10.1007/s10071-005-0002-7

Macellini, S., Maranesi, M., Bonini, L., Simone, L., Rozzi, S., Ferrari, P. F., & Fogassi, L. (2012). Individual and social learning processes involved in the acquisition and generalization of tool use in macaques. *Philosophical Transactions of the Royal Society B*, *367*, 24-36. https://doi.org/10.1098/rstb.2011.0125

Magnusson, M. S., Burgoon, J. K., & Casarrubea, M. (2016). *Discovering hidden temporal patterns in behavior and interaction: T-pattern detection and analysis with THEME*. Humana Press. https://doi.org/10.1007%2F978-1-4939-3249-8

Makowski, D., Ben-Shachar, M. S., & Lüdecke, D. (2019). bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software*, *4*, 1541. https://doi.org/10.21105/joss.01541

Mangalam, M., & Fragaszy, D. M. (2016). Transforming the body-only system into the body-plus-tool system. *Animal Behaviour*, *117*, 115-122. https://doi.org/10.1016/j.anbehav.2016.04.016

Martin, P., & Bateson, P. P. G. (1993) *Measuring behaviour: An introductory guide*. Cambridge University Press. https://doi.org/10.1017/cbo9781139168342

Martin, P., & Caro, T. M. (1985). On the functions of play and its role in behavioral development. *Advances in the Study of Behavior, 15,* 59-103. https://doi.org/10.1016%2Fs0065-3454%2808%2960487-8

Martin-Ordas, G., Call, J., & Colmenares, F. (2008). Tubes, tables and traps: great apes solve two functional equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition*, *11*, 423-430. https://doi.org/10.1007/s10071-007-0132-1

Marzke, M. W. (2013). Tool making, hand morphology and fossil hominins. *Philosophical Transactions of the Royal Society B*, *368*, 20120414. https://doi.org/10.1098/rstb.2012.0414

Mather, J. A. (2008). Cephalopod consciousness: Behavioral evidence. *Consciousness and Cognition*, *17*, 37-48. https://doi.org/10.1016/j.concog.2006.11.006

Matthews, L. J., Paukner, A., & Suomi, S. J. (2010). Can traditions emerge from the interaction of stimulus enhancement and reinforcement learning? An experimental model. *American Anthropologist*, *112*, 257-269. https://doi.org/10.1111/j.1548-1433.2010.01224.x

McCall, R. B. (1974). Exploratory manipulation and play in the human infant. *Monographs of the Society for Research in Child Development*, 1-88. https://doi.org/10.2307/1166007

Melin, A. D., Young, H. C., Mosdossy, K. N., & Fedigan, L. M. (2014). Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. *Journal of Human Evolution*, *71*, 77-86. https://doi.org/10.1016/j.jhevol.2014.02.009

Meulman, E. J. M., Seed, A. M., & Mann, J. (2013). If at first you don't succeed… Studies of ontogeny shed light on the cognitive demands of habitual tool use. *Philosophical Transactions of the Royal Society B*, *368*, 20130050. https://doi.org/10.1098/rstb.2013.0050

Miller, S. (1973). Ends, means, and galumphing: Some leitmotifs of play 1. *American Anthropologist*, *75*, 87-98. https://doi.org/10.1525/aa.1973.75.1.02a00050

Moran, G. (1985). Behavioral description and its impact on functional inference. *Behavioral and Brain Sciences*, *8*, 186–187. https://doi.org/10.1017%2Fs0140525x0002032x

Morand-Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological Reviews*, *91*, 367-389. https://doi.org/10.1111/brv.12174

Morgan, B. J. T. (2010). *Applied stochastic modelling* (2nd ed.). CRC Press. https://doi.org/10.1201/b17188

Morgante, J. D., & Keen, R. (2008). Vision and action: The effect of visual feedback on infants' exploratory behaviors. *Infant Behavior and Development*, *31*, 729-733. https://doi.org/10.1016/j.infbeh.2008.04.007

Nadler, R. D., & Bartlett, E. S. (1997). Penile erection: A reflection of sexual arousal and arousability in male chimpanzees. *Physiology & Behavior*, *61*, 425-432. https://doi.org/10.1016%2Fs0031-9384%2896%2900454-4

Nahallage, C. A. D., & Huffman, M. A. (2007a). Acquisition and development of stone handling behavior in infant Japanese macaques. *Behaviour*, *144*, 1193-1215. https://doi.org/10.1163/156853907781890959

Nahallage, C. A. D., & Huffman, M. A. (2007b). Age-specific functions of stone handling, a solitary-object play behavior, in Japanese macaques (*Macaca fuscata*). *American Journal of Primatology*, *69*, 267-281. https://doi.org/10.1002/ajp.20348

Nahallage, C. A. D., & Huffman, M. A. (2008). Comparison of stone handling behavior in two macaque species: implications for the role of phylogeny and environment in primate cultural variation. *American Journal of Primatology*, *70*, 1124-1132. https://doi.org/10.1002/ajp.20610

Nahallage, C. A. D., Leca, J.-B., & Huffman, M. A. (2016). Stone handling, an object play behaviour in macaques: Welfare and neurological health implications of a bio-culturally driven tradition. *Behaviour*, *153*, 845-869. https://doi.org/10.1163%2F1568539x-00003361

Napier, J. R. (1956). The prehensile movements of the human hand. *Journal of Bone and Joint Surgery*, *38*, 902-913. https://doi.org/10.1302/0301-620x.38b4.902

Navarrete, A. F., Reader, S. M., Street, S. E., Whalen, A., & Laland, K. N. (2016). The coevolution of innovation and technical intelligence in primates. *Philosophical Transactions of the Royal Society B*, *371*, 20150186. https://doi.org/10.1098/rstb.2015.0186

Neilands, P. D., Jelbert, S. A., Breen, A. J., Schiestl, M., & Taylor, A. H. (2016). How insightful is 'insight'? New Caledonian crows do not attend to object weight during spontaneous stone dropping. *PLoS One*, *11*, e0167419. https://doi.org/10.1371/journal.pone.0167419

Neumann, C, Duboscq, J, Dubuc, C, Ginting, A, Irwan, AM, Agil, M, Widdig, A & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*, 911-921. https://doi.org/10.1016/j.anbehav.2011.07.016

Newell, K. M. (1986). Constraints on the development of coordination. In M. G. Wade & H. T. Whiting (Eds.), *Motor development in children: Aspects of coordination and control* (pp. 341–360). Martinus Nijhoff. https://doi.org/10.1007/978-94-009-4460-2_19

Newell, K. M., & Jordan, K. (2007). Task constraints and movement organization: A common language. In G. D. Broadhead & W. E. Davis (Eds.), *Ecological task analysis and movement* (pp. 5–23). Human Kinetics. https://doi.org/10.5040/9781492595434.ch-001

Newell, K. M., McDonald, P. V., & Baillargeon, R. (1993). Body scale and infant grip configurations. *Developmental Psychobiology*, *26*, 195-205. https://doi.org/10.1002/dev.420260403

Newell, K. M., Scully, D. M., Tenenbaum, F., & Hardiman, S. (1989). Body scale and the development of prehension. *Developmental Psychobiology, 22,* 1-13. https://doi.org/10.1002/dev.420220102

Nord, C. M. (2021). *The contexts of social learning in wild vervet monkeys*. [Doctoral thesis, University of Lethbridge].

Osiurak, F., & Badets, A. (2016). Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychological Review*, *123*, 534-568. https://doi.org/10.1037/rev0000027

Osiurak, F., & Danel, S. (2018). Tool use and dexterity: Beyond the embodied theory. *Animal Behaviour*, *139*, e1-e4. https://doi.org/10.1016/j.anbehav.2018.03.016

Osiurak, F., Jarry, C., & Le Gall, D. (2010). Grasping the affordances, understanding the reasoning: Toward a dialectical theory of human tool use. *Psychological Review*, *117*, 517-540. https://doi.org/10.1037/a0019004

Overington, S. E., Morand-Ferron, J., Boogert, N. J., Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour*, *78,* 1001-1010. https://doi.org/10.1016/j.anbehav.2009.06.033

Packard, A. (1972). Cephalopods and fish: The limits of convergence. *Biological Reviews*, *47*, 241-307. https://doi.org/10.1111/j.1469-185x.1972.tb00975.x

Palmer, C. F. (1989). The discriminating nature of infants' exploratory actions. *Developmental Psychology*, *25*, 885-893. https://doi.org/10.1037/0012-1649.25.6.885

Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, *45*, 525-567. https://doi.org/10.1111/j.1469-185x.1970.tb01176.x

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in *Cebus* monkeys and great apes. *Journal of Human Evolution,* 6, 623-641. https://doi.org/10.1016%2Fs0047-2484%2877%2980135-8

Pavličev, M., & Wagner, G. (2016). The evolutionary origin of female orgasm: evolution of female orgasm. *Journal of Experimental Zoology*, *326*, 326–337. https://doi.org/10.1002/jez.b.22690 https://doi.org/10.1002/jez.b.22690

Pellegrini, A. D., & Gustafson, K. (2005). Boys' and girls' uses of objects for exploration, play, and tools in early childhood. In A. D. Pellegrini & P. K. Smith (Eds.) *The nature of play: Great apes and humans* (pp. 113–138). New York: Guilford.

Pelletier, A. N., Kaufmann, T., Mohak, S., Milan, R., Nahallage, C. A. D., Huffman, M. A., …, & Leca, J.-B. (2017). Behavior systems approach to object play: Stone handling repertoire as a measure of propensity for complex foraging and percussive tool use in the genus *Macaca*. *Animal Behavior and Cognition*, *4*, 455-473. https://doi.org/10.26451%2Fabc.04.04.05.201

Pellis, S. M. (1991). How motivationally distinct is play? A preliminary case study. *Animal Behaviour*, *42*, 851-853. https://doi.org/10.1016/s0003-3472(05)80129-0

Pellis, S. M., & Pellis, V. C. (1987). Play-fighting differs from serious fighting in both target of attack and tactics of fighting in the laboratory rat Rattus norvegicus. *Aggressive Behavior*, *13*, 227-242. https://doi.org/10.1002/1098-2337(1987)13:4<227::aid-ab2480130406>3.0.co;2-c

Pellis, S. M., & Pellis, V. C. (1998). The structure-function interface in the analysis of play fighting. In M. Bekoff & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative and ecological perspectives* (pp. 115-140). Cambridge, UK: Cambridge University Press. https://doi.org/10.1017%2Fcbo9780511608575.007

Pellis, S. M., Pellis, V. C., Pelletier, A., & Leca, J.-B. (2019). Is play a behavior system, and, if so, what kind? *Behavioural Processes*, *160*, 1-9. https://doi.org/10.1016/j.beproc.2018.12.011

Peshek, K. R., & Blumstein, D. T. (2011). Can rarefaction be used to estimate song repertoire size in birds? *Current Zoology*, *57*, 300-306. https://doi.org/10.1093/czoolo/57.3.300

Peterson, J. V., Fuentes, A., & Wandia, I. N. (2021). Affiliation among subadult males varies between populations of long-tailed macaques. *Acta Ethologica*, *24*, 9-21. https://doi.org/10.1007/s10211-020-00356-5

Pierce Jr, J. D. (1986). A review of tool use in insects. *Florida Entomologist*, *69*, 95-104. https://doi.org/10.2307/3494748

Polizzi di Sorrentino, E. P., Sabbatini, G., Truppa, V., Bordonali, A., Taffoni, F., Formica, …, & Visalberghi, E. (2014). Exploration and learning in capuchin monkeys (*Sapajus* spp.): the role of action–outcome contingencies. *Animal Cognition*, *17*, 1081–1088. https://doi.org/10.1007/s10071-014-0740-5

Pouydebat, E., Gorce, P., Coppens, Y., & Bels, V. (2009). Biomechanical study of grasping according to the volume of the object: human versus non-human primates. *Journal of Biomechanics*, *42*, 266-272. https://doi.org/10.1016/j.jbiomech.2008.10.026

Povinelli, D. J. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford University Press. https://doi.org/10.1097/01.nmd.0000106127.32329.d1

Power, T. G. (1999). *Play and exploration in children and animals*. Psychology Press. https://doi.org/10.4324/9781410603623

Quiatt, D., & Huffman, M. A. (1993). On home bases, nesting sites, activity centers, and new analytic perspectives. *Current Anthropology*, *34*, 68–70. https://doi.org/10.1086/204139

R Core Team. (2013). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org

Ramsey, J. K., & McGrew, W. C. (2005). Object play in great apes: Studies in nature and captivity. In A.D. Pellegrini & J.P. Smith (Eds.), *The nature of play: Great apes and humans*, (pp. 89-112). Guilford Press.

Randerath, J., Goldenberg, G., Spijkers, W., Li, Y., & Hermsdörfer, J. (2011). From pantomime to actual use: how affordances can facilitate actual tool-use. *Neuropsychologia*, *49*, 2410-2416. https://doi.org/10.1016/j.neuropsychologia.2011.04.017

Rasa, O. A. E. (1984). A motivational analysis of object play in juvenile dwarf mongooses (*Helogale undulata rufula*). *Animal Behaviour*, *32*, 579-589. https://doi.org/10.1016%2Fs0003-3472%2884%2980295-x

Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, *22*, 787-805. https://doi.org/10.1023/a:1012069500899

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

Reaux, J. E., & Povinelli, D. J. (2000). The tube-trap problem. In D. J. Povinelli (Ed.) *Folk physics for apes: The chimpanzee's theory of how the world works* (pp. 108-131). Oxford University Press. https://doi.org/10.1097/01.nmd.0000106127.32329.d1

Rius, M. M., Cozzi, A., Bienboire-Frosini, C., Teruel, E., Chabaud, C., Monneret, P., ... & Pageat, P. (2018). Selection of putative indicators of positive emotions triggered by object and social play in mini-pigs. *Applied Animal Behaviour Science, 202*, 13-19. https://doi.org/10.1016/j.applanim.2018.02.002

Root-Bernstein, M., Narayan, T., Cornier, L., & Bourgeois, A. (2019). Context-specific tool use by *Sus cebifrons*. *Mammalian Biology*, *98*, 102-110. https://doi.org/10.1016/j.mambio.2019.08.003

Roth, L., Briken, P., & Fuss, J. (2022). Masturbation in the animal kingdom. *Journal of Sex Research.* https://doi.org/10.1080/00224499.2022.2044446

Rowe, C., & Healy, S. D. (2014). Measuring variation in cognition. *Behavioral Ecology*, *25*, 1287-1292. https://doi.org/10.1093/beheco/aru090

Russon, A. E., van Schaik, C. P., Kuncoro, P., Ferisa, A., Handayani, D. P., & van Noordwijk, M. A. (2009). Innovation and intelligence in orangutans. In S. A., Wich, T. M., Setia, & C. P., van Schaik (Eds.). *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 279-298). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199213276.003.0020

Rutz, C., & St Clair, J. J. (2012). The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behavioural Processes*, *89*, 153-165. https://doi.org/10.1016/j.beproc.2011.11.005

Samuni, L., Lemieux, D., Lamb, A., Galdino, D., & Surbeck, M. (2022). Tool use behavior in three wild bonobo communities at Kokolopori. *American Journal of Primatology*, *84*, e23342. https://doi.org/10.1002/ajp.23342

Sanz, C. M., & Morgan, D. B. (2013). The social context of chimpanzee tool use. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 161-175). Cambridge University Press. https://doi.org/10.1017/cbo9780511894800.011

Sanz, C. M., Call, J., & Boesch, C. (2013). *Tool use in animals: Cognition and ecology*. Cambridge University Press. https://doi.org/10.1017/cbo9780511894800

Sciaky, L., Gunst, N., Wandia, I. N., & Leca, J.-B. (2022). Dyadic response facilitation of object play in Balinese long-tailed macaques. *Behavioural Processes*, *203*, 104765. https://doi.org/10.1016/j.beproc.2022.104765

Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology*, *16*, 697-701. https://doi.org/10.1016/j.cub.2006.02.066

Seed, A., Emery, N., & Clayton, N. (2009). Intelligence in corvids and apes: A case of convergent evolution? *Ethology*, *115*, 401-420. https://doi.org/10.1111/j.1439-0310.2009.01644.x

Shively, C. A., Willard, S. L., Register, T. C., Bennett, A. J., Pierre, P. J., Laudenslager, M. L., ... & Kritchevsky, S. B. (2012). Aging and physical mobility in group-housed Old World monkeys. *Age*, *34*, 1123-1131. https://doi.org/10.1007/s11357-011-9350-1

Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. JHU Press.

Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences*. McGraw-HiU Book Company.

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P. O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology & Evolution*, *30*, 50-60. https://doi.org/10.1016/j.tree.2014.11.004

Simberloff, D. (1978). Use of rarefaction and related methods in ecology. In K. L. Dickson, J. Jr. Cairns, & R.J. Livingston (Eds.). *Biological Data in Water Pollution Assessment: Quantitative and Statistical Analyses* (pp. 150-165). American Society for Testing and Materials.

Simon, T., & Smith, P. K. (1985). Play and problem-solving: a paradigm questioned. *Merrill-Palmer Quarterly*, *31*, 265–277.

Sinha, A. (1997). Complex tool manufacture by a wild bonnet macaque, *Macaca radiata*. *Folia Primatologica, 68*, 23-25. https://doi.org/10.1159/000157227

Sirianni, G., Wittig, R. M., Gratton, P., Mundry, R., Schüler, A., & Boesch, C. (2018). Do chimpanzees anticipate an object's weight? A field experiment on the kinematics of hammer-lifting movements in the nut-cracking Taï chimpanzees. *Animal Cognition, 21*, 109-118. https://doi.org/10.1007/s10071-017-1144-0

Slater, P. J. B. (1981). Individual differences in animal behavior. In P.P.G. Bateson, & P.H. Klopfer, (Eds.), *Perspectives in Ethology, Volume 4* (pp. 35-49). Springer. https://doi.org/10.1007/978-1-4615-7575-7_2

Smith, P. K. (1988). Children's play and its role in early development: A re-evaluation of the 'play ethos' In A. D. Pellegrini (Ed.), *Psychological bases for early education* (pp. 207–226). John Wiley & Sons.

Smith, P. K. (2010). *Children and play*. Wiley-Blackwell. https://doi.org/10.1002/9781444311006

Smith, P. K., & Connolly, K. J. (1980). *The ecology of preschool behaviour*. Cambridge University Press.

Smith, P. K., & Dutton, S. (1979). Play training in direct and innovative problem solving. *Child Development*, *4*, 830–836. https://doi.org/10.2307/1128950

Smith, P. K., Simon, T., & Emberton, R. (1985). Play, problem-solving and experimenter effects: a replication of Simon and Smith (1983). *British Journal of Developmental Psychology*, *3*, 105–107. https://doi.org/10.1111/j.2044-835x.1985.tb00961.x

Sol, D., Griffin, A. S., & Bartomeus, I. (2012). Consumer and motor innovation in the common myna: the role of motivation and emotional responses. *Animal Behaviour*, *83*, 179-188. https://doi.org/10.1016/j.anbehav.2011.10.024

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PloS one*, *6*, e19535. https://doi.org/10.1371/journal.pone.0019535

Sosnowski, M. J., Benítez, M. E., & Brosnan, S. F. (2022). Endogenous cortisol correlates with performance under pressure on a working memory task in capuchin monkeys. *Scientific Reports*, *12*, 1-10. https://doi.org/10.1038/s41598-022-04986-6

Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P., & Fragaszy, D. (2011). Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of Human Evolution*, *61*, 97-107. https://doi.org/10.1016/j.jhevol.2011.02.010

Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: training for the unexpected. *The Quarterly Review of Biology*, *76*, 141-168. https://doi.org/10.1086/393866

St Clair, J. J. H., & Rutz, C. (2013). New Caledonian crows attend to multiple functional properties of complex tools. *Philosophical Transaction of the Royal Society B, 368*, 20120415. https://doi:10.1098/rstb.2012.0415

St. Amant, R., & Horton, T. E. (2008). Revisiting the definition of animal tool use. *Animal Behaviour*, *75*, 1199-1208. https://doi.org/10.1016/j.anbehav.2007.09.028

Stephens, J. & Krebs, D. (1986). *Foraging Theory*. Princeton University Press. https://doi.org/10.1515/9780691206790

Stephenson, G. R. (1973). Testing for group-specific communication patterns in Japanese macaques. In E.W. Menzel (Ed.), *Precultural Primate Behavior* (pp. 51-75). Karger.

Sutton-Smith B. (2001). *The ambiguity of play*. Harvard University Press.

Sylva, K., Bruner, J., & Genova, P. (1976). The role of play in the problem-solving of children 3–5 years old. In J. Bruner, A. Jolly, & K. Sylva (Eds.), *Play: Its role in development and evolution* (pp. 244–257). Penguin.

Tan, A. W. (2017). From play to proficiency: The ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. *Journal of Comparative Psychology*, *131*, 89-114. https://doi.org/10.1037/com0000068

Taylor, A. H., Hunt, G. R., Medina, F. S., & Gray, R. D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society of London B*, *276*, 247-254. https://doi.org/10.1098/rspb.2008.1107

Temerlin, M. K. (1975). *Lucy: growing up human: a chimpanzee daughter in a psychotherapist's family*. Science & Behavior Books.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B*, *364*, 2405–2415. https://doi.org/10.1098/rstb.2009.0052

Teschke, I., Wascher, C. A. F., Scriba, M. F., von Bayern, A. M. P., Huml, V., Siemers, B., & Tebbich, S. (2013). Did tool-use evolve with enhanced physical cognitive abilities? *Philosophical Transactions of the Royal Society B*, *368*, 20120418. https://doi.org/10.1098/rstb.2012.0418

Thierry, B., Anderson, J. R., Demaria, C., Desportes, C. & Petit, O. (1994). Tonkean macaque behavior from the perspective of the evolution of Sulawesi macaques. In J. J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt, (Eds.) *Current primatology, Vol. II: Social development, learning and behavior* (pp. 103-117). Université Louis Pasteur.

Thomsen, R., & Soltis, J. (2004). Male masturbation in free-ranging Japanese macaques. *International Journal of Primatology*, *25*, 1033-1041. https://doi.org/10.1023/b:ijop.0000043350.75897.89

Thomsen, R., Soltis, J., & Teltscher, C. (2003). Sperm competition and the function of male masturbation in non-human primates. In C. B., Jones (Ed.), *Sexual selection and reproductive competition in primates: new perspectives and directions* (pp. 437-453). American Society of Primatologists.

Thornton, A., & Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B*, *367*, 2773-2783. https://doi.org/10.1098/rstb.2012.0214

Thouless, C. R., Fanshawe, J. H., & Bertram, B. C. R. (1989). Egyptian vultures *Neophron percnopterus* and ostrich *Struthio camelus* eggs: the origins of stone-throwing behavior. *Ibis*, *131*, 9-15. https://doi.org/10.1111/j.1474-919x.1989.tb02737.x

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford University Press.

Torigoe, T. (1985). Comparison of object manipulation among 74 species of non-human primates. *Primates*, *26*, 182-194. https://doi.org/10.1007/bf02382017

Torigoe, T. (1987). Further report on object manipulation in non-human primates: A comparison within 13 species of the genus *Macaca*. *Primates, 28*, 533-538. https://doi.org/10.1007/bf02380867

Tudor-Hart, B. (1955). *Toys, play and discipline in childhood.* Routledge & Kegan Paul.

van Elk, M., van Schie, H. T., & Bekkering, H. (2009). Action semantic knowledge about objects is supported by functional motor activation. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1118–1128. https://doi.org/10.1037/a0015024

van Schaik, C. P., & van Noordwijk, M. A. (1985). Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology, 206*, 533-549. https://doi.org/10.1111/j.1469-7998.1985.tb03557.x

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., ... & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, *299,* 102-105. https://doi.org/10.1126/science.1078004

van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, *36*, 719-741. https://doi.org/10.1006/jhev.1999.0304

Vandenberg, B. (1981). The role of play in the development of insightful tool-using strategies. *Merrill-Palmer Quarterly, 27*, 97-109.

Vandenberg, B. (1990). Play and problem solving: An elusive connection*. Merrill-Palmer Quarterly*, *36*, 261-272.

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27,* 1413-1432. https://doi.org/10.1007/s11222-016-9696-4

Visalberghi, E., & Fragaszy, D. (2006). What is challenging about tool use? The capuchin's perspective. In T. R. Zentall, & E. A. Wasserman (Eds.), *Comparative cognition:*

*Experimental explorations of animal intelligence* (pp. 529-552). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195377804.003.0028

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

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P., & Fragaszy, D. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*, *19*, 213–17. https://doi.org/10.1016/j.cub.2008.11.064

Visalberghi, E., Di Bernardi, C., Marino, L. A., Fragaszy, D., & Izar, P. (2017). Female bearded capuchin monkeys (*Sapajus libidinosus*) use objects to solicit the sexual partner. *Journal of Comparative Psychology*, *131*, 207. https://doi.org/10.1037/com0000072

Völter, C. J., & Call, J. (2014). The cognitive underpinnings of flexible tool use in great apes. *Journal of Experimental Psychology: Animal Learning and Cognition*, *40*, 287-302. https://doi.org/10.1037/xan0000025

von Bayern, A. M., Jacobs, I., & Osvath, M. (2020). Tool-using puffins prickle the puzzle of cognitive evolution. *Proceedings of the National Academy of Sciences, 117*, 2737-2739. https://doi.org/10.1073/pnas.1922117117

Wasserman, E. A. (2021). *As if by design: How creative behaviors really evolve*. Cambridge University Press. https://doi.org/10.1017/9781108774895

Waterman, J. M. (2010). The adaptive function of masturbation in a promiscuous African ground squirrel. *PLoS One*, *5,* e13060. https://doi.org/10.1371/journal.pone.0013060

Webber, Q. M. R., Schneider, D. C., & Vander Wal, E. (2020). Is less more? A commentary on the practice of 'metric hacking' in animal social network analysis. *Animal Behaviour*, *168*, 109-120. https://doi.org/10.1016/j.anbehav.2020.08.011

Webster, M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, *582*, 337–340. https://doi.org/10.1038/d41586-020-01751-5

Westergaard, G. C., & Fragaszy, D. M. (1987). The manufacture and use of tools by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *101*, 159-168. https://doi.org/10.1037/0735-7036.101.2.159

Wheatley, B. P. (1988). Cultural behavior and extractive foraging in *Macaca fascicularis*. *Current Anthropology*, *29*, 516-519. https://doi.org/10.1086/203670

Whiten, A., & Mesoudi, A. (2008). Establishing an experimental science of culture: Animal social diffusion experiments. *Philosophical Transactions of the Royal Society B*, *363*, 3477–3488. https://doi.org/10.1098/rstb.2008.0134

Whiten, A., Harrison, R. A., McGuigan, N., Vale, G. L., & Watson, S. K. (2022). Collective knowledge and the dynamics of culture in chimpanzees. *Philosophical Transactions of the Royal Society B*, *377*, 20200321. https://doi.org/10.1098/rstb.2020.0321

Wu, H. G., Miyamoto, Y. R., Castro, L. N. G., Ölveczky, B. P., & Smith, M. A. (2014). Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. *Nature Neuroscience*, *17*, 312-321. https://doi.org/10.1038/nn.3616

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, *106*, 283-295. https://doi.org/10.1002/(sici)1096-8644(199807)106:3<283::aid-ajpa2>3.0.co;2-o

Yerkes, R. M. (1907). *The dancing mouse: A study in animal behavior*. Macmillan. https://doi.org/10.5962/bhl.title.1047

Zou, H., Liu, M., Luan, Y., Xie, Q., Cheng, Z., Zhao, G., ... & Yu, L. (2017). Pattern of novel object exploration in cynomolgus monkey *Macaca fascicularis*. *Journal of Medical Primatology*, *46*, 19-24. https://doi.org/10.1111/jmp.12251

Zullo, L., & Hochner, B. (2011). A new perspective on the organization of an invertebrate brain. *Communicative & Integrative Biology*, *4*, 26-29. https://doi.org/10.4161/cib.13804

# APPENDICES

## Appendix A

**Supplementary Material S2.1 –** Ethogram comprised of 38 stone handling behaviors performed by the Balinese long-tailed macaques of Ubud (Bali, Indonesia). Updated from Pelletier et al. (2017).

**Bite (BIT):** To bring a stone to the mouth and place it between the teeth.

*Comments:* This pattern is typically performed using one or both hands, occasionally accompanied by foot support. Though most frequently performed by bringing a stone up to the mouth, this pattern may also occur when an individual brings their face down to a stone that is placed on a surface, though not when embedded in a substrate. It may extend with the individual holding the stone, still visible, between its teeth without manual support. However, this pattern is different from Move Inside Mouth, during which the stone disappears inside the mouth.

**Carry (CAR):** To hold or cradle a stone while moving from one place to another.

*Comments:* This pattern can be performed by using either the hands or mouth to grasp the stone. Stones are either held or cuddled against the body while the individual moves in a bipedal, tripedal, or quadrupedal manner.

**Clack (CLK):** To strike two stones, or a stone and an object, together with both hands moving in a symmetrical clapping gesture.

*Comments:* This pattern is performed utilizing either a precision or power grip, and always occurring while the stones are being held in front of the individual, away from the ground and other body parts.

**Cover (COV):** To lightly place an object upon or over a stone with the hands.

*Comments:* This pattern often resembles a peek-a-boo type of activity, where the stone is fully covered, and then frequently uncovered. Items regularly used to perform this activity are leaves, plastic, cloth, or dried grass. This pattern was not distinguished from "Wrap" (WRP) in previous papers on Japanese macaques (Leca et al., 2007b).

**Cuddle (CUD):** To grab a stone with the hand and hold it against a body part.

*Comments:* Body parts frequently utilized in this activity include the chest, abdomen, groin, and side of leg. This pattern can be performed with stones of various sizes, however frequently occurs with one large stone, or a series of smaller stones. Can be performed either on the ground, or away from the ground while held against the upper body. Occasionally, this pattern may occur without manual support, by placing a stone onto a body part (e.g., inner thigh), away from the ground.

**Dislodge (DSL):** To (potentially attempt to) remove a stone embedded in a substrate by scratching or rubbing it with the fingertips or mouth.

*Comments:* Stones are not always extracted from the substrate, however when they are, individuals either incorporate the newly unearthed stone(s) into the SH activities, or discard them immediately after dislodging. This pattern is most frequently performed on a dirt surface. When using the mouth to dislodge a stone, the teeth are used in place of the fingertips, moving in a similar motion.

**Flint (FLN):** To strike a stone held in one hand against another stone or object, that is held stationary in another body part.

*Comments:* Though this pattern is performed most frequently with the hands, utilizing either a power or precision grip, it is sometimes performed by using the mouth to hold the stationary stone (i.e., Flint in mouth). This pattern is always performed away from the ground.

**Gather (GAT):** To bring a stone to oneself, often collecting stones into a pile in front of oneself.

*Comments:* This pattern can be performed in a number of different ways, including picking motions, gathering large amounts of stones by sliding them towards oneself on the ground using the arms to guide them towards oneself, or the stacking of stones on top of one another. Stones can be gathered using both the hands and the feet.

**Grasp (GRP):** To clutch or touch a stone placed on the ground, in front of, or beside, oneself.

*Comments:* This pattern can be performed with the hands or the feet, with either a (tight or loose) power grip or an open palm. This pattern frequently occurs while the individual's attention is elsewhere, or while another SH pattern is being performed.

**Grasp-Walk (GRW):** To clutch a stone in the palm of the hand while walking.

*Comments:* This pattern can be performed by either the hands or the feet, however it is most frequently held in the palm of the hand while the individual moves in a quadrupedal manner.

**Groom (GRM):** To pick at or scratch a stone with the fingertips or with the teeth.

*Comments:* Stones may be held or grasped in the hand or foot, or placed on the ground. This pattern resembles what would be observed during allo- or self-grooming sessions, however the actions are directed towards stones rather than a monkey's fur. Often, this pattern is performed on a stone covered by, or wrapped in, other objects, such as leaves or cloth. When performed with the teeth, the stone is usually held away from the ground, and the individual uses its teeth to pick at the stone, usually wrapped in other objects, such as leaves and cloth. However, this pattern is different from Bite because the front teeth pick at and pluck the stone, and the stone is not put between the teeth to bite it.

**Hold (HLD):** To pick up a stone and hold onto or clutch it for some time, keeping it away from both the body and other surfaces.

*Comments:* This pattern can be performed by both the hands and the feet, most frequently utilizing a power grip. Occasionally, the arm holding the stone may be resting on the individual's thigh, but the stone is kept away from the body.

**Lick (LIC):** To bring a stone to the mouth and touch it with the tongue.

*Comments:* This pattern is typically performed using one or both hands, occasionally accompanied by foot support. This pattern is most frequently performed by bringing a stone to the face, rather than bringing the face down towards a stone that is placed on a substrate.

**Move And Push/Pull (MAP):** To clutch a stone that is placed on the ground with the arm(s) extended in front of oneself, and walk either forward or backward while the stone is rubbed against the ground.

*Comments:* This pattern can be performed using either one or both hands, and is sometimes performed in combination with a “bite” (BIT).

**Move Inside Mouth (MIM):** To insert a stone inside the mouth and move it with the tongue or the hands.

*Comments:* During this activity, the stone fully disappears inside the mouth. Stones can often be seen moving through cheek when performed.

**Pick And Drop (PAD):** To repeatedly take a hold of a stone with the hands and let it fall to the ground or into a cavity.

*Comments:* This pattern may be performed by picking up a stone and dropping it straight onto the ground, or the individual may let the stone roll down a body part, such as the arms, when the stone is being dropped. When using smaller stones, individuals frequently utilize a precision grip, and the action may resemble picking up small food items and quickly discarding them. Occasionally, this pattern is performed closely to the ground, but the release of the stone by the hand occurs before contact with the ground, differentiating this pattern from Pound.

**Pick Up (PUP):** To take hold of a stone with one hand and place it into the other hand.

*Comments:* This action requires that the stone picked up be completely let go of by the original hand once placed into the open supporting hand. This action is performed most frequently when hands are placed in front of the body, away from any surface or other body parts.

**Pound (PND):** To strike a stone on the ground or an object, using a power grip.

*Comments:* Stones are typically pounded on a hard surface such as concrete or packed dirt. Most frequently utilized target objects are leaves, cloth, nuts or other stones. This pattern may also be performed using a fluid motion and instantaneously pushing the stone forward once contact with the ground is made. When handling small stones, the hand may open while approaching the surface, to strike the stone on the ground. However, this pattern is different from Pick and Drop, because the release of the stone by the hand occurs just before reaching the ground.

**Pound-Drag (PDR):** To strike a stone on the ground using a fluid motion and instantaneously drag the stone backwards once contact with the ground is made.

*Comments:* This pattern may resemble a “Pound” (PND) that is combined with a “Rub” (RUB), however, the pattern is performed without interruption as one fluid motion, and the latter rubbing portion of the pattern is interrupted as it does not include both a forward and backwards motion, only a backwards dragging motion of the hand.

**Push-Through (PTH):** To exert force on a stone, typically with the palm of the hand or the fingers, in an apparent attempt to move the stone through a cavity, like a hole or a pipe.

*Comments:* This SH behavioral element (or SH pattern) may resemble Pick and Drop, when repeatedly performed; however, when performing a Push-Through the stone is not dropped. It may also resemble Dislodge, but in Push-Through, the stone is pushed or clutched, rather than scratched or rubbed with the fingertips. Most frequently, stones are stuck in the cavity and the monkey aims to free the stone from the cavity by performing a pushing action.

**Roll (ROL):** To move a stone back and forth on a substrate, or body part, in a rolling or rubbing motion, performed with a loose grip or open palms.

*Comments:* Though this pattern is most frequently performed with the hands, it is sometimes performed with the feet. This pattern resembles “Rub” (RUB), however the hand grip utilized for this activity is different.

**Roll In Hands (RIH):** To roll or rotate a stone back and forth in both hands, moving in an alternating sliding gesture, with a loose grip.

*Comments:* Stones are typically rolled along the length of the hand, utilizing the palms and fingers of both hands. This action can be performed either slowly or quickly. Stones are always held away from the ground or body when this pattern is performed.

**Roll With Fingers (RWF):** To move a stone back and forth on a substrate in a rolling motion using only the fingertips.

*Comments:* This pattern differs from “roll” (ROL) as only the fingertips are used to perform this pattern rather than utilizing the palm. A traditional grip is not utilized, rather the fingertips are pressed onto the stone with enough pressure as to guide the stone a short distance back and forth. This pattern is most frequently performed directly in front of the individual, using both hands to presumably stabilize and guide the stone. Stones used for this activity are very round.

**Rub (RUB):** To slide or move a stone back and forth on a substrate, or a body part, utilizing a power or precision grip.

*Comments:* Though this pattern may resemble “Roll” (ROL) the hand grip utilized in this activity is different. This pattern can be performed on the ground, or other substrates; when a stone is rubbed on a body part, the stone can slide, move back and forth, or in circular motion, with a power or precision grip. When used to groom other individuals, this pattern differs from “Groom” (GRM), as the focus is to rub the stone along the fur of an individual, potentially using it to assist in the grooming process, rather than to groom the stone itself.

**Rub Together (RBT):** To touch and move (in a rubbing motion) the surface of two stones together in an alternating sliding gesture.

*Comments:* This pattern is always performed with the hands placed in front of the individual, away from the ground and other body parts, utilizing either a power or precision grip.

**Rub With Hands (RWH):** To hold or grasp a stone with one hand (or foot) and move the palm of the other hand along the surface of the stone while applying firm pressure.

*Comments:* The hand performing the rubbing motion can either move back and forth along the surface of the stone(s), or perform the rubbing action in only one direction multiple times. Though this pattern most frequently occurs when stones are being held away from the ground or body, or in the water, it can also be performed when a stone is being grasped on the ground.

**Scatter (SCA):** To disperse a stone with the hands in a scattering motion on a substrate, in front of oneself.

*Comments:* This pattern utilizes an open hand moving in a sweeping gesture across a substrate. This pattern differs from "gather" (GAT) as it does not bring stones towards the performer, rather moves them away, sweeping them to the side.

**Shake In Hands (SIH):** To move a stone in an open palmed hand by moving the hand back and forth, up and down, or repeatedly flexing fingers towards palm and back out again.

*Comments:* The placement of the hand in this activity may sometimes resemble "cuddle" (CUD) as the back of the hand can be held against or close to the body when performed. This pattern is always performed while the hand is away from the ground.

**Shift In Hands (SFH):** To completely transfer a stone from one hand to the other repeatedly, utilizing a cupping motion of the hands.

*Comments:* The entire hand is utilized in this activity as the curving of the fingers allows for the cupping motion required to completely pass the stone(s) off into the other hand each time. This pattern can be performed either slowly or quickly. Stones are always held away from the ground or body when this pattern is performed.

**Slam (SLM):** To pick up a stone and shove it to a substrate (e.g., ground) or an object, without using a power grip, but accompanying the stone by applying pressure on its top and/or side surfaces with the hand, either by pushing or slapping.

*Comments:* This SH behavioral element (or SH pattern) may resemble Pound, but the stone is not grasped by using a power grip. Most frequently, the stones used to Slam are larger than the monkey's hand. This SH pattern may also resemble Pick and Drop, when repeatedly performed; however, when performing a Slam, the stone is pushed or slapped with the hand instead of dropped from the hand.

**Slap (SLA):** To hit a stone in a slapping motion with the palm or fingertips of the hand.

*Comments:* This pattern may resemble "tap" (TAP); however, it typically occurs one to few times, and is not used to hit or move a stone towards another stone, object, or body part. This pattern can be performed while a stone is being held, grasped, or on the ground, and can be performed with one or both hands.

**Slap-Roll (SLR):** To hit a stone in a slapping motion with the palm or fingertips of one hand, immediately followed by the rotation or rolling of the stone back and forth between both hands, moving in an alternating sliding gesture.

*Comments:* This pattern resembles a combination of two other SH patterns, namely a "slap" (SLA), followed by a "roll in hands" (RIH); however, it is performed only on the ground, rather than being held away from the ground or body while performing. This pattern is idiosyncratic, performed by only one individual.

**Sniff (SNF):** To bring a stone to the nose and smell it by inhaling.

*Comments:* This pattern is most frequently performed by bringing a stone to the nose using the hands, however it can also occur when an individual brings their face down to a stone that is placed on a substrate. The duration of this pattern is typically very short, however longer durations are sometimes achieved by performing repeatedly.

**Tap (TAP):** To move or tap a stone in a repeated sweeping gesture using the fingertips, against a substrate, object, or body part.

*Comments:* This pattern may resemble “slap” (SLA); however, it occurs multiple times, and the stone is tapped against another object, stone, or body part. Body parts most frequently involved include the hands, feet, tail, groin, and legs. This pattern can be performed in combination with objects and body parts (i.e., to tap a stone against a stone that is held by the foot) or just involving a body part (i.e., to tap a stone against the genital region, onto the side of the leg, or onto the other hand). This pattern is performed with one or both hands.

**Throw (THR):** To toss a stone underhand, either in front of or behind the individual.

*Comments:* This pattern differs from the locomotive pattern “toss-walk” (TSW) as the individual generally performs this action while remaining stationary. Stones are thrown with the hands only, utilizing either one or both hands to perform the action.

**Toss And Catch (TAC):** To lightly throw a stone upwards and catch it with one or both hands, or with the mouth.

*Comments:* This pattern is idiosyncratic, only performed by one individual.

**Toss-Walk (TSW):** To lightly throw a stone, underhand, ahead of oneself while walking, then take hold of and clutch it in the palm of the hand.

*Comments:* This pattern differs from “throw” as it is not performed stationary, but while the individual is walking in a quadrupedal manner. The distance travelled by the stone is generally much shorter than with the pattern “throw,” allowing the stone to be retrieved again after the tossing action occurs.

**Wrap (WRP):** To encase or enclose a stone in an object, using the hands, either tightly or loosely, in what appears to be an attempt to bend or fold the object around the stone.

*Comments:* Items frequently used to wrap stones include leaves, cloth, plastic, twigs, and bundles of dried grass. This action can be performed either while the stone is placed on the ground, or while the stone is being held. The unwrapping of a stone that was previously wrapped with an object is also classified under this pattern.

**Note.** “Object” refers to a variety of objects other than stones, including vegetal materials and man-made items (e.g., wooden stick, leaves, grass, nuts, cloth, nylon rope, plastic bag, metallic rod).

**Supplementary Material S2.2 –** Example of stone handling behavior in three old juvenile Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/wuSkQ08wr20

**Supplementary Material S2.3** – *Z-Scores for Percentage of Duration for Each SH Behavior for 40 Individuals. Green Cells Indicate Preferred SH Behaviors for Each Individual (Z-Score > 1.96). † = Variable Log-Transformed; ‡ = Variable Not Normally Distributed.*

| Subject | Bite† | Carry | Clack‡ | Cover† | Cuddle† | Dislodge‡ | Flint‡ | Gather† | Grasp |
|---|---|---|---|---|---|---|---|---|---|
| Cipria | 1.00 | 1.24 | 0.40 | 0.09 | 1.33 | 0.00 | -0.45 | 1.80 | 0.45 |
| Gnome | 1.00 | 2.02 | -0.28 | 0.65 | 0.95 | -0.12 | -0.45 | -0.82 | 2.51 |
| Lady-Qui-Louche | 0.85 | 2.08 | -0.28 | 1.36 | 1.03 | -0.22 | -0.45 | 2.27 | 1.07 |
| Megamind | 0.32 | 0.08 | -0.11 | 0.42 | 0.43 | -0.22 | -0.30 | 0.96 | -0.40 |
| Benji | 1.13 | 0.21 | -0.28 | 1.14 | 0.51 | -0.22 | -0.45 | 1.38 | 0.01 |
| Gennaro | 2.37 | -0.74 | -0.28 | -0.90 | -0.74 | -0.22 | -0.45 | 0.35 | -0.02 |
| Morty | 0.82 | 0.86 | -0.20 | -0.18 | 0.11 | 0.10 | -0.45 | 0.40 | -0.04 |
| Scarface | -0.71 | 0.31 | -0.28 | -1.56 | -1.26 | -0.18 | -0.45 | 0.44 | 0.80 |
| Grinch | 0.57 | 0.79 | -0.28 | -1.12 | 1.66 | -0.22 | -0.45 | -0.72 | -1.59 |
| Kappa | 0.63 | 1.38 | -0.28 | 0.04 | 2.43 | -0.22 | 0.21 | -1.33 | -0.53 |
| Kyla | -0.21 | 0.24 | -0.28 | -0.18 | -0.36 | -0.22 | 0.11 | -1.19 | 1.78 |
| Pirata | -0.68 | -0.02 | -0.28 | -1.40 | 0.21 | -0.22 | -0.03 | 0.35 | -1.72 |
| Bass | 1.35 | -0.68 | -0.28 | 1.53 | 0.43 | -0.22 | -0.30 | 0.82 | -0.71 |
| C-17 | 0.66 | -1.40 | -0.28 | 1.53 | -1.04 | -0.22 | -0.45 | -1.10 | -0.66 |
| Lookout | -0.21 | -0.85 | 5.65 | -0.62 | -0.80 | -0.22 | 1.77 | -0.07 | -0.09 |
| Sick Boy | -0.15 | -0.84 | -0.28 | 1.14 | -0.22 | -0.22 | 0.53 | 0.44 | -0.34 |
| Duchess | 1.04 | -0.11 | -0.28 | 2.41 | 1.31 | -0.04 | -0.45 | -0.96 | 0.05 |
| Encrenca | 0.85 | 0.68 | 0.06 | -1.62 | -0.58 | -0.10 | 4.03 | 0.96 | -0.79 |
| Langur | 0.69 | 0.29 | -0.28 | 0.37 | 0.49 | -0.22 | -0.45 | -1.28 | 0.95 |
| S3 | -0.96 | -0.87 | -0.28 | -0.62 | -1.15 | -0.22 | -0.45 | 1.52 | 0.61 |
| Charlie | -1.55 | 0.76 | 1.73 | 0.15 | -0.03 | -0.22 | -0.45 | 1.66 | -0.77 |
| Littlefinger | -1.27 | -0.47 | -0.20 | 0.26 | -0.44 | -0.22 | -0.45 | 0.16 | -0.18 |
| Pinocchio | -1.27 | -1.38 | -0.28 | -0.29 | -1.26 | -0.22 | -0.45 | -0.07 | 0.68 |
| White Eyebrows | -0.15 | -1.11 | -0.28 | 0.20 | -0.22 | -0.22 | -0.45 | -0.72 | 0.30 |
| Beardy | -0.18 | -0.35 | 0.04 | -1.62 | -0.74 | -0.22 | -0.45 | 0.16 | 1.47 |
| Musty | 0.76 | 0.50 | -0.28 | -0.84 | 0.73 | -0.22 | -0.45 | -0.40 | 0.48 |
| Punk | 1.47 | 2.93 | -0.28 | 0.09 | 0.57 | -0.12 | -0.45 | -0.40 | -1.02 |
| S12 | 0.10 | -0.28 | -0.28 | -0.18 | 2.48 | -0.22 | -0.45 | -1.33 | 1.37 |
| Danger | -0.33 | -0.76 | -0.28 | -1.17 | -0.63 | -0.22 | -0.45 | -0.44 | -0.28 |
| Ramsey | -1.27 | -0.48 | -0.28 | 1.75 | -0.06 | -0.22 | -0.45 | 0.58 | 0.67 |
| Ronald | 0.38 | -0.21 | -0.28 | -0.95 | -0.11 | -0.22 | -0.30 | 1.24 | -0.91 |
| Temple Baggy | -0.08 | -1.10 | -0.28 | -0.29 | -0.80 | -0.22 | -0.45 | -0.26 | -0.12 |
| Baffo | -1.61 | 0.19 | -0.28 | 0.53 | 1.01 | -0.22 | -0.45 | -1.75 | -0.96 |
| Sorry | -1.61 | 0.18 | -0.20 | 1.20 | 0.49 | 0.31 | -0.15 | 1.00 | 1.49 |
| T5 | -1.02 | -1.24 | -0.22 | -0.07 | -1.21 | 0.12 | 1.69 | -0.82 | -0.98 |
| Yetta | -0.83 | -0.15 | -0.28 | 0.53 | -0.20 | -0.22 | 3.12 | 0.30 | -0.17 |
| Anvil | -1.39 | -1.24 | -0.28 | -0.02 | -0.55 | -0.22 | 0.45 | -0.72 | 0.48 |
| Baggy | -0.12 | 0.51 | -0.28 | -0.51 | -1.26 | -0.22 | -0.45 | -0.63 | 0.40 |
| Nigel | 0.82 | 0.17 | -0.28 | 0.20 | -1.26 | 0.20 | -0.45 | -0.77 | -1.04 |
| Splash | -1.24 | -1.13 | 1.22 | -1.45 | -1.26 | 6.12 | 0.92 | -1.05 | -2.27 |

| Subject | Grasp-Walk‡ | Groom | Hold† | Lick‡ | Move and Push/Pull‡ | Move in Mouth‡ | Pick and Drop‡ | Pick Up‡ | Pound‡ |
|---|---|---|---|---|---|---|---|---|---|
| Cipria | 0.49 | -1.12 | 1.59 | -0.11 | 0.35 | -0.46 | -0.58 | 4.21 | -0.74 |
| Gnome | -0.53 | 0.37 | 0.15 | 2.31 | 0.60 | -0.46 | -0.58 | -0.61 | -0.74 |
| Lady-Qui-Louche | -0.51 | 0.19 | -0.09 | -0.37 | 1.64 | -0.46 | -0.58 | 0.27 | -0.74 |
| Megamind | -0.66 | 0.68 | 0.21 | -0.56 | 0.52 | -0.46 | -0.58 | -0.61 | -0.46 |
| Benji | -0.89 | 0.52 | 0.33 | -0.13 | 0.09 | -0.46 | -0.58 | -0.61 | -0.74 |
| Gennaro | 0.07 | -0.36 | -0.48 | -0.63 | 1.36 | 1.54 | -0.58 | -0.61 | -0.67 |
| Morty | -0.66 | 0.63 | 1.62 | -0.56 | 4.39 | -0.46 | -0.38 | -0.43 | -0.74 |
| Scarface | 0.54 | 1.20 | 1.23 | 3.04 | -0.08 | -0.45 | -0.58 | -0.25 | -0.74 |
| Grinch | -0.51 | -0.94 | -0.15 | -0.34 | 0.05 | -0.37 | -0.20 | -0.61 | 0.92 |
| Kappa | -0.69 | -0.36 | -0.42 | 2.14 | 0.06 | -0.46 | -0.58 | -0.61 | -0.67 |
| Kyla | -0.69 | 0.81 | -1.71 | 1.94 | 2.01 | -0.46 | -0.58 | -0.61 | -0.74 |
| Pirata | -0.61 | -1.39 | -0.03 | -0.63 | -0.50 | -0.46 | -0.58 | -0.61 | -0.72 |
| Bass | 0.64 | 0.54 | -0.24 | -0.43 | -0.60 | 0.50 | -0.58 | -0.24 | 0.05 |
| C-17 | -0.29 | -0.48 | -0.51 | -0.57 | -0.60 | -0.46 | 0.26 | -0.61 | 1.49 |
| Lookout | 0.92 | -0.28 | 0.57 | 0.34 | -0.18 | -0.28 | -0.21 | -0.07 | -0.69 |
| Sick Boy | -0.54 | -0.15 | -0.69 | -0.63 | 0.19 | -0.46 | -0.25 | 0.28 | 0.66 |
| Duchess | -0.53 | 0.34 | 0.90 | -0.24 | 0.04 | -0.46 | -0.58 | -0.61 | -0.74 |
| Encrenca | 4.27 | -0.62 | 1.80 | -0.56 | -0.60 | 0.56 | 1.56 | 2.82 | -0.66 |
| Langur | -0.91 | 0.29 | -0.09 | -0.11 | -0.60 | -0.46 | -0.58 | -0.61 | -0.74 |
| S3 | 1.96 | -0.97 | -0.15 | -0.53 | -0.60 | -0.46 | 0.64 | -0.61 | 2.33 |
| Charlie | -0.11 | -0.41 | -0.06 | 0.09 | -0.60 | 0.76 | -0.24 | -0.32 | -0.25 |
| Littlefinger | 0.29 | -0.94 | -0.69 | -0.63 | 1.01 | -0.46 | 0.43 | -0.11 | 0.78 |
| Pinocchio | 0.45 | -0.69 | 0.39 | -0.36 | 1.25 | -0.30 | 0.88 | 0.68 | -0.48 |
| White Eyebrows | -0.11 | 0.27 | -0.06 | 0.71 | -0.60 | -0.46 | -0.58 | -0.61 | 3.03 |
| Beardy | 0.69 | -0.77 | 1.38 | -0.47 | -0.60 | -0.46 | -0.29 | 0.07 | -0.73 |
| Musty | 0.62 | -1.22 | 1.41 | -0.63 | -0.60 | -0.28 | -0.58 | -0.24 | -0.72 |
| Punk | -0.13 | -0.33 | 1.71 | -0.63 | -0.45 | -0.37 | -0.41 | 0.63 | -0.68 |
| S12 | -0.97 | 0.31 | -1.77 | -0.63 | -0.60 | -0.46 | -0.35 | -0.61 | -0.70 |
| Danger | -0.52 | -0.50 | -1.62 | -0.24 | -0.60 | -0.46 | -0.58 | -0.25 | 2.41 |
| Ramsey | -0.57 | 3.16 | -1.26 | -0.63 | -0.39 | -0.46 | -0.58 | -0.42 | -0.73 |
| Ronald | -0.35 | -0.21 | -0.12 | -0.37 | -0.60 | 2.32 | 0.28 | -0.25 | 0.01 |
| Temple Baggy | -0.89 | 0.37 | -0.39 | 2.66 | -0.47 | -0.35 | 1.62 | 0.32 | 1.38 |
| Baffo | 0.05 | -0.68 | -0.60 | -0.63 | -0.60 | -0.46 | -0.58 | -0.61 | -0.13 |
| Sorry | -0.70 | 0.13 | -0.90 | -0.63 | -0.60 | -0.46 | -0.58 | -0.07 | 0.60 |
| T5 | 0.97 | 1.13 | -1.59 | -0.63 | -0.08 | -0.25 | 0.89 | -0.47 | 0.37 |
| Yetta | -0.75 | -1.01 | -0.27 | -0.57 | -0.55 | -0.46 | 0.50 | 1.71 | 1.02 |
| Anvil | -0.75 | 3.38 | 0.90 | -0.23 | -0.60 | 0.39 | 4.84 | -0.42 | -0.69 |
| Baggy | 0.93 | -0.80 | -1.41 | 0.80 | -0.60 | 3.81 | 0.53 | 0.52 | 0.07 |
| Nigel | 1.58 | -0.03 | 1.38 | 0.24 | -0.60 | 0.28 | 0.79 | 1.48 | 0.30 |
| Splash | -0.60 | -0.08 | -0.27 | -0.58 | -0.60 | 3.10 | 0.06 | -0.33 | 0.23 |

| Subject | Pound-Drag‡ | Push-Through‡ | Roll† | Roll in Hands‡ | Roll with Fingers‡ | Rub Together‡ | Rub with Hands‡ | Rub |
|---|---|---|---|---|---|---|---|---|
| Cipria | -0.64 | 5.19 | 1.20 | 1.19 | -0.32 | -0.25 | -0.41 | -1.49 |
| Gnome | -0.64 | -0.30 | -0.72 | -0.57 | -0.33 | -0.25 | -0.41 | -0.67 |
| Lady-Qui-Louche | -0.64 | -0.30 | -1.03 | -0.68 | -0.60 | -0.25 | -0.41 | -1.09 |
| Megamind | -0.45 | -0.30 | 1.52 | 0.57 | -0.48 | -0.25 | 0.03 | 0.78 |
| Benji | -0.64 | -0.30 | -0.79 | -0.68 | -0.22 | -0.25 | -0.41 | 0.87 |
| Gennaro | 3.32 | -0.30 | -0.16 | -0.41 | 0.20 | -0.25 | -0.41 | 0.01 |
| Morty | -0.64 | -0.30 | -0.16 | -0.59 | -0.48 | -0.25 | -0.37 | -0.50 |
| Scarface | -0.53 | -0.30 | 1.27 | -0.68 | -0.66 | -0.25 | -0.37 | -0.26 |
| Grinch | 0.58 | -0.30 | -0.30 | -0.68 | -0.09 | -0.25 | -0.41 | 0.44 |
| Kappa | -0.64 | 0.35 | -0.72 | -0.36 | 0.33 | -0.25 | 0.09 | -0.31 |
| Kyla | -0.64 | -0.30 | -0.41 | -0.68 | -0.57 | -0.25 | -0.41 | -0.09 |
| Pirata | 0.46 | -0.30 | -0.96 | 0.49 | -0.66 | -0.25 | -0.26 | 3.71 |
| Bass | -0.60 | -0.30 | -1.56 | -0.68 | 0.42 | -0.25 | -0.41 | -0.24 |
| C-17 | -0.56 | 0.41 | 0.61 | -0.16 | 4.25 | -0.25 | -0.41 | -0.63 |
| Lookout | -0.09 | -0.30 | -0.51 | -0.50 | 0.02 | 0.28 | -0.33 | 1.52 |
| Sick Boy | 0.21 | -0.30 | -1.35 | -0.68 | -0.51 | -0.25 | -0.35 | 1.29 |
| Duchess | -0.64 | -0.30 | 1.34 | 2.17 | -0.04 | -0.25 | -0.41 | -0.32 |
| Encrenca | 0.87 | -0.30 | 0.33 | -0.41 | 0.81 | -0.25 | -0.13 | -1.15 |
| Langur | -0.64 | -0.30 | -1.73 | -0.68 | -0.66 | -0.25 | -0.41 | 1.62 |
| S3 | 1.06 | -0.30 | -0.51 | -0.54 | -0.41 | -0.25 | -0.41 | -0.87 |
| Charlie | 1.44 | -0.30 | 0.12 | -0.61 | 0.32 | -0.25 | 0.49 | -0.87 |
| Littlefinger | 1.92 | -0.30 | -0.44 | 0.56 | -0.55 | -0.08 | -0.34 | 1.12 |
| Pinocchio | -0.56 | -0.30 | 1.97 | -0.41 | 0.29 | -0.25 | 0.42 | 0.10 |
| White Eyebrows | -0.64 | -0.30 | -0.72 | -0.48 | -0.04 | -0.25 | -0.41 | -0.75 |
| Beardy | -0.64 | -0.30 | 0.15 | -0.12 | 0.43 | -0.25 | 1.37 | 0.67 |
| Musty | -0.11 | -0.30 | 1.13 | 0.60 | 0.01 | -0.25 | 1.17 | 0.12 |
| Punk | -0.64 | 1.26 | 0.75 | -0.24 | -0.54 | -0.25 | -0.05 | -0.56 |
| S12 | -0.64 | -0.30 | -2.05 | -0.68 | -0.66 | -0.25 | -0.41 | -0.11 |
| Danger | 0.32 | -0.30 | 0.61 | -0.23 | -0.66 | -0.25 | -0.41 | 0.29 |
| Ramsey | -0.64 | -0.30 | 0.26 | -0.04 | 2.48 | -0.25 | -0.41 | 0.51 |
| Ronald | -0.49 | -0.30 | 0.05 | 1.81 | 2.66 | -0.25 | 0.31 | -0.99 |
| Temple Baggy | -0.48 | -0.30 | 1.66 | -0.68 | -0.37 | -0.25 | -0.41 | -0.38 |
| Baffo | -0.61 | -0.30 | -0.20 | 3.93 | -0.52 | -0.25 | -0.07 | 0.22 |
| Sorry | 0.42 | -0.30 | 0.43 | 0.57 | -0.23 | 5.56 | -0.37 | -0.90 |
| T5 | 0.08 | -0.30 | 0.08 | -0.68 | -0.24 | -0.25 | -0.41 | 0.90 |
| Yetta | -0.64 | -0.30 | -1.70 | -0.52 | -0.40 | -0.25 | -0.41 | 0.93 |
| Anvil | -0.64 | -0.30 | 0.68 | 1.95 | -0.32 | 0.11 | 4.95 | -1.29 |
| Baggy | -0.41 | 0.47 | 1.31 | -0.59 | -0.66 | -0.25 | -0.41 | -0.35 |
| Nigel | 1.52 | -0.30 | 0.71 | -0.20 | -0.55 | 2.44 | 2.51 | -0.95 |
| Splash | 2.87 | 2.62 | -0.16 | 0.63 | -0.45 | 0.03 | -0.41 | -0.32 |

| Subject | Scatter‡ | Shake in Hands‡ | Shift in Hands‡ | Slam‡ | Slap‡ | Sniff† | Tap‡ | Toss-Walk‡ | Throw‡ | Wrap† |
|---|---|---|---|---|---|---|---|---|---|---|
| Cipria | 1.63 | -0.44 | 0.16 | -0.38 | -0.31 | 1.78 | -0.69 | -0.50 | -0.43 | 0.71 |
| Gnome | -0.22 | 0.11 | -0.47 | -0.38 | 0.24 | -0.83 | 0.03 | -0.50 | -0.43 | -1.35 |
| Lady-Qui-Louche | 3.57 | -0.44 | -0.47 | -0.38 | 1.04 | -1.14 | -0.29 | -0.50 | -0.43 | 0.71 |
| Megamind | -0.38 | -0.44 | -0.47 | -0.38 | 0.94 | 0.24 | -0.68 | -0.50 | 0.85 | -0.08 |
| Benji | -0.73 | -0.44 | -0.47 | -0.38 | -0.50 | -1.22 | 0.57 | -0.50 | -0.43 | 0.81 |
| Gennaro | -0.56 | -0.44 | -0.47 | -0.38 | 0.19 | 0.09 | -0.30 | 0.99 | -0.43 | 0.15 |
| Morty | 2.34 | -0.44 | -0.21 | -0.38 | -0.57 | -0.37 | -0.60 | -0.50 | -0.43 | 2.73 |
| Scarface | 0.08 | -0.44 | -0.10 | -0.38 | 3.27 | 0.94 | -0.68 | 0.53 | -0.43 | -0.55 |
| Grinch | -0.14 | 3.64 | -0.47 | -0.38 | 0.80 | -0.37 | 0.30 | 0.97 | -0.43 | -0.93 |
| Kappa | 1.28 | -0.30 | -0.31 | -0.38 | -0.25 | 0.17 | 0.90 | -0.50 | -0.43 | -0.88 |
| Kyla | -0.27 | -0.44 | -0.47 | -0.38 | -0.55 | -0.76 | 3.88 | -0.50 | -0.43 | -1.49 |
| Pirata | -0.74 | -0.44 | -0.47 | -0.38 | -0.62 | 0.17 | -0.32 | -0.50 | -0.43 | 0.15 |
| Bass | -0.33 | 0.19 | -0.47 | -0.38 | 3.31 | -1.22 | 0.14 | -0.50 | -0.43 | 0.99 |
| C-17 | -0.74 | -0.44 | -0.47 | -0.27 | 0.02 | -0.76 | 2.00 | -0.50 | -0.43 | -0.51 |
| Lookout | -0.57 | 0.79 | -0.47 | -0.38 | -0.62 | 1.17 | -0.17 | -0.50 | -0.43 | 0.15 |
| Sick Boy | -0.69 | -0.44 | -0.44 | -0.37 | -0.56 | 1.01 | -0.16 | 0.53 | -0.43 | 0.71 |
| Duchess | -0.48 | -0.44 | -0.47 | -0.38 | -0.28 | -1.06 | -0.32 | -0.50 | -0.43 | 0.71 |
| Encrenca | -0.59 | -0.13 | 4.69 | -0.38 | -0.49 | -0.83 | -0.52 | -0.50 | -0.43 | -1.30 |
| Langur | -0.54 | -0.44 | -0.47 | -0.38 | -0.65 | -0.37 | -0.69 | -0.50 | -0.43 | 1.65 |
| S3 | 2.05 | -0.44 | -0.47 | -0.38 | -0.61 | 0.01 | -0.44 | -0.50 | -0.43 | -1.30 |
| Charlie | 0.10 | 0.05 | 0.23 | 3.09 | -0.08 | 0.48 | 0.15 | -0.50 | 1.59 | -0.55 |
| Littlefinger | -0.24 | -0.44 | -0.47 | -0.38 | -0.04 | -0.91 | -0.68 | 0.27 | -0.43 | 0.53 |
| Pinocchio | -0.08 | -0.44 | 0.86 | -0.38 | -0.51 | -0.68 | 0.72 | 3.34 | 2.18 | 1.04 |
| White Eyebrows | -0.79 | -0.44 | -0.25 | -0.38 | -0.37 | 1.40 | -0.43 | -0.50 | -0.43 | 1.13 |
| Beardy | -0.07 | -0.44 | -0.47 | -0.38 | -0.38 | 1.01 | -0.46 | -0.50 | -0.43 | 0.06 |
| Musty | -0.30 | -0.44 | 0.17 | -0.38 | -0.27 | 1.40 | -0.52 | -0.50 | -0.43 | 0.48 |
| Punk | 1.90 | -0.44 | 1.32 | -0.38 | -0.02 | 0.24 | -0.69 | -0.50 | -0.43 | 0.85 |
| S12 | -0.76 | -0.44 | -0.47 | 1.71 | -0.33 | -0.29 | -0.69 | -0.50 | -0.43 | -1.49 |
| Danger | -0.59 | -0.44 | -0.47 | 0.38 | -0.52 | 2.01 | -0.62 | 0.13 | -0.43 | -0.32 |
| Ramsey | -0.14 | 0.19 | 0.47 | -0.31 | -0.57 | -0.14 | -0.69 | 0.13 | -0.43 | -1.16 |
| Ronald | 0.39 | 2.33 | 2.71 | -0.21 | 0.22 | -1.60 | 1.46 | 2.41 | -0.43 | 1.70 |
| Temple Baggy | -0.68 | -0.44 | -0.25 | 0.26 | -0.63 | 1.78 | -0.44 | 3.27 | 2.86 | 0.06 |
| Baffo | -0.59 | -0.44 | -0.47 | 4.31 | -0.47 | -0.29 | -0.62 | -0.50 | -0.43 | -0.46 |
| Sorry | 0.74 | -0.44 | -0.47 | -0.32 | 2.82 | -0.68 | -0.52 | -0.50 | -0.43 | -1.40 |
| T5 | -0.46 | 3.32 | -0.47 | -0.38 | -0.59 | -0.99 | 1.66 | 0.29 | 1.51 | -0.60 |
| Yetta | -0.56 | 0.13 | -0.47 | 0.56 | -0.58 | 0.32 | -0.49 | -0.50 | 3.11 | 0.43 |
| Anvil | -0.73 | -0.44 | 0.39 | 1.72 | -0.09 | -1.53 | -0.61 | -0.50 | 2.16 | -1.26 |
| Baggy | -0.31 | -0.28 | 0.65 | -0.38 | -0.62 | 0.32 | -0.30 | 1.24 | -0.43 | -0.60 |
| Nigel | -0.26 | 1.78 | 0.79 | -0.38 | -0.13 | 1.86 | -0.50 | -0.50 | -0.43 | 0.57 |
| Splash | -0.51 | -0.32 | -0.47 | -0.38 | -0.65 | -0.37 | 2.31 | -0.50 | -0.43 | -0.08 |

**Supplementary Material S2.4** – *Z-Scores for Percentage of Duration for Each SH Behavior for The Original and Resampled SH Activity of 9 Individuals. Green Cells Indicate Preferred SH Behaviors for Each Individual (Z-Score > 1.96). † = Variable Log-Transformed; ‡ = Variable Not Normally Distributed.*

| SH behavioral pattern | Gennaro | Gennaro Resampled | C-17 | C-17 Resampled | Grinch | Grinch Resampled | Duchess | Duchess Resampled |
|---|---|---|---|---|---|---|---|---|
| Bite† | 2.37 | 0.30 | 0.66 | 0.09 | 0.57 | 0.02 | 1.04 | 1.30 |
| Carry | -0.74 | -0.25 | -1.40 | -1.27 | 0.79 | 0.73 | -0.11 | 0.40 |
| Clack‡ | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 |
| Cover† | -0.90 | -0.47 | 1.53 | 0.79 | -1.12 | -0.70 | 2.41 | 2.72 |
| Cuddle† | -0.74 | 0.43 | -1.04 | -1.02 | 1.66 | 1.28 | 1.31 | 1.00 |
| Dislodge‡ | -0.22 | -0.22 | -0.22 | 0.09 | -0.22 | -0.22 | -0.04 | -0.21 |
| Flint‡ | -0.45 | -0.45 | -0.45 | -0.45 | -0.45 | -0.45 | -0.45 | -0.45 |
| Gather† | 0.35 | 2.13 | -1.10 | -0.65 | -0.72 | 0.54 | -0.96 | -0.91 |
| Grasp | -0.02 | -0.35 | -0.66 | -1.02 | -1.59 | -0.47 | 0.05 | -0.06 |
| Grasp-Walk‡ | 0.07 | -0.93 | -0.29 | 0.45 | -0.51 | -0.23 | -0.53 | -0.22 |
| Groom | -0.36 | 0.04 | -0.48 | -0.45 | -0.94 | -0.47 | 0.34 | -0.50 |
| Hold† | -0.48 | -0.51 | -0.51 | -0.45 | -0.15 | -0.67 | 0.90 | -0.41 |
| Lick‡ | -0.63 | -0.52 | -0.57 | -0.37 | -0.34 | -0.37 | -0.24 | -0.56 |
| Move and Push/Pull‡ | 1.36 | 1.10 | -0.60 | -0.60 | 0.05 | 1.55 | 0.04 | 3.05 |
| Move in Mouth‡ | 1.54 | -0.33 | -0.46 | -0.46 | -0.37 | -0.46 | -0.46 | -0.46 |
| Pick and Drop‡ | -0.58 | -0.52 | 0.26 | -0.32 | -0.20 | -0.57 | -0.58 | -0.58 |
| Pick Up‡ | -0.61 | -0.61 | -0.61 | -0.61 | -0.61 | -0.61 | -0.61 | -0.44 |
| Pound‡ | -0.67 | -0.74 | 1.49 | 1.87 | 0.92 | -0.07 | -0.74 | -0.74 |
| Pound-Drag‡ | 3.32 | -0.29 | -0.56 | -0.45 | 0.58 | -0.36 | -0.64 | -0.64 |
| Push-Through‡ | -0.30 | -0.30 | 0.41 | -0.29 | -0.30 | -0.30 | -0.30 | -0.30 |
| Roll† | -0.16 | -1.51 | 0.61 | -0.65 | -0.30 | -1.76 | 1.34 | 1.69 |
| Roll in Hands‡ | -0.41 | -0.67 | -0.16 | -0.66 | -0.68 | -0.68 | 2.17 | -0.30 |
| Roll with Fingers‡ | 0.20 | 0.13 | 4.25 | 2.10 | -0.09 | -0.59 | -0.04 | 0.17 |
| Rub Together‡ | -0.25 | -0.25 | -0.25 | -0.25 | -0.25 | -0.25 | -0.25 | -0.25 |
| Rub with Hands‡ | -0.41 | -0.34 | -0.41 | -0.41 | -0.41 | -0.41 | -0.41 | -0.41 |
| Rub | 0.01 | 1.15 | -0.63 | -0.09 | 0.44 | 1.07 | -0.32 | -0.67 |
| Scatter‡ | -0.56 | -0.12 | -0.74 | -0.68 | -0.14 | -0.53 | -0.48 | -0.16 |
| Shake in Hands‡ | -0.44 | -0.02 | -0.44 | -0.44 | 3.64 | -0.42 | -0.44 | -0.44 |
| Shift in Hands‡ | -0.47 | -0.41 | -0.47 | -0.47 | -0.47 | -0.47 | -0.47 | -0.27 |
| Slam‡ | -0.38 | -0.38 | -0.27 | -0.37 | -0.38 | -0.38 | -0.38 | -0.38 |
| Slap‡ | 0.19 | 1.31 | 0.02 | -0.13 | 0.80 | 0.81 | -0.28 | 0.56 |
| Sniff† | 0.09 | -0.66 | -0.76 | 0.96 | -0.37 | -0.96 | -1.06 | -1.14 |
| Tap‡ | -0.30 | -0.44 | 2.00 | 1.99 | 0.30 | -0.12 | -0.32 | -0.28 |
| Toss-Walk‡ | 0.99 | 0.99 | -0.50 | -0.50 | 0.97 | 5.68 | -0.50 | -0.50 |
| Throw‡ | -0.43 | -0.43 | -0.43 | -0.43 | -0.43 | 2.89 | -0.43 | -0.43 |
| Wrap† | 0.15 | 2.75 | -0.51 | -0.05 | -0.93 | -1.02 | 0.71 | 1.50 |

| SH behavioral pattern | Pinocchio | Pinocchio Resampled | Ramsey | Ramsey Resampled | S12 | S12 Resampled | Anvil | Anvil Resampled |
|---|---|---|---|---|---|---|---|---|
| Bite† | -1.27 | -1.33 | -1.27 | 0.69 | 0.10 | -0.98 | -1.39 | -1.59 |
| Carry | -1.38 | -1.02 | -0.48 | -1.09 | -0.28 | 1.16 | -1.24 | -0.99 |
| Clack‡ | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 | -0.28 |
| Cover† | -0.29 | 0.08 | 1.75 | 2.57 | -0.18 | -0.66 | -0.02 | 1.09 |
| Cuddle† | -1.26 | -0.66 | -0.06 | -0.80 | 2.48 | 1.89 | -0.55 | -0.39 |
| Dislodge‡ | -0.22 | -0.22 | -0.22 | -0.22 | -0.22 | -0.22 | -0.22 | -0.22 |
| Flint‡ | -0.45 | -0.45 | -0.45 | -0.45 | -0.45 | -0.45 | 0.45 | 0.45 |
| Gather† | -0.07 | 1.05 | 0.58 | 1.29 | -1.33 | 0.27 | -0.72 | 0.10 |
| Grasp | 0.68 | -0.80 | 0.67 | 0.52 | 1.37 | 1.47 | 0.48 | 1.78 |
| Grasp-Walk‡ | 0.45 | 0.83 | -0.57 | -0.48 | -0.97 | -0.97 | -0.75 | -0.44 |
| Groom | -0.69 | -1.05 | 3.16 | -0.13 | 0.31 | -1.22 | 3.38 | -0.09 |
| Hold† | 0.39 | -0.53 | -1.26 | -0.74 | -1.77 | -0.88 | 0.90 | -0.54 |
| Lick‡ | -0.36 | -0.62 | -0.63 | -0.63 | -0.63 | -0.63 | -0.23 | -0.62 |
| Move and Push/Pull‡ | 1.25 | -0.01 | -0.39 | -0.39 | -0.60 | -0.50 | -0.60 | -0.45 |
| Move in Mouth‡ | -0.30 | -0.23 | -0.46 | -0.46 | -0.46 | -0.46 | 0.39 | -0.44 |
| Pick and Drop‡ | 0.88 | -0.44 | -0.58 | -0.58 | -0.35 | -0.57 | 4.84 | -0.18 |
| Pick Up‡ | 0.68 | 0.53 | -0.42 | -0.60 | -0.61 | -0.61 | -0.42 | -0.25 |
| Pound‡ | -0.48 | -0.58 | -0.73 | -0.74 | -0.70 | -0.15 | -0.69 | 1.39 |
| Pound-Drag‡ | -0.56 | -0.52 | -0.64 | -0.64 | -0.64 | -0.64 | -0.64 | -0.52 |
| Push-Through‡ | -0.30 | -0.30 | -0.30 | -0.30 | -0.30 | -0.30 | -0.30 | -0.30 |
| Roll† | 1.97 | 2.60 | 0.26 | 1.78 | -2.05 | -2.05 | 0.68 | 0.27 |
| Roll in Hands‡ | -0.41 | -0.31 | -0.04 | -0.22 | -0.68 | -0.68 | 1.95 | -0.64 |
| Roll with Fingers‡ | 0.29 | -0.26 | 2.48 | 0.61 | -0.66 | -0.66 | -0.32 | -0.50 |
| Rub Together‡ | -0.25 | 0.10 | -0.25 | -0.25 | -0.25 | -0.25 | 0.11 | -0.24 |
| Rub with Hands‡ | 0.42 | -0.14 | -0.41 | -0.41 | -0.41 | -0.41 | 4.95 | -0.47 |
| Rub | 0.10 | 0.41 | 0.51 | 0.17 | -0.11 | 0.98 | -1.29 | -0.90 |
| Scatter‡ | -0.08 | -0.21 | -0.14 | -0.53 | -0.76 | -0.69 | -0.73 | -0.43 |
| Shake in Hands‡ | -0.44 | -0.44 | 0.19 | -0.43 | -0.44 | -0.44 | -0.44 | -0.44 |
| Shift in Hands‡ | 0.86 | 4.11 | 0.47 | 1.77 | -0.47 | -0.47 | 0.39 | -0.45 |
| Slam‡ | -0.38 | -0.38 | -0.31 | -0.29 | 1.71 | 0.01 | 1.72 | 1.44 |
| Slap‡ | -0.51 | -0.45 | -0.57 | -0.33 | -0.33 | 0.18 | -0.09 | -0.32 |
| Sniff† | -0.68 | -0.38 | -0.14 | -1.31 | -0.29 | -0.52 | -1.53 | -1.38 |
| Tap‡ | 0.72 | -0.03 | -0.69 | -0.60 | -0.69 | -0.69 | -0.61 | -0.65 |
| Toss-Walk‡ | 3.34 | -0.48 | 0.13 | 0.34 | -0.50 | -0.50 | -0.50 | 0.55 |
| Throw‡ | 2.18 | -0.39 | -0.43 | -0.43 | -0.43 | -0.43 | 2.16 | 5.48 |
| Wrap† | 1.04 | 0.04 | -1.16 | 0.63 | -1.49 | -1.00 | -1.26 | -0.16 |

| SH behavioral pattern | Sorry | Sorry Resampled |
|---|---|---|
| Bite† | -1.61 | -1.35 |
| Carry | 0.18 | 1.45 |
| Clack‡ | -0.20 | -0.28 |
| Cover† | 1.20 | 1.55 |
| Cuddle† | 0.49 | 0.28 |
| Dislodge‡ | 0.31 | 0.68 |
| Flint‡ | -0.15 | 0.44 |
| Gather† | 1.00 | 1.57 |
| Grasp | 1.49 | 1.11 |
| Grasp-Walk‡ | -0.70 | -0.96 |
| Groom | 0.13 | 0.65 |
| Hold† | -0.90 | -1.67 |
| Lick‡ | -0.63 | -0.37 |
| Move and Push/Pull‡ | -0.60 | 1.58 |
| Move in Mouth‡ | -0.46 | -0.46 |
| Pick and Drop‡ | -0.58 | -0.58 |
| Pick Up‡ | -0.07 | -0.59 |
| Pound‡ | 0.60 | -0.18 |
| Pound-Drag‡ | 0.42 | -0.61 |
| Push-Through‡ | -0.30 | -0.30 |
| Roll† | 0.43 | 1.07 |
| Roll in Hands‡ | 0.57 | -0.65 |
| Roll with Fingers‡ | -0.23 | -0.65 |
| Rub Together‡ | 5.56 | -0.23 |
| Rub with Hands‡ | -0.37 | -0.29 |
| Rub | -0.90 | -0.97 |
| Scatter‡ | 0.74 | 0.71 |
| Shake in Hands‡ | -0.44 | -0.44 |
| Shift in Hands‡ | -0.47 | -0.47 |
| Slam‡ | -0.32 | -0.25 |
| Slap‡ | 2.82 | 3.87 |
| Sniff† | -0.68 | -0.68 |
| Tap‡ | -0.52 | -0.66 |
| Toss-Walk‡ | -0.50 | -0.50 |
| Throw‡ | -0.43 | -0.43 |
| Wrap† | -1.40 | -1.35 |

## Appendix B

**Supplementary Material S3.1 –** Three examples of stone handling behavior with stones of different sizes in one juvenile male Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/VD7q24I5xlw

**Supplementary Material S3.2 –** *Two New Behavioral Patterns in Stone Handling Behavior of Balinese Long-Tailed Macaques and Their Definitions.*

| SH behavioral pattern | Definition |
|---|---|
| **Slam** | To pick up a stone and shove it to a substrate (e.g., ground) or an object, without using a power grip, but accompanying the stone by applying pressure on its top and/or side surfaces with the hand, either by pushing or slapping. *Comments: This SH behavioral pattern (or SH pattern) may resemble Pound, but the stone is not grasped by using a power grip. Most frequently, the stones used to Slam are larger than the monkey's hand. This SH pattern may also resemble Pick and Drop, when repeatedly performed; however, when performing a Slam, the stone is pushed or slapped with the hand instead of dropped from the hand.* |
| **Push-Through** | To exert force on a stone, typically with the palm of the hand or the fingers, in an apparent attempt to move the stone through a cavity, like a hole or a pipe. *Comments: This SH behavioral pattern (or SH pattern) may resemble Pick and Drop, when repeatedly performed; however, when performing a Push-Through the stone is not dropped. It may also resemble Dislodge, but in Push-Through, the stone is pushed or clutched, rather than scratched or rubbed with the fingertips. Most frequently, stones are stuck in the cavity and the monkey aims to free the stone from the cavity by performing a pushing action.* |

**Supplementary Material S3.3 –** Two new behavioral patterns in stone handling behavior of Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/QGWvYOvgbbQ

## Appendix C

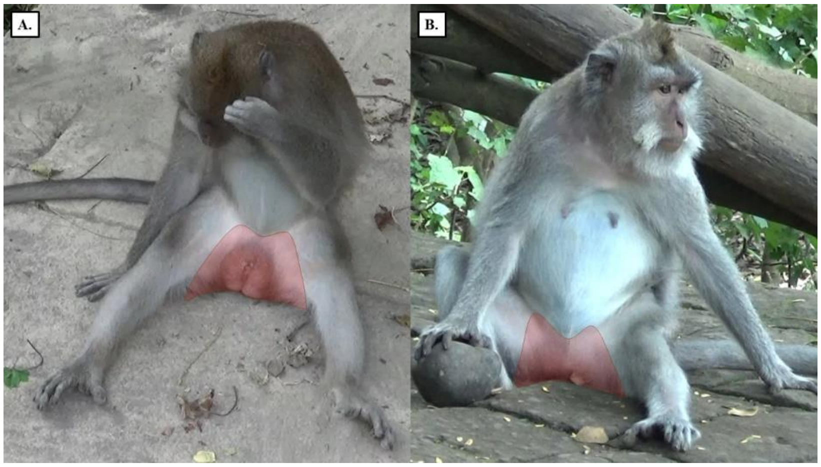
**Supplementary Material S4.1 -** Terminal strings (i.e., SH behavioral elements constituent of T-patterns in brackets) detected in SH sequences with TOG/ROG (i.e., “TOG/ROG”) and SH sequences without TOG/ROG (i.e., “no TOG/ROG”). In TPA, each behavioral state (i.e., with a measurable duration) is characterized by a beginning ("b") and an end ("e"). Numbers on the right-side columns indicate length (i.e., number of behavioral elements) and occurrences (Occs) of each string.

To be retrieved at URL:

https://drive.google.com/file/d/1CRumdrYJ2u5uDVYBmEzd8UtFeVpfIdbx/view?usp=sharing

## Appendix D

**Supplementary Material S5.1** – Genital and inguinal regions in (A.) males and (B.) females used to score the SH behavioral patterns belonging to the category *genital stone-tapping/-rubbing*.




**Supplementary Material S5.2 –** Examples of "Tap On Groin", "Rub On Groin", "Pelvic Thrusting", and "Roll On Groin" in male and female Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/d2TiQGBx4KA

**Supplementary Material S5.3 -** Examples of "Tap On Other body parts", and "Rub On Other body parts" in male and female Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/Km62I5mX4Rw

**Supplementary Material S5.4** – *Number of Days of Data Collection per Subject, Total Duration of Stone Handling Recorded for Each Subject Across Multiple Days, Mean Stone Handling Duration (± SD) per Day and per Subject.*

| Subject | Age | Sex | Obs day | Total SH (mm:ss) | M SH (mm:ss) |
|---|---|---|---|---|---|
| Duchess | Young | Female | 8 | 33:31 | 04:11 (± 02:55) |
| Encrenca | Young | Female | 6 | 36:00 | 05:37 (± 04:51) |
| Fake Robin | Young | Female | 9 | 25:59 | 02:53 (± 04:40) |
| Grinch | Young | Female | 9 | 33:40 | 03:44 (± 03:43) |
| Kappa | Young | Female | 8 | 30:16 | 03:47 (± 03:50) |
| Kyla | Young | Female | 7 | 34:35 | 04:56 (± 03:40) |
| Lady Deadpool | Young | Female | 9 | 23:13 | 02:35 (± 02:01) |
| Langur | Young | Female | 3 | 30:09 | 06:02 (± 04:11) |
| Marilyn | Young | Female | 10 | 32:33 | 03:15 (± 02:49) |
| Pirata | Young | Female | 5 | 33:27 | 06:41 (± 03:55) |
| Robin | Young | Female | 8 | 35:36 | 04:27 (± 03:15) |
| S3 | Young | Female | 8 | 39:34 | 04:57 (± 04:15) |

| Subject | Age | Sex | Obs day | Total SH (mm:ss) | M SH (mm:ss) |
|---|---|---|---|---|---|
| Samanta | Young | Female | 7 | 33:17 | 04:45 (± 04:01) |
| Wax | Young | Female | 8 | 37:18 | 04:40 (± 03:52) |
| Bass | Young | Male | 5 | 38:11 | 07:38 (± 03:42) |
| C-17 | Young | Male | 5 | 30:56 | 06:11 (± 03:53) |
| Carlo | Young | Male | 7 | 30:28 | 04:21 (± 03:29) |
| Dome | Young | Male | 5 | 30:17 | 06:03 (± 03:19) |
| Inmate | Young | Male | 6 | 30:01 | 05:00 (± 03:43) |
| Lookout | Young | Male | 7 | 30:27 | 04:21 (± 02:41) |
| Newby | Young | Male | 5 | 30:43 | 06:09 (± 02:31) |
| Nyoman | Young | Male | 10 | 30:09 | 03:01 (± 02:28) |
| Paggio | Young | Male | 6 | 32:34 | 05:26 (± 02:21) |
| Paul | Young | Male | 6 | 31:35 | 05:16 (± 03:32) |
| Scarface | Young | Male | 4 | 34:52 | 08:43 (± 02:35) |
| Sick Boy | Young | Male | 4 | 31:07 | 07:47 (± 02:27) |
| Sugar | Young | Male | 7 | 31:54 | 04:34 (± 03:47) |
| Watson | Young | Male | 5 | 30:26 | 06:05 (± 02:32) |
| Beardy | Adult | Female | 7 | 30:01 | 04:17 (± 03:07) |
| Big Eyes | Adult | Female | 6 | 30:36 | 05:06 (± 03:03) |
| Carmen | Adult | Female | 9 | 34:27 | 03:50 (± 03:20) |
| Chifu | Adult | Female | 5 | 31:43 | 06:21 (± 03:32) |
| Deadpool Lard | Adult | Female | 7 | 30:37 | 04:22 (± 04:04) |
| Izma | Adult | Female | 8 | 29:36 | 03:42 (± 02:26) |
| Musty | Adult | Female | 6 | 30:01 | 05:00 (± 04:01) |
| Punk | Adult | Female | 5 | 32:12 | 06:26 (± 02:57) |
| S12 | Adult | Female | 4 | 31:35 | 07:54 (± 03:12) |
| S9 | Adult | Female | 9 | 32:04 | 03:34 (± 02:46) |
| Selma | Adult | Female | 8 | 32:40 | 04:05 (± 02:01) |
| Sorry | Adult | Female | 7 | 37:01 | 05:17 (± 04:28) |
| T5 | Adult | Female | 10 | 32:06 | 03:13 (± 01:45) |
| Yetta | Adult | Female | 7 | 31:12 | 04:27 (± 02:15) |
| Anvil | Adult | Male | 4 | 31:20 | 07:50 (± 02:33) |
| Baggy | Adult | Male | 8 | 30:54 | 03:52 (± 02:46) |
| Danger | Adult | Male | 5 | 30:48 | 06:10 (± 07:19) |
| Lancelot | Adult | Male | 8 | 30:50 | 03:51 (± 02:50) |
| Ned | Adult | Male | 4 | 23:26 | 05:52 (± 06:53) |
| Nigel | Adult | Male | 9 | 32:21 | 03:36 (± 03:07) |
| Obelix | Adult | Male | 6 | 20:11 | 03:22 (± 01:49) |
| Pinocchio | Adult | Male | 5 | 31:11 | 06:33 (± 03:46) |
| Ramsey | Adult | Male | 7 | 31:07 | 04:27 (± 03:39) |
| Ronald | Adult | Male | 4 | 34:38 | 08:39 (± 01:14) |
| Splash | Adult | Male | 5 | 35:54 | 07:11 (± 03:30) |
| Temple Baggy | Adult | Male | 3 | 30:00 | 10:00 (± 05:19) |

| Subject | Age | Sex | Obs day | Total SH (mm:ss) | M SH (mm:ss) |
|---|---|---|---|---|---|
| White Eyebrows | Adult | Male | 8 | 31:15 | 03:54 (± 02:01) |
| Zeus | Adult | Male | 7 | 30:13 | 04:19 (± 04:10) |

*Note*. Total duration (in minutes and seconds). Young = juvenile/subadult. SH = stone handling.

**Supplementary Material S5.5** – Examples of twig-assisted masturbation in an adult female Balinese long-tailed macaque (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/w3qUlBt7WaA

## Appendix E

**Supplementary Material S6.1** – Stone handling (SH) behavioral patterns included in the Dropping and Percussive SH profiles of Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/aIYtxNtow00

**Supplementary Material S6.2** – Example of a successful trial for a juvenile/subadult male Balinese long-tailed macaque (Ubud, Monkey Forest, Bali, Indonesia).

To be retrieved at URL: https://youtu.be/QeApbg91sJI