WHAT CAN BEHAVIOURAL STRUCTURE TELL US ABOUT MOTIVATION? INSIGHTS FROM OBJECT PLAY AND FORAGING IN BALINESE LONG-TAILED MACAQUES

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ABSTRACT

Current research is not unanimous on whether object play is motivationally linked to foraging, due to a lack of systematic comparison of the behavioural structure of both activities. This thesis aimed to address this gap by comparing the ethograms and kinematics of two object-directed activities, a seemingly playful one (stone handling), and a functional one (food processing) in Balinese long-tailed macaques. My results indicated that percussive stone handling in this species was more frequent, prevalent, and complex than in other macaque species. I also found that stone pounding was a playful activity motivationally distinct from foraging (nut pounding), and that some of the defining structural characteristics of play (e.g., exaggeration, variability, incompleteness) were not simply a consequence of immaturity, but indeed inherent components of playful actions, regardless of the age of the performer. This work contributes to understanding the mechanisms and evolution of questionably adaptive behaviours, like play.

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CHAPTER ONE

Introduction

Theoretical advances require adequate working definitions and measures.

- Burghardt (2005) *The Genesis of Animal Play: Testing the Limits*

These words are applicable to all fields of scientific research. When Burghardt made this statement, he was referring specifically to the field of play behaviour. The purpose of play in animals has been a puzzling and hotly debated topic among researchers for decades (reviewed in Bateson, 2014; Hall, 1998). To determine the underlying causes and functions of play behaviour, numerous theories have been proposed, but many still lack strong empirical support (Fagen, 1981; Pellis, Burghardt, Palagi, & Mangel, 2015). Despite extensive research effort, play behaviour remains an evolutionary puzzle (Bateson, 2014; Fagen, 1981; Power, 2000). Part of this ambiguity stems from a lack of consensus regarding the terms used to define, the criteria used to characterize, and the theories used to explain different forms of play (i.e., social play, locomotor play, object play). In order to better understand the current state of knowledge of playful behaviour in the scientific literature, some common operational and functional definitions and theories must first be reviewed.

Definitions and Theories of Object Play

Like other forms of play, such as locomotor play and social play, object play can be challenging to identify and define (Bjorklund & Gardiner, 2011; Burghardt, 2005). Object play contains behavioural patterns that may look similar to those found in more obviously functional behavioural categories, such as foraging; however, it typically occurs in a non-functional context, and is often structurally modified from the functional version of the behaviour it resembles (Power, 2000). Some common items used in most definitions include the following: the seemingly non-functional and solitary manipulation of inanimate objects (Bjorklund & Pellegrini, 2002; Burghardt, 2005), including both man-made and naturally occurring items (Fagen, 1981; Greene, Mellilo-Sweeting, & Dudzinski, 2011; Hall, 1998), that may occasionally be accompanied by the presence of play signals, such as species-specific body postures, facial expressions, or pheromones to distinguish the behaviour from analogous but non-playful activities (Burghardt, 2005; Ramsey & McGrew, 2005; Smith, 1982). Though the aforementioned composite definition encompasses some of the commonly used criteria for defining object play, many definitions are seldom this thorough. For example, Watson (1992) characterizes an anecdotal observation of an object-oriented activity as object play in a bird species (the laughing kookaburra, *Dacelo noveaguineae*), based on the criteria that the actions performed were repeated, differed in sequence from foraging behaviour, and was performed in solitude. Greene et al. (2011) characterized object play in captive and wild dolphins (*Tursiops truncatus* and *Stenella frontalis*) as either one or more individuals playing with or sharing an object. Broad and vague definitions like the ones in these examples highlight the challenges that arise from different interpretations and perspectives coming from different authors (Pellis & Pellis, 2009). The lack of clear and precise definitions not only makes the distinction of play behaviour from its functional counterparts more difficult, but also hinders the future identification of object play in these species, or replication for future studies.

In addition to the clear absence of a collective definitional criteria, a lack of agreement for universal terminology used to characterize play can also be problematic. For example, the term object manipulation is frequently viewed as a general label for several types of behavioural patterns directed towards objects (Power, 2000). However, this label fails to distinguish object manipulation from other forms of object-directed activities, including object exploration, object play, and tool use (cf. Pellegrini & Gustafson, 2005). Such amalgamation can impede the identification of potential functions inherent to each of these activities, as they often display subtle structural differences, but lack obvious distinguishing characteristics (Fagen, 1981; Ramsey & McGrew, 2005; Sutton-Smith, 2006). In addition, some definitions for object play tend to emphasize the inferred functional components of the behaviour, or lack thereof (see Fagen, 1981; Pellis & Pellis, 2009), whereas others focus more on the structural characteristics, such as exaggeration, variability, and incompleteness in the body movements or behavioural sequence (Burghardt, 2005; Martin & Caro, 1985).

Along with the lack of definitional and terminological cohesiveness, theoretical disagreement is also present when considering potential functions (i.e., ultimate aspects) and underlying psychological mechanisms (i.e., proximate aspects) of object play (Pellis, Pellis, & Bell, 2010; Spinka, Newberry, & Bekoff, 2001). For example, historic theories of play typically fall under two categories: Surplus Energy or Relaxation, and Pre-exercise/Practice or Recapitulation (Saracho & Spodec, 1995). While the "surplus energy" theory posits that the excess metabolic energy produced by humans and animals is eliminated through play (after Spencer, 1898, cited in Saracho & Spodec, 1995; Barber 1991), the "relaxation" theory (after Lazarus, 1883, cited in Saracho & Spodec, 1995) states that play derives from a need to relax, and therefore replenishes energy used through work. The "pre-exercise/practice" theory (after Groos, 1901, cited in Saracho & Spodec, 1995) states that practice of adult roles and behaviour allows for the reinforcement of instinct, helping individuals to prepare for their futures. The "recapitulation" theory (after Hall, 1906, cited in Saracho & Spodec, 1995) postulates that evolutionary developmental stages are reached or acted out through play, and helps to free individuals from primitive instincts that may no longer be beneficial to them. As seen with some of these historic theories, claims on how and why individuals engage in playful behaviour typically aim to understand the underlying psychological processes, or the (either immediate or long-term) benefits accrued, though it is important to note that these explanations may occur simultaneously (Pellis et al., 2010). More modern research and reviews attempt to bridge this gap by acknowledging the value of addressing these concurrent theories and explanations. It is noteworthy that, while these coexisting theories are being addressed, there is still a lack of a fully integrative theoretical framework to explain both the proximate and ultimate causes of play (Burghardt, 2005). Additionally, age is a potential confounding variable, as these theories tend to provide different explanations for different age classes, or focus mainly on young individuals. For example, the "surplus energy" theory argues that, because immature mammals are often not limited in energy, play behaviour should be more frequent and more vigorous in younger than in older individuals (Barber, 1991). Likewise, the "training for the unexpected" hypothesis states that play allows individuals, especially young ones, to cope with unpredictable circumstances, as play can lead to unexpected outcomes, making them more resilient to novel situations (Bateson, 2014; Spinka et al., 2001). The "behavioural flexibility" hypothesis holds that object play can provide similar benefits to mainly younger performers, as the expression of novel actions during play activity could lead to more functional behavioural patterns (Fagen, 1981). A more modern view of the "pre-exercise/practice" theory is the "needing-to-learn" theory (Ross & Jones, 1999), which postulates that play in immature individuals could provide delayed benefits, allowing for training or practice for the execution of more functional and efficient behavioural patterns by mature individuals (Bateson, 2014; Fagen, 1981). Indeed, because young individuals have reduced sensori-motor control compared to adults, object play behaviour could facilitate the development of skills leading to complex and coordinated manual actions characteristic of adulthood (Brownlee, 1954). Similarly, the "affordance learning" theory asserts that object play allows individuals to become more familiar with the properties of an object through non-instrumental manipulation and innovative exploration (Gibson, 1979; Parker & Gibson, 1977), and enables practice for more functional behaviour, such as tool use (Kahrs & Lockman, 2014), which in turn, could lead to the emergence of adaptive solutions to specific environmental problems. Finally, the "motor-training" hypothesis postulates that play in juveniles prepares an individual's muscular and nervous system for the challenges and constraints of adult behaviour (Brownlee, 1954; Pellis et al., 2010). Taken together, these theories take into account developmental changes and learning mechanisms to address key ultimate forces driving the evolution of (object) play behaviour. However, many of them still lack strong empirical support (Martin & Caro, 1985).

Other theories emphasize the proximate causation of play behaviour, such as motivational processes or other psychological mechanisms. The "arousal modulation" theory (after Berlyne, 1960; Ellis, 1973, cited in Verenikina, Harris, & Lysaght, 2003) asserts that play allows an individual to encounter novel environmental conditions and engage in complex activities, which can either raise or lower levels of external stimulation leading to an adequately balanced level of individual arousal (Verenikina et al., 2003). The "autotelic" theory argues that play is performed for its own sake, in the sense that the goal of the behaviour is the behaviour itself (after Groos, 1898, cited in Mitchell, 1990). The "semblance" theory emphasizes the view that play involves pretense (i.e., make-believe; Baldwin, 1902 cited in Burghardt, 2005). In the context of object play in animals, acting “as if” could have implications for understanding predatory actions.

Each of these theories contribute to explaining how and why play activities may have arisen and are performed today. However, it is important to note that even object play behaviour is multifunctional, often having more than one adaptive value. Play-related benefits may be either immediate or delayed, as is often the case for individuals from different age classes, and environmental stressors may impact the occurrence or frequency of play (Pellis et al., 2010). Therefore, to better understand, distinguish, or compare play behaviour with the more functional behavioural counterpart(s) it may often outwardly structurally resemble, it is crucial to consider both mechanistic and functional perspectives (Burghardt, 2005). Without some consistently used criteria for defining and categorizing play, these behaviours can be easily mistaken. The level of theoretical and definitional ambiguity surrounding play behaviour led Gordon Burghardt to survey the literature, and establish the five most widely used criteria to characterize a playful behaviour (2005). These five criteria tie together previous literature to address the structural components, psychological mechanisms, and functional aspects of play.

Burghardt’s first criterion states that play should not be fully functional in the form or context in which it is expressed. This is not to say that play has no adaptive value. Play may serve a function, though it is possible that we do not recognize it yet. Play could have fitness-enhancing benefits that it was not originally selected for, or benefits may be delayed rather than immediate. The second criterion states that play is spontaneously performed for its own sake, meaning that it is intrinsically pleasurable or rewarding in itself. The third criterion states that play must differ from its more “serious” (i.e., functional) behavioural counterpart(s), either in its kinematic structure (i.e., being more exaggerated, incomplete, or highly variable in its form), or in its temporal organization (i.e., occurring earlier or later than it normally should, or in an inappropriate context, or in a more random sequential expression of the behavioural patterns). The fourth criterion states that play is repeated in a similar (but not abnormal or stereotypic) manner, typically in play bouts, for at least a short period during an individual's life. With regards to object play, this criterion helps to distinguish object play from behaviours such as object exploration (as exploration would not occur in the same repeated manner as play), and can take into account any potential adaptive roles found for repetition, such as skill development in the context of practice. The fifth and last criterion states that play is initiated in the absence of severe stress, and occurs only when an individual is in a relaxed state, and all other behavioural and functional needs have been met. Typically, elements from each of the five criteria must be present in order to identify a behaviour as playful. Therefore, a clear definition for object play must include or address each of these points. These five criteria help to provide a clear method for characterizing object play behaviour, and can also be used across age classes.

Object Play in Different Age Classes

As stated above, play may be expressed differently in different age classes. Object play is known to occur in numerous mammal and bird species, but is rarely observed in adult animals, with the exception of some domestic species and captive individuals (Hall, 1998; Power, 2000). As discussed above, many theories focus on describing or inferring the play-related benefits accrued to young individuals, as it occurs most frequently at this age (Bateson, 2014; Jensen, 1999; Pellis & Pellis, 2009). However, the benefits of object play in adult individuals are less clear. Unlike object play in juveniles, the sequential expression of play behavioural patterns performed by adults is typically not random, more closely resembling that of serious behaviour (Hall, 1998). Therefore, the developmental theories arguing that play may serve as practice for future more functional and adult-like behaviour are less valuable in this case, as adults have typically mastered all the related sensory-motor and cognitive skills needed for survival. If play is ever being used as practice in adults, the function and motivation to engage in play behaviour may change (Cappiello, 2017). Practice in adults would be more likely to occur in animals with a more complex behavioural repertoire, and could help to rehearse, enhance, and maintain the precision of already established motor skills in a new setting, or to slow down the age-related degeneration of sensori-motor coordination, while also adding slight modifications to the behavioural repertoire (Bateson & Young, 1979; Cappiello, 2017; Hall, 1998; Lacreuse, Woods, & Herndon, 2007; Nahallage, Leca, & Huffman, 2016).

Most literature however, tends to focus on play in juveniles, as this behaviour is observed most frequently in immature individuals (Burghardt, 2005; Fagen, 1981; Pellis & Pellis, 2009; Pellis et al., 2010). This narrow focus can be problematic when attempting to understand play in different age classes. A common criticism is that the exaggeration of body movement during play bouts, the increased variability in the form or duration of the execution of playful actions, and incompleteness in the basic temporal organization of a play sequence, are simply due to immaturity, as young individuals do not yet have the well-developed sensori-motor coordination to appropriately execute the behavioural patterns (Fentress, 1983). Because object play occurs more rarely in adult individuals, this immaturity confounder is typically not controlled for. To date, very few studies aimed to compare the structure of object play across age classes within the same species (but see Leca, Gunst, & Huffman, 2011). Additionally, finding a comparable form of object play performed in both juvenile and adult animals may not be possible in some species (but see

Cappiello, 2017; Greene et al., 2011 in dolphins, *Tursiops truncatus* and *Stenella frontalis*; Gamble & Cristol, 2002 in herring gulls, *Larus argentatus*; Huffman & Quiatt, 1986; Leca, Gunst & Huffman, 2007; Nahallage & Huffman, 2007a in macaques, *Macaca fuscata* and *M. mulatta*). Species-related and age-related variation in the potential costs, benefits, and motivations associated with object play (Ahloy Dallaire & Mason, 2016; Caro, 1995), makes this task even more challenging.

Motivation

As discussed in previous paragraphs, in order to understand the evolution of play behaviour, it is important to consider the underlying psychological mechanisms, such as motivational processes (Burghardt, 2005). However, as opposed to play behaviour, motivation, and particularly the motivational correlates of different forms of play, are not directly measurable. Therefore, we must first provide an adequate definition. The term motivation refers to *why* an individual engages in certain behaviour, or *why* the behaviour is being produced (Mook, 1996). However, in order to understand *why*, we also need to know *what* motivates this behaviour. For example, in order to understand object play behaviour, we seek to understand *what* external stimuli and internal psychological mechanisms are driving the behaviour.

Three main theoretical views aim to explore and understand motivational processes (reviewed in Mook, 1996). First, the mediationist perspective emphasizes the role of an individual's mental processes in behavioural expression. Within this view, psychodynamic theorists argue that conflicting emotional mechanisms (e.g., drives, impulses, and desires) and personality dimensions motivate behaviour, whereas cognitive theorists suggest that learning processes, beliefs, and rational thought do. However, approaching motivation in non-human animals can be difficult from this perspective, because such internal mechanisms are not directly accessible and measurable, and non-verbal subjects cannot simply be asked about their desires and beliefs. Second, the behaviourist perspective suggests that an individual's behaviour is fully determined by external stimuli rather than internal factors. In other words, actions are considered behavioural contingencies produced and reinforced (via classical or operant conditioning) by a variety of physical or social environmental situations that individuals are presented with, and respond to. Third, the biological perspective emphasizes *how* the integration between environmental influences, learning experiences, genetic factors and physiological processes contribute to causing behaviour in an individual, viewed as a biological system, while considering the fitness consequences of the behavioural traits under study within the species' evolutionary history.

Since motivation cannot be observed or measured directly, researchers typically examine various physiological and behavioural correlates (or intervening variables) of motivational states in order to infer motivation, such as hunger levels (by measuring how much or how fast an individual eats; cf. Hall & Bradshaw, 1998; Mook, 1996), the detailed kinematic structure of behaviour (Ansuini, Giosa, Turella, Altoè, & Castielle, 2008; Cohen & Rosenbaum, 2004), or its sequential organization (Eilam, 2015; Eilam, Zor, Szechtman, & Hermesh, 2006; Miller, Galanter, & Pribram, 1960). With regards to the latter, it is noteworthy that the words 'motor', 'motion', 'motivation', and 'emotion' are etymologically related, from *movere*, meaning "to move" in Latin. However, the current scientific literature investigating the motivational basis for object play is limited (but see Ahloy Dallaire & Mason, 2015; Gamble & Cristol, 2002; Hall & Bradshaw, 1998; Kuba, Byrne, Meisel, & Mather, 2006; Pellis, 1991; Rasa, 1984). Some authors suggest there is a single play-specific motivation system, arguing that play behaviour could have its own neural circuitry in the brain (Panksepp, 1998; Rasa, 1984). Other authors state that object play is underlain by basic drives involved in more functional behaviour systems (e.g., by using elements and movements taken from functional repertoires), and the expression of behavioural repertoires that evolved to solve survival and reproductive problems, such as foraging, fighting, anti-predator responses, nest building, courtship, and sexual behaviour (Burghardt, 2005). For example, object play was found to be motivationally linked to foraging activities in some species (domestic cats, *Felis silvestris catus*, Hall & Bradshaw, 1998; Japanese macaques, *M. fuscata*, Leca, Gunst, & Huffman, 2008a; oriental small-clawed otters, *Anonyx cinerea*, Pellis, 1991). This view suggests that if play derived from more functional behaviour, it may include behavioural patterns that structurally resemble the more functional and specific ethogram it may have evolved from. For example, Pellis (1983, 1991) found that object play in oriental small-clawed otters involved behavioural patterns reminiscent of those performed during a foraging sequence, and their expression was linked to a foraging motivational system.

The transformational model of play aims to address whether play evolved to aid in survival (Burghardt, 2005). This model proposes an evolutionary scenario in which play evolves through different proximate and ultimate processes. Primary process play is considered the most basic or rudimentary form of play (i.e., a behavioural pattern barely meeting Burghardt’s five criteria, 2005) and may not serve a function at this stage. Secondary process play can be considered a transformation of the already established primary process play, through the acquisition of new function(s); however the behaviour would have changed very little at this stage. Once these potential functions have emerged, the behaviour can then undergo further transformations. This level of play is called tertiary process play, and may look very different from the first two levels, as structural modifications are likely to occur with the emergence of additional functions. Though this model proposes a broader evolutionary perspective, it also has an ontogenetical component that may help to explain how the motivational systems underlying play might also change with age (e.g., as individuals develop, predatory actions could be incorporated into object play; Bateson, 2014; Hall, 1998).

Since object play can be considered a complex activity that involves the combination of discrete actions within a sequence, it is logical to assume that these actions share a common underlying motivation, leading them to be performed together to fulfil a specific goal (Burghardt & Bowers, 2017). If object play does share a common underlying motivation to a specific functional activity, such as foraging, then these two behavioural categories should also be structurally similar. However, current studies investigating object play-related motivation fail to provide a systematic comparison between the different levels of the behavioural structure of object play and foraging activities (e.g., the sequence of behavioural patterns, the kinematic structure of how individual patterns are performed). This seriously hinders our examination of the motivational processes underlying object play activities. In order to further our understanding of the motivational and cognitive bases of both object play and the most likely functional behavioural counterpart it is associated with, a detailed and comparative investigation of the different levels of the behavioural structure (e.g., exaggeration, variability, incompleteness; Burghardt, 2005) of these two activities is necessary (Power, 2000). One way to do this is by using hierarchically organized models.

Importance of Hierarchical Organization and Behaviour Systems Approaches

Hierarchically organized models are structured systems that allow complex questions about behaviour to be answered (Burghardt & Bowers, 2017). As discussed in the above section, understanding what motivates behaviour is one of these complex questions. A behaviour systems framework is a hierarchically organized model that can be used to identify and explore the motivational processes underlying various behaviours with different levels of complexity, expressed in multiple contexts (e.g., lab or natural settings) and by different species (Timberlake, 2001). This structural approach allows behavioural patterns within a specific activity to be descriptively categorized and hierarchically organized into multiple interconnected levels, based on stimulus-processing modules and motivational modes that stem from a major functional behaviour system (e.g., foraging, defense, reproduction, parental care, socializing, and body care; Timberlake, 2001). Behaviour systems are concerned with both the structural components and functional aspects of behaviour, as they integrate individual-environment interactions (Timberlake, 1993; Burghardt & Bowers, 2017). They are often used as *explanations* for behaviour after its expression. However, the detailed and organized nature of behaviour systems can also make them a powerful tool in *predicting* behaviour as a theoretical model, if used with the appropriate observations (Timberlake, 1993). The different levels of the behaviour systems model are designed to mirror the chronological sequence of any functional behaviour, typically starting with an appetitive or seeking phase (e.g., food search, investigation, and extraction in foraging behaviour; Burghardt, 2005; Panksepp, 1998).

The behaviour system approach is theoretically applicable to any form of object play, as long as this activity can be motivationally linked to the more functional behaviour it is hypothesized to originate from (Burghardt, 2005; Burghardt & Bowers, 2017; Pellegrini, 2009; Pellis & Pellis, 2009). Because most of the playful actions are (1) performed during the appetitive phase of behaviour (i.e., in the absence of a consummatory phase, such as eating the food item processed in a foraging context; Burghardt, 2005; Burghardt & Bowers 2017), (2) context-specific, and (3) species-specific, a model that aims to understand play-related motivational processes by categorizing behavioural patterns for different forms of species-typical play behaviour (e.g., social play, object play) is crucial. This approach can provide the theoretical foundations for hypothesis-testing and kinematic structural analysis of object play behaviour in different species.

Stone Handling as a Candidate for Object Play

Stone handling (SH), defined as the solitary, versatile, and seemingly playful manipulation of stones with no apparent function (e.g., pounding a stone on the ground, clacking two stones together, or rubbing stones on a substrate; Leca et al., 2008a) is considered one of the longest studied forms of culturally-transmitted object play in non-human primates, spanning over 30 years of continuous research in some macaque populations (Leca, Gunst & Huffman, 2012). SH is one of the few forms of object play routinely performed throughout an individual's lifespan in both captive and free-ranging groups, and has been described in four closely related species of macaques: Japanese macaques, rhesus macaques, *M. mulatta*, long-tailed macaques (*M. fascicularis*), and Taiwanese macaques (*M. cyclopis*) (Huffman & Quiatt, 1986; Leca, et al., 2007; Nahallage & Huffman, 2008; Nahallage et al., 2016). Additionally, the SH activity typically comprises a variety of stone-directed behavioural patterns, involving different body parts (e.g., hands, feet, mouth) and are performed in a sequence, which is either repeated (e.g., a few recurring

SH patterns being performed over and over) or varied (e.g., many different SH patterns that are more or less randomly expressed with little repetition throughout the SH sequence).

Though SH has been observed in four closely related species with the genus *Macaca*, it has only been well documented and reported in Japanese macaques and rhesus macaques (Leca et al., 2007; Nahallage & Huffman, 2012). Research on Japanese macaques highlight both the cultural and potentially playful aspects of this behaviour (Leca et al., 2012). In order for a behaviour to be considered cultural, it should (1) be performed by several members of a group, (2) be persistent over generations, (3) be transmitted through social means, and (4) typically show inter-group differences in frequency and form (Fragaszy & Perry, 2003). Longitudinal studies of SH in the Arashiyama-Kyoto troop of free-ranging, provisioned Japanese macaques over a 30-year span has shown that this behaviour develops (at the individual level) and evolves (at the group level) through four consecutive phases (Huffman, 1984; Huffman & Quiatt, 1986; Huffman, 1996; Huffman & Hirata, 2003; Leca et al., 2012). The initial stage in acquiring SH is referred to as the innovation phase, in which an individual (the innovator) begins to perform basic forms of the activity (e.g., gathering stones into a pile and scattering them around). The next two stages deal with the propagation of the behaviour across group members; they are referred to as the diffusion phase, which consists of both the early transmission of SH among peer playmates, and the tradition phase in which SH is passed down from mothers to offspring. The final stage is referred to as the transformation phase, and is characterized by an increase in the size of the SH repertoire, the diversity of contexts in which SH is performed, and the complexity of the SH behavioural patterns performed (Huffman, 1996; Leca et al., 2007, 2008a). In the Japanese macaques of Arashiyama, Leca et al. (2008a) found a temporal link between SH and foraging activities, with SH behaviour occurring most frequently in the post-provisioning period. This result suggests that food provisioning may have played a role in the transformation of SH, as it provides both free time, and new contexts in which to engage in the activity. Food provisioning also appears to be a key feature in the emergence of SH in a group of macaques. SH only occurs in provisioned groups, and it is suggested that food provisioning reduces environmental pressures, creates a more sedentary lifestyle, and provides individuals with free time to engage in non-subsistence and leisure-like activities, such as object play (Huffman & Hirata, 2003).

Similar to what has been demonstrated in Japanese macaques (Leca et al., 2007), rhesus macaques show age-related differences in the performance of SH. Young individuals performed more diverse SH patterns, with more but relatively short SH bouts, whereas adults performed fewer and longer SH bouts with a lower diversity in SH patterns (Nahallage & Huffman, 2012). Some structural and contextual characteristics of SH meet three of the five criteria for playful behaviour, as defined by Burghardt (2005). More specifically, SH appears to be intrinsically motivated, is performed repeatedly throughout an individual's lifespan, and occurs in the absence of stressful conditions (Nahallage & Huffman, 2012).

The first step towards a thorough understanding of the structure and underlying motivation of SH is to establish species-specific SH ethograms. Indeed, detailed descriptions of the form of SH in multiple species is a prerequisite for future kinematic and possible phylogenetic analyses of SH with the genus *Macaca*. If SH behaviour has evolved from foraging behaviour, a systematic cross-species comparison could help to determine the complex evolutionary relationships between behavioural adaptations, by-products, and possible exaptations, and elucidate at least part of the evolutionary scenario linking object play activities and foraging strategies. While the SH ethograms of Japanese and rhesus macaques have been published (Leca et al., 2007; Nahallage & Huffman, 2012), those of long-tailed and Taiwanese macaques have yet to be established. Moreover, SH has not yet been examined in terms of two major criteria of object play, namely being functionally incomplete in the context in which it is expressed, and being more exaggerated and/or more variable than its more "serious" (i.e., functional) behavioural counterpart (cf. Burghardt, 2005).

The Long-tailed Macaque

The long-tailed macaque is a non-human primate species known for its enhanced object manipulative abilities (Gumert, Kluck, & Malaivijitnond, 2009; Parker & Gibson, 1977; Torigoe, 1985, 1987). Burmese long-tailed macaques (*M. fascicularis aurea*) have been documented using stones as tools in a foraging context. This stone tool use (STU) comprises a range of stone-assisted percussive foraging techniques (e.g., stone-axe chipping, stone-hammer pounding) in order to extract and eat molluscs protected by tough shells, like oysters and sea snails (Gumert et al., 2009; Gumert & Malaivijitnond, 2012). The long-tailed macaques of Ubud, Central Bali (*M. fascicularis fascicularis*), have been observed performing similar percussive type actions in both a seemingly playful context (i.e., SH) and a functional context – nut handling (NH), a foraging technique directed towards hard-shelled nuts (Leca et al., 2016).

From an outward appearance, the percussive actions performed in SH closely resemble those executed in both STU and NH, signifying that percussive behavioural patterns are present in the natural foraging repertoire of long-tailed macaques. This similar appearance could indicate that SH and foraging actions share a common underlying motivation in this species. A structural kinematic analysis of similar patterns (i.e., pounding actions) performed in SH and NH would provide valuable information on whether these activities are motivationally linked, and provide a first step in understanding the evolution of SH behaviour. Since long-tailed macaques are known to perform similar types of complex object-directed actions in multiple contexts, it makes them an excellent candidate species to answer questions on the motivational aspects of potentially playful behaviour.

Objectives of this Thesis

As discussed in previous sections, it is important to consider both the proximate and ultimate aspects of play. However, in order to understand potential functions of object play behaviour, we must first investigate its motivational underpinnings by analyzing its kinematic structure. This thesis aims to examine the behavioural structure of SH in Balinese long-tailed macaques in order to answer the following questions: (1) Can SH truly be considered a form of object play? (2) Is SH motivationally linked to foraging? (3) Are the structural components of play, such as exaggeration, variability, and incompleteness, constrained by the immaturity of the performer, or are they intrinsic features of playful behaviour in all age classes?

SH is performed throughout the lifespan, and therefore provides an excellent opportunity to address questions pertaining to motivation. As discussed above, object play has been motivationally linked to foraging activities in some species (Hall & Bradshaw, 1998; Pellis, 1991). Because long-tailed macaques perform similar types of object-directed actions in both a seemingly playful context (i.e., SH) and a functional foraging context (i.e., NH), they are an excellent candidate species to study these behaviours.

Study one (Chapter Two) adds to the existing SH literature by presenting the SH ethogram in a third species, the Balinese long-tailed macaque, and utilizes a behaviour systems framework to propose the hypothesis that SH is motivationally linked to foraging activities. This ethogram provides a basis for examining the kinematic structure of SH behavioural patterns by comparing them with similar actions performed in a foraging context. Additionally, a comparison of the SH repertoires in three macaque species (*M. fascicularis, M. fuscata,* and *M. mulatta*) is made in order to test for species differences in SH patterns, and to better understand the evolution of percussive SH.

Study Two (Chapter Three) begins to test the motivational link between foraging and object play behaviour using the proposed hypothesis outlined in Chapter Two, by delving into the kinematics of percussive pounding actions in both SH and NH. As discussed above, if object play and foraging share a common underlying motivation, they should also be structurally similar. If SH is motivationally linked to foraging, it should involve movements taken from foraging repertoires (Burghardt, 2005), and therefore, the kinematic structure of percussive patterns should be similar in both SH and NH. If SH is a playful activity motivationally distinct from foraging activities, then SH should exhibit structural characteristics of play, such as exaggeration, variability, and incompleteness (Burghardt, 2005) that are absent in a functional behaviour such as NH. Additionally, since play is performed most frequently in young individuals (Bateson, 2014), a common criticism for play displaying these characteristics is the immaturity confounder (Fentress, 1983). This chapter utilizes a unique study design by comparing percussive actions of SH in adults and juveniles to test whether structural aspects of play (variability, exaggeration, incompleteness) are associated with immaturity, or are in fact a component of play. This chapter is the first study to perform a direct test on Burghardt's third criteria for play that addresses variability, exaggeration, and incompleteness.

CHAPTER TWO

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*[1]

Abstract

Stone handling (SH), has been identified in four closely related primate species of the *Macaca* genus. We provide the first ethogram of SH in long-tailed macaques (*Macaca fascicularis*), a primate species known to use stones for extractive foraging. A total of 62.7 hrs of video recorded data were scored from a population of Balinese long-tailed macaques living in Ubud, Bali, Indonesia, and a total of 36 stone handling patterns were identified. Behavior discovery curves were generated and showed that the minimum threshold of completeness was exceeded for the SH repertoire in this group. A "foraging substitute" hypothesis for the expression of SH was proposed, suggesting that SH consists of performing foraging-like actions on non-edible objects. We used a "behavior systems" framework to test this prediction, finding that all 36 stone handling patterns could be reliably categorized in a foraging behavior system, supporting the hypothesis that stone handling can be considered pseudo-foraging behavior. Our "behavior systems" approach will serve as a foundation for the future testing of the motivational basis of stone handling. Additionally, a comparison of 39 stone handling patterns performed by three macaque species (*M. fascicularis, M. fuscata* and *M. mulatta*) showed overlapping

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behavioral propensities to manipulate stones; however, the differences suggest that long-tailed macaques might be more prone to use stones as percussive tools in a foraging context. This work could offer insights into the development and evolution of complex activities such as percussive stone tool use in early humans.

Keywords: object play, percussive tool use, behavior systems, motivation, foraging, ethogram

Introduction

> What we need are more detailed observations of play from the viewpoint of the various systems involved within what seems to be a single kind of play...
>
> - Burghardt (2005) *The Genesis of Animal Play: Testing the Limits*

Despite the lack of a definitional and theoretical consensus, object-oriented play is known to occur in numerous mammal and bird species (Fagen, 1981; Power, 2000). For the purpose of this study, object play will be defined as the spontaneous, repeated, seemingly relaxed, incompletely functional, and usually solitary manipulation of inanimate objects, which differs structurally, sequentially, and contextually from more serious versions of object handling (Bjorklund & Pellegrini, 2002; Burghardt, 2005; Hall, 1998). Research on object play behavior in non-human primates has key implications for the development of foraging competence, the motivation underlying tool use, and the evolution of material culture in humans (Parker & Gibson, 1977; Ramsey & McGrew, 2005). The development of ethograms across a wider range of species is an important first step to better understanding object play. Because object play is rarely observed in adult animals – with the exception of some domestic species and captive individuals (Hall, 1998) – more detailed descriptions of adult animals playing with non-edible objects are also needed. Such data would aid in determining what actions are specific to play and which actions arise from immaturity when performed by young animals.

Stone handling (SH) is one of the few types of object play routinely performed throughout an individual's lifespan in both captive and free-ranging groups, and has been described in four closely related species of macaques: Japanese macaques (*Macaca fuscata*), rhesus macaques (*M. mulatta*), long-tailed macaques (*M. fascicularis*), and Taiwanese macaques (*M. cyclopis,* Nahallage et al., 2016). SH consists of the non-instrumental manipulation of stones in various ways (e.g., clacking two stones together or rubbing stones on a substrate), and is structurally complex: the stones may be manipulated in combination with other objects (including edible ones, like fruits and leaves) and may involve various other body parts than just the hands (e.g., feet, mouth; Leca et al., 2008a). In free-ranging provisioned groups of Japanese macaques, SH has been motivationally linked to foraging due to the similarities in the actions performed and the temporal association between these two object-oriented activities (Leca et al., 2008a). Additionally, SH is probably the best-known example of non-adaptive and culturally-transmitted behavior in non-human primates (Leca et al., 2012). Overall, SH is an ideal candidate behavior to examine the motivational processes underlying object play from a cross-species comparative perspective.

The first objective of this study was to contribute to the limited descriptive database of object play activities in both young and adult monkeys by providing a comprehensive written and video-illustrated SH ethogram in long-tailed macaques. The long-tailed macaque is an excellent candidate species to make this contribution, as one of the subspecies (i.e., Burmese long-tailed macaque, *Macaca fascicularis aurea*) is known for its manual dexterity and routine stone tool use skills in an extractive foraging context (Gumert et al., 2009).

Our second objective was to propose a “foraging substitute” hypothesis for the motivation underlying the expression of SH in this species. In line with previous research on Japanese macaques (Leca et al., 2008a), we suggest that SH consists of performing foraging-like actions on non-edible objects (i.e., stones) because this activity involves motivational processes typically associated with foraging. To explore this hypothesis, we used a “behavior systems” approach. This approach allows for the descriptive grouping of activity-specific behavioral patterns under multi-level, interrelated and hierarchically nested perceptual, central, and motor units, by inferring stimulus processing modules and more integrated internal states or motivational modes, which originate from a few major functional behavior systems (e.g., foraging, defense, sex/reproduction, parental care, socializing, and body care; Timberlake, 2001).

Our third objective was to compare the SH patterns performed by long-tailed macaques with the SH ethograms available for Japanese macaques (Leca et al., 2007) and rhesus macaques (Nahallage & Huffman, 2008). Cross-species comparative analysis is one of the most powerful methodological tools to explore the origins and evolution of biological features (Martins, 1996). This approach is particularly useful to reconstruct scenarios for the evolutionary history of behavioral traits, which do not leave any direct fossil traces. It can be used to decide whether similar behavioral patterns are due to common ancestry or the result of independent adaptations to similar environmental pressures (Martins, 1996). Such a comparative approach should be relevant to understanding the evolution of object play behavior because it can distinguish adaptive from non-adaptive traits by indicating which ones have predated, accompanied, or followed the modification of some of their structural and functional attributes. The lack of functional constraints, and thus the flexibility and versatility of SH activity, makes it a good candidate for cross-species comparative analysis. If SH is most reliably assigned to the foraging behavior system in the long-tailed macaques, and the SH ethograms vary across these three macaque species, one could test whether this variation in object play behavior reflects inter-specific differences in foraging strategies. We put a special emphasis on the cross-species comparison of percussive SH patterns. Indeed, a higher diversity in percussive SH patterns and more frequent percussive stone-tool using in long-tailed macaques than in the other two macaque species could indicate differential adaptive foraging styles in relation to the behavioral propensity to manipulate stones.

Methods

Study Site

The study site was located at the Sacred Monkey Forest Sanctuary, Ubud (central Bali, Indonesia). The study population was composed of five neighboring groups of Balinese long-tailed macaques (*Macaca fascicularis fascicularis*), totaling approximately 600 individuals. In this study, we focused on one group (called “Cemetery”), totaling 136 individuals. The monkeys were free-ranging within the temple grounds and provisioned with fruits and vegetables by the temple staff twice daily.

This research was exclusively observational and non-invasive, and followed all Indonesian laws for foreign research. 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 approved by our federally mandated institutional animal welfare committee.

Data Collection Procedure

During three weeks in August 2008, between 09:00 hours and 18:00 hours, CADN, MAH and JBL used two main observational sampling methods: continuous focal-animal sampling and *ad libitum* sampling (Altmann, 1974). All focal and ad libitum samples were video-recorded with Sony digital video cameras (DCR-TRV22 and DCR-TRV33). Overall conditions of visibility were ideal for obtaining good quality video. Whenever possible, the subjects were filmed from the front or side, within 3 - 5 m, and about 2 m square in frame. A total of 62.7 hrs (i.e., 55.9 hrs of focal and 6.8 hrs of ad libitum samples) were collected from a representative subset of the population including all age and sex classes (namely, male and female infants, juveniles, and adults). Focal subjects were randomly selected, independently of their activities, and the age and sex class with least cumulative data was given priority. We followed Huffman's (1996) protocol, which previously determined that the optimal time period to record a complete SH bout of a randomly selected individual after feeding time was 15 min. If the focal individual performed SH activity during the last 2 min of this 15 min period, the observation was extended for another 5 minutes before ending, unless SH was still in progress.

Data Analysis

In 2016, ANP used The Observer XT 12 (by Noldus) software to score the start and end time of each SH pattern down to the second, from a total of 14.0 hrs of video-recorded SH activity. For the quantitative analyses of Balinese long-tailed macaques presented in this study, we used a sample of 7.3 hrs of SH performed by 75 individuals from all age/sex classes, which represented 205 SH bouts. The basic unit of analysis that we employed to establish the SH ethogram was the SH pattern: a single, non-instrumental, stone-directed, and specifically defined manipulative action (see Appendix for a comprehensive list of distinct SH patterns in Balinese long-tailed macaques). We used The Observer XT 12 duration-sequence option to assess intra-scorer reliability for ANP when transcribing the same samples of SH video-records twice, involving a total of 15.6 min of video containing SH activity, with a total of 78 SH patterns performed (k = 0.99, Martin & Bateson, 1993).

To visually demonstrate the rate at which new SH patterns were identified over the course of observation time, we generated two behavior discovery curves – one generated from our focal sample and one from our *ad libitum* sample – by mapping the cumulative corresponding timecode (x-axis) at which all SH patterns first appeared (y-axis), using the order in which the videos were originally scored (Figures 2.1 and 2.2). In order to assess the completeness of the behavioral repertoire of SH patterns, we created an asymptotic model describing the relationship between the sampling effort and the observation of new SH patterns via a derivation of the Clench equation: $S(t) = at/(1 + bt)$ (Soberón & Llorente, 1993), where t is a measure of effort, a is the rate of increase at the beginning of sampling, and b is the accumulation of behavioral acts. After adjusting this equation to our data, we estimated the maximum theoretical number of SH patterns in our study group by calculating a/b and the proportion of observed SH patterns (Dias, Rangel-Negrín, Covohua-Fuentes, & Canales-Espinosa, 2009).

To reduce the possible effect of behavioral idiosyncrasy on the SH behavior discovery curve, we sampled a large number of individuals performing SH, from all age and sex classes. Indeed, a previous study aiming to establish the ethogram of red pandas (*Ailurus fulgens fulgens)* and using a similar model showed that, if the total number of observation hours exceeds the number of animals observed, and if the degree of behavioral idiosyncrasy in the population is relatively low, the number of behaviors observed per hour increases at a more rapid rate when observing several animals within an observation time than when observing one single animal for the same length of time. In other words, it is better to observe more individuals in any given observation period than one individual for a long period of time (Jule, Lea, & Leaver, 2009). Our study met these two requirements. First, 73 individuals (i.e., 97% of identified stone handlers in the Cemetery group) were sampled over 55.9 hrs to generate the curve based on focal data, and 22 individuals (i.e., 29% of identified stone handlers) were sampled over 6.8 hrs to generate the curve based on ad libitum data (Figure 2.2). Second, we aimed to establish the ethogram of SH, a cultural behavior with relatively low levels of idiosyncrasy (*cf*. Leca et al., 2007).

To conduct a cross-species comparison of SH with the genus *Macaca*, we used previously published data on the SH behavior in Japanese macaques and rhesus macaques. The first data set was collected in 2004, in the free-ranging provisioned group of Japanese macaques, totaling 141 individuals living at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture, Japan (*cf*. Leca et al., 2007). For the quantitative analyses of Japanese macaques presented in this study, we used a sample of 7.1 hours of SH performed by 63 individuals from all age/sex classes, which represented 149 SH bouts. The second data set was collected in 2004, in the captive group of rhesus macaques, totaling 29 individuals housed in an outside enclosure at the Kyoto University Primate Research Institute, Inuyama, Japan (cf. Nahallage & Huffman, 2008). For the quantitative analyses of rhesus macaques presented in this study, we used a sample of 5.2 hrs of SH performed by 29 individuals from all age/sex classes, which represented 103 SH bouts.

To investigate possible differences in the occurrence (i.e., presence/absence) of each of the 39 SH patterns (i.e., dichotomous nominal data) across three macaque species (namely, *M. fascicularis*, *M. mulatta*, and *M. fuscata*), we used a Cochran's Q test, followed by a series of post-hoc paired McNemar’s tests. The qualitative comparison of percussive SH patterns (namely, Clack, Flint, Pound, Pound-Drag, Slap, Slap-Roll, Swipe, and Tap; Appendix) was based on the occurrence of these eight SH patterns across the three macaque species. The quantitative comparison of percussive SH patterns could be done only between *M. fascicularis* and *M. fuscata*. To compare the relative frequency of percussive SH patterns (i.e., how *often* percussive SH patterns were performed in a given SH bout, relative to other SH patterns) and the relative duration of percussive SH patterns (i.e., how *long* percussive SH patterns were performed in a given SH bout, relative to other SH patterns) between the two species, we used Mann-Whitney U tests. To compare the prevalence of percussive SH (i.e., how *many* group members engaged in this form of object play) between the two species, we used a 2 x 2 contingency chi-square test. For statistical analyses, we used IBM SPSS Statistics 24©. Because none of our predictions were directional, we conducted two-tailed tests. Significance levels were set at $\alpha = 0.05$.

Results

SH Ethogram

The SH ethogram of the Balinese long-tailed macaques of Ubud included 36 behavioral patterns (Appendix A; Figure 2.3). Descriptions and comments were included for each SH pattern. For clarity and simplicity, descriptions defined the actions as if they were performed using only one stone, even though most SH patterns could be performed using more than one stone. Corresponding videos were included in supplementary materials. The SH ethogram is available at: https://youtu.be/oRDvBbywJus. Examples of SH sequences are available at: https://youtu.be/MvvSg5Jo3JE.

To assess the completeness of the SH ethogram, we fit the observed cumulative number of newly scored SH patterns over the course of observation time with the predicted discovery curve for both focal samples (Figure 2.1) and *ad libitum* samples (Figure 2.2). The fit of our data to the Clench equation was very good for both the focal data ($r^2 \geq 0.96$) and the *ad libitum* data ($r^2 \geq 0.98$). Most SH patterns were discovered within the first hour of video recording for both sampling methods and the number of new behavioral patterns discovered decreased with more hours of observation. We found 35 behavioral patterns from the focal data, which closely matched (99.3%) the expected theoretical number of 35.3 ($a = 49.448$, $b = 1.402$). Likewise, we found 34 behavioral patterns from the ad *libitum data*, also closely matching (96.8%) the expected theoretical number of 35.1 ($a = 70.139$, $b = 1.997$). These two curves revealed a plateau at 22.3 and 5.2 hrs of observation, respectively. Overall, we exceeded the minimum threshold of completeness for the SH ethogram in this group (i.e., 90%; Dias et al., 2009). Thus, the behavior discovery curves (Figure 2.1 and Figure 2.2) provide evidence that this comprehensive ethogram is representative of the SH patterns performed in the Ubud population of long-tailed macaques in 2008.

“Behavior Systems” Approach to SH

In order to explore the motivational processes underlying the SH activity, we utilized a “behavior systems” approach (Timberlake, 2001). We provided the best possible descriptive correspondence between each of the 36 SH behavioral patterns and upper-level perceptual and central units from the most likely behavior system that has been previously associated with SH in macaques, namely the foraging behavior system (Huffman & Quiatt, 1986; Leca et al., 2008a; Figure 2.4). Based on the behavioral repertoire of the long-tailed macaques (Brotcorne, 2014), we found that all 36 SH patterns could most reliably be categorized in a nested and hierarchically organized foraging behavior system, including all the typical motivational modes characteristic of the chronological sequence of this activity, namely food search, food investigation, food processing, food extraction, and food consumption (Figure 2.4).

Cross-Species Comparative Analysis of SH, with an Emphasis on Percussive SH

The patterns of SH performed by long-tailed macaques were compared to those previously described in Japanese macaques (Leca et al., 2007) and rhesus macaques (Nahallage & Huffman, 2008). Previous classifications of SH patterns in both Japanese macaques and rhesus macaques were categorized based on general activity patterns and the combination with other objects (Leca et al., 2007; Nahallage & Huffman, 2008). For this comprehensive SH ethogram in long-tailed macaques, SH patterns were specifically examined in relation to the precise movement being performed by the body parts executing the action (i.e., the hands or feet), rather than classifying SH patterns solely on the objects and body parts involved. Because long-tailed macaques often incorporate various objects and body parts into their SH activities (e.g., "Tap" on foot, groin, leg, tail; Pelletier, Huffman, Nahallage, Gunst, & Leca, 2016), this method allowed us to create a smaller but more precise repertoire that labeled the behavioral patterns as general categories rather than splitting them when the general action being performed was the same (e.g., "Rub" includes patterns that involve a stone being moved back and forth along a substrate, and contains the previously labeled patterns: "Rub in mouth," "Rub with mouth," "Rub/put on fur," and "Stone-groom").

Table 2.1 shows how the previously labeled SH patterns (*cf*. Leca et al., 2007; Nahallage & Huffman, 2008) not included in this ethogram have now been categorized. Previous patterns such as "Insert into cavity," "Wash," "Combine with objects," and "Flint in mouth," were represented under broader categories based on the specific actions being performed by the hands or feet. These SH patterns were also present in long-tailed macaques; however, because our study group lives in a highly anthropogenic environment (Brotcorne, 2014), these monkeys have been observed to perform numerous SH patterns in combination with a variety of objects other than stones, including vegetal materials and human-made items (e.g., "Cover" with leaves, grass, cloth; "Pound" on leaf, nut, plastic; Pelletier et al., 2016), the previous method of classification would have led to a long and potentially confusing ethogram (e.g., "Cover with leaf," "Cover with cloth," "Cover with grass," "Cover with plastic"). This systematic method of classification prevented us from generating an ethogram that would have been either too general (e.g., "Combine with object" which could contain different actions such as "Cover" or "Wrap"), too specific (e.g., “Wrap with leaf,” “Wrap with plastic”), or based on environmental factors including the objects or substrates involved (e.g., “Wash” and “Rub With Hands” were patterns in which the actions performed are the same, only the presence of water distinguishes them from one another). Because inserting stones into a cavity could also be viewed as the previously categorized pattern, “Combine with objects” (e.g., a bamboo stalk used as the cavity the stones are being inserted into and removed from), and because this action can be performed in a number of different ways by both the same individual, and between individuals, this previously identified category has now been categorized according to how the action is being performed (i.e., “Insert into cavity” frequently resembles a combination of the actions “Pick and drop” when the stone is dropped into a bamboo stalk, and “Gather” when the stone is then retrieved).

From this new categorization, a list of 39 distinct SH patterns was generated. Of the 39 SH patterns, 36 were present in long-tailed macaques, 31 in Japanese macaques and 17 in rhesus macaques (Table 2.1). The occurrence of these 39 SH patterns significantly differed across the three macaque species (Cochran's Q (2) = 26.4, $p < 0.001$). Post-hoc paired comparisons showed significant differences in the SH repertoires of *M. mulatta* and *M. fascicularis* (McNemar’s test, $p < 0.001$), and that of *M. mulatta* and *M. fuscata* ($p < 0.001$). The size of the SH repertoire of *M. mulatta* was about half as large than that of *M. fascicularis* and *M. fuscata,* and there was no SH pattern that was present in *M. mulatta* and absent in *M. fascicularis* or *M. fuscata*. The SH repertoires of *M. fascicularis* and *M. fuscata* did not differ significantly neither in profile (McNemar’s test, $p = 0.227$), nor in size (Table 2.1).

Long-tailed macaques showed a higher diversity in *percussive* SH patterns than Japanese and rhesus macaques. Among the eight percussive SH patterns documented in the genus *Macaca* to date, *M. fascicularis* performed seven (namely, Clack, Flint, Pound, Pound-Drag, Slap, Slap-Roll, and Tap), *M. fuscata* three (Flint, Pound, and Swipe), and *M. mulatta* one (Clack; Appendix). Even though *M. fascicularis* and *M. fuscata* did not differ significantly in the duration of SH bouts (mean ± SD, 2.2 ± 3.2 min and 2.9 ± 3.7 min, respectively; Mann-Whitney U test, $U = 13405$, $p = 0.050$), percussive SH patterns were significantly more frequent ($U = 7199$, $p < 0.001$) and lasted significantly longer ($U = 7146$, $p < 0.001$) in *M. fascicularis* than in *M. fuscata*. Although *M. fascicularis* and *M. fuscata* did not differ significantly in the prevalence of SH activity (55.1% and 44.7% of sampled individuals performed SH, respectively; $\chi^2(1)= 3.03$, $p = 0.082$), the prevalence of percussive SH patterns was significantly higher in *M. fascicularis* than in *M. fuscata* (74.7% and 4.8% of sampled stone handlers performed percussive SH, respectively; $\chi^2(1)= 68.36$,, $p < 0.001$).

It is also noteworthy that percussive SH patterns were performed by numerous individuals from all age and sex classes in *M. fascicularis*. Of the 75 stone handlers sampled in this species, including 11 adult males, 23 adult females, 21 juvenile males, and 20 juvenile females, 58 individuals performed percussive SH patterns, including 10 adult males, 21 adult females 15 juvenile males, and 10 juvenile females. By contrast, of the 63 stone handlers sampled in *M. fuscata*, including eight adults males, 44 adult females, five juvenile males, and six juvenile females, only three individuals performed percussive SH patterns, including two adult females and one juvenile male.

Discussion

This paper provided the first SH ethogram in Balinese long-tailed macaques. Categorizing behavior by using descriptive observations is a first step towards understanding these motivations, as it provides a thorough foundation on which to base future sequential and kinematic analyses. We used a theoretical model (i.e., the behavior systems approach) to propose structural connections between SH, an object play activity in this primate species, and more functional behavioral categories. By doing so, we inferred potential motivations for this playful and thus, incompletely functional behavior. Understanding the motivations underlying object play behavioral patterns, specifically SH actions that are performed throughout the lifespan, can offer insight into the fitness consequences of playful activities. Because SH is routinely performed by both young individuals and adults, health-related and welfare benefits of this behavior have been suggested (see Nahallage & Huffman, 2007a; Nahallage et al., 2016).

Our preliminary behavior systems approach suggested that, while showing most characteristics of object play, SH might be considered a foraging-like activity which consists of pseudo-foraging behavioral patterns directed toward non-edible objects. First, Balinese long-tailed macaques were as much manipulative with stones as with food items that are difficult to process. Of the 36 SH patterns exhibited by Balinese long-tailed macaques (i.e., all those listed in Table 2.1, except Rub Together, and Toss And Catch), 34 have also been observed being performed in an extractive foraging context: nut handling, a food-processing activity aimed at weakening the hard shell of three types of local fruits and nuts (i.e., *Cocos nucifera*, *Aleurites moluccanus* and *Pangium edule*) in order to crack them open and feed on the seeds inside (Pelletier et al., 2017a). Second, we argued that a given SH pattern (i.e., Grasp) could be ascribed to the most relevant perceptual-motor modules (i.e., collection/accumulation/hoarding), which in turn, could be included in the most putative motivational modes (i.e., food search) within a specific behavior system (i.e., foraging). Third, SH could be viewed as the appetitive phase of the foraging behavior system, with obviously no consummatory phase, because the object being manipulated (i.e., a stone) is not edible. Fourth, in free-ranging groups of Japanese macaques, most SH activity occurred within 20 min following food provisioning time and while the monkeys were still chewing their food (Leca et al., 2008a). As such, our findings were consistent with the view that the structure of play behavior is amenable to a behavior systems approach (Pellegrini, 2009; Pellis & Pellis, 2009). Object play behavior has also been motivationally linked to foraging activities in other mammals (oriental small-clawed otters: Pellis, 1991; domestic cats: Hall & Bradshaw, 1998).

Of course, the involvement of other behavior systems is also possible. For example, we argued that the SH pattern "Throw" should primarily be ascribed to the foraging behavior system because it was reminiscent of the underhand throwing motion of a hard-shelled food item (e.g., coconut) up in the air to crack it open, an innovative foraging technique observed in several macaque species (e.g., rhesus macaques: Comins, Russ, Humbert, & Hauser, 2011; Balinese long-tailed macaques: Gunst, personal observation). However, we acknowledge that a similar stone-directed upward throwing action could also fit into a defense behavior system (e.g., Japanese macaques: Leca, Nahallage, Gunst, & Huffman, 2008b). Still, we believe that our study provides a basis for the "foraging substitute" hypothesis that should be tested using a principal component analysis. If the SH patterns assigned to particular modules (e.g., Pick Up, Gather, Grasp) frequently co-occur within a given SH bout, it could suggest that their expression is indeed underlain by a unique and so-called "collection, accumulation, hoarding" motivational module under the "foraging behavior system" (Figure 2.4).

Alternative functional hypotheses pertaining to the expression of SH have been tested in Japanese macaques, two of which received some support. In line with the "surplus energy" hypothesis, proposing that play behavior enables the adaptive expenditure of excess metabolic energy, SH bouts in juveniles (often not limited in energy) were more frequent, versatile, and vigorous, but shorter, than in adults (Leca et al., 2007). Consistent with the "motor training" hypothesis, SH could have beneficial consequences both in immature individuals by allowing a faster development of manipulative skills (Nahallage & Huffman, 2007a) and in senescent individuals by maintaining neural pathways through the daily practice of fined-tuned manual activity, and potentially slowing down the deterioration of sensorimotor and cognitive abilities associated with advanced age (Nahallage et al., 2016). Additionally, even though the "misdirected foraging" hypothesis was not supported in a captive group of Japanese macaques (Nahallage & Huffman, 2007a), it was supported in all free-ranging provisioned groups of this species, where there was a clear temporal connection between SH occurrence and the post-provisioning period (Leca et al., 2008a). Despite sometimes conflicting results, these alternative hypotheses are not mutually exclusive; they suggest that SH could be underlain by various motivational, cognitive, and maturational processes depending on the age class and the context in which this activity occurs. Future experimentally controlled studies should also examine whether the foraging behavior system approach to SH is causal in the context of free-ranging provisioned macaques. More specifically, individuals more frequently performing SH patterns that we ascribed to the food extraction module (i.e., "Clack," "Flint," "Pound") should be more likely to engage in experimentally-induced percussive stone tool use in a foraging context, due to their familiarity with stone-striking actions in a playful context.

A previous study of SH in Japanese and rhesus macaques showed some similarities in the SH patterns performed, suggesting a common behavioral propensity for SH in these two macaque species (Nahallage & Huffman, 2008). Our SH ethogram in long-tailed macaques provided the basis for a comparison with a third species within the same genus.

Table 2.1 showed only the presence or absence of SH patterns in these three species, and though this comparison should be viewed as preliminary, it is noteworthy that the SH profile of Balinese long-tailed macaques overlapped more with that of Japanese macaques than with that of rhesus macaques. Our results also showed that SH was significantly more diverse in Balinese long-tailed macaques and Japanese macaques than in rhesus macaques. With regards to percussive SH, we found that percussive SH patterns were more diverse in Balinese long-tailed macaques than in Japanese and rhesus macaques. Percussive SH activity was also more prevalent, more frequent, and more enduring in Balinese long-tailed macaques than in Japanese macaques.

Even if our cross-species comparison was preliminary, these differences suggest that long-tailed macaques of all age and sex classes are more prone to use a variety of combinatorial and percussive actions during stone play activity than Japanese and rhesus macaques. Our results are consistent with a comparative analysis of object manipulation within the genus *Macaca*, and show that, among all four closely related macaque species exhibiting SH (i.e., *M. fascicularis*, *M. fuscata*, *M. mulatta*, and *M. cyclopis*; cf. Nahallage et al., 2016), long-tailed macaques displayed the greatest variety of finger use manipulation patterns (Torigoe, 1987). They are also consistent with a recent comparative analysis of manipulation complexity across 36 nonhuman primate species, using a scaling method with increasing complexity levels from 1 to 8, based on the (a)synchronous (un)coordinated use of hands and digits with same/different objects; this study showed that Japanese macaques reached complexity level 6, whereas long-tailed macaques reached level 7 (Heldstab et al., 2016).

Interestingly, these findings on the playful manipulation of stones in Balinese long-tailed macaques parallel other stone-directed behavioral data collected in a more functional context in a closely related subspecies: Burmese long-tailed macaques are more frequent stone tool users than Japanese and rhesus macaques, and the only macaques spontaneously exhibiting percussive stone tool use techniques to crack shellfish in coastal environments (Gumert et al., 2009; Tan, 2016). Developmental evidence indicates that percussive stone tool use in Burmese long-tailed macaques may be facilitated by a biological predisposition to handle stones at a very young age, via exploratory and non-instrumental actions that are gradually incorporated into foraging routines (Tan, 2017). From an evolutionary viewpoint, our study suggests that cross-species variation in manual dexterity and the behavioral propensity to manipulate stones in a playful context could reflect, and possibly explain, differential adaptive foraging styles, including stone tool use, within the genus *Macaca.*

To further explore the behavior systems pertaining to SH, one should test whether percussive SH and percussive stone tool use are underlain by similar motivational and cognitive processes. Future analyses will compare the kinematic structure of pounding actions with different objects in different contexts, as well as the temporal organization of different types of pounding sequences, in Balinese and Burmese long-tailed macaques. After controlling for age, and thus physical maturity, we expect higher structural complexity of pounding actions and more predictable behavioral sequences as the apparent functionality of the activity, the food-related interest in the objects being handled, and the difficulty to manipulate them increase. More specifically, we predict that among adults, the variability in the execution of arm/hand movements and the level of randomness in the behavioral sequences will decrease from non-percussive SH (i.e., bouts including stone-gathering and stone-rubbing) to percussive SH (i.e., bouts including stone-pounding on the ground) to percussive food handling (i.e., bouts including nut-pounding on the ground) to stone tool use (i.e., bouts including stone-hammering on shellfish). This work could offer insights into the emergence of complex foraging activities such as percussive stone tool use in early humans.

Like other behavioral traditions (Fragaszy & Perry, 2003), SH is socially learned, performed by most members of the group, transmitted over generations, and can be viewed as developing through numerous phases (Huffman, 1984; Huffman & Quiatt, 1986; Huffman, 1996; Leca et al., 2012; Nahallage & Huffman, 2007b). The beginning phase can be described as the innovation phase, where an individual performs a novel activity. The second phase, transmission, is the early part of the behavioral diffusion, and can be described as the diffusion of SH behavior from individuals through social means, typically horizontally among individuals in a close social network, such as playmates. In the later period of diffusion, when the behavior reaches the tradition phase, SH is passed down through generations, primarily from mothers to their offspring, and is performed by most members of the group (Huffman & Hirata, 2003). An additional phase, the transformation phase, occurs after the behavior has reached a cultural level, and new patterns and modifications are added, leading to an increase in both repertoire size and complexity, and expanding the contexts in which they are performed (Huffman & Quiatt, 1986; Leca et al., 2012). From this perspective, patterns such as “Slap-roll” and “Pound-drag” could be viewed as part of the transformation phase of SH, as they may involve the combination of already established SH patterns to create new and more complex ones. Table 2.1 shows a total of 8 new SH patterns identified in long-tailed macaques that have not been observed previously in other species. Patterns such as “Slap-roll” and “Toss and Catch” were idiosyncratic, being very rare and performed by only one to three individuals, much like the “Flip,” “Swipe,” and “Spin” patterns in Japanese macaques, potentially speaking to the novelty or complexity of the patterns.

The transformation phase could also involve the combination of already established SH patterns with a variety of objects other than stones, body parts, and substrates. Patterns such as “Roll With Fingers,” and different variants of “Throw” (i.e., “Throw and run,” “Throw and jump,” and “Throw and sway” performed in a group of Japanese macaques) are consistent with this view, as they involve previously established patterns being performed in a new way. Stone throwing in Japanese macaques is a perfect example of this. When a “Throw” is performed in combination with an agonistic display, it provides an effective signal to other individuals within the group, and can be considered a form of spontaneous tool use (Leca et al., 2008b). The “Tap” pattern in long-tailed macaques could also be viewed as part of the Transformation phase of SH as it also encompasses several different variants. This pattern can be performed using numerous body parts including tapping a stone onto the hands, feet, leg, tail, and groin, and often involves the combination with non-stone objects. Still, the primary focus on stones during the SH activity could be due to the fact that they are small, graspable, hard, sound-producing, multifunctional, and ubiquitous objects. As such, our research has implications for the evolution of combinatory object-directed actions, including stone tool use, in our primate ancestors.

Conclusion

The lack of definitional and theoretical agreement regarding object play activities suggests that more detailed descriptions are needed. We presented the first SH ethogram in Balinese long-tailed macaques. The behavior systems approach provides a likely hypothesis for future research on the underlying motivations of SH. A systematic comparison of SH across multiple macaque species utilizing this framework could enhance our understanding of the development and evolution of complex manipulative activities in hominins, such as percussive stone tool use in a foraging context.

Table 2.1

Presence (X) or absence (-) of 39 SH behavioral patterns, based on previously published and slightly modified classifications (cf. last column on the far right) of SH patterns across three species in the Macaca genus (for M. mulatta, see Nahallage & Huffman, 2008; for M. fuscata, see Leca et al., 2007). (*): idiosyncratic behaviors, i.e. very rare and performed by only one to three individuals.

SH Behavioural Pattern	*Macaca fascicularis*	*Macaca mulatta*	*Macaca fuscata*	Previous Classification of SH Patterns
Bite	X	X	X	
Carry	X	X	X	Carry in mouth
Clack	X	X	X	
Cover	X	-	X	Wrap in leaf was not previously distinguished from Cover, Combine with objects
Cuddle	X	X	X	
Dislodge	X	-	-	
Flint	X	-	X	Flint in mouth
Flip*	-	-	X	
Gather	X	-	X	Pick, Put in water
Grasp	X	-	X	Grasp with hands
Grasp-Walk	X	X	X	
Groom	X	-	-	
Hold	X	X	X	
Lick	X	X	X	
Move And Push/Pull	X	X	X	
Move Inside Mouth	X	X	X	Put in mouth
Pick And Drop	X	X	X	Pick up small stones, Insert into cavity
Pick Up	X	-	X	
Pound	X	-	X	
Pound-Drag	X	-	-	
Roll	X	X	X	Rub on surface was not previously distinguished from Roll
Roll In Hands	X	X	X	
Roll With Fingers	X	-	-	
Rub	X	X	X	Rub/put on fur, Stone-groom, Rub with mouth, Rub in mouth
Rub Together	X	X	X	
Rub With Hands	X	-	X	Wash when performed in water
Scatter	X	X	X	
Shake In Hands	X	-	X	
Shift In Hands	X	-	-	
Slap	X	-	X	Tap in mouth
Slap-Roll*	X	-	-	
Sniff	X	X	X	
Spin*	-	-	X	
Swipe*	-	-	X	
Tap	X	-	-	
Toss And Catch*	X	-	-	
Toss-Walk	X	X	X	
Throw	X	-	X	Throw and jump, Throw and run, Throw and sway
Wrap	X	-	X	Wrap in leaf, Combine with objects
Total SH Patterns	36	17	31	

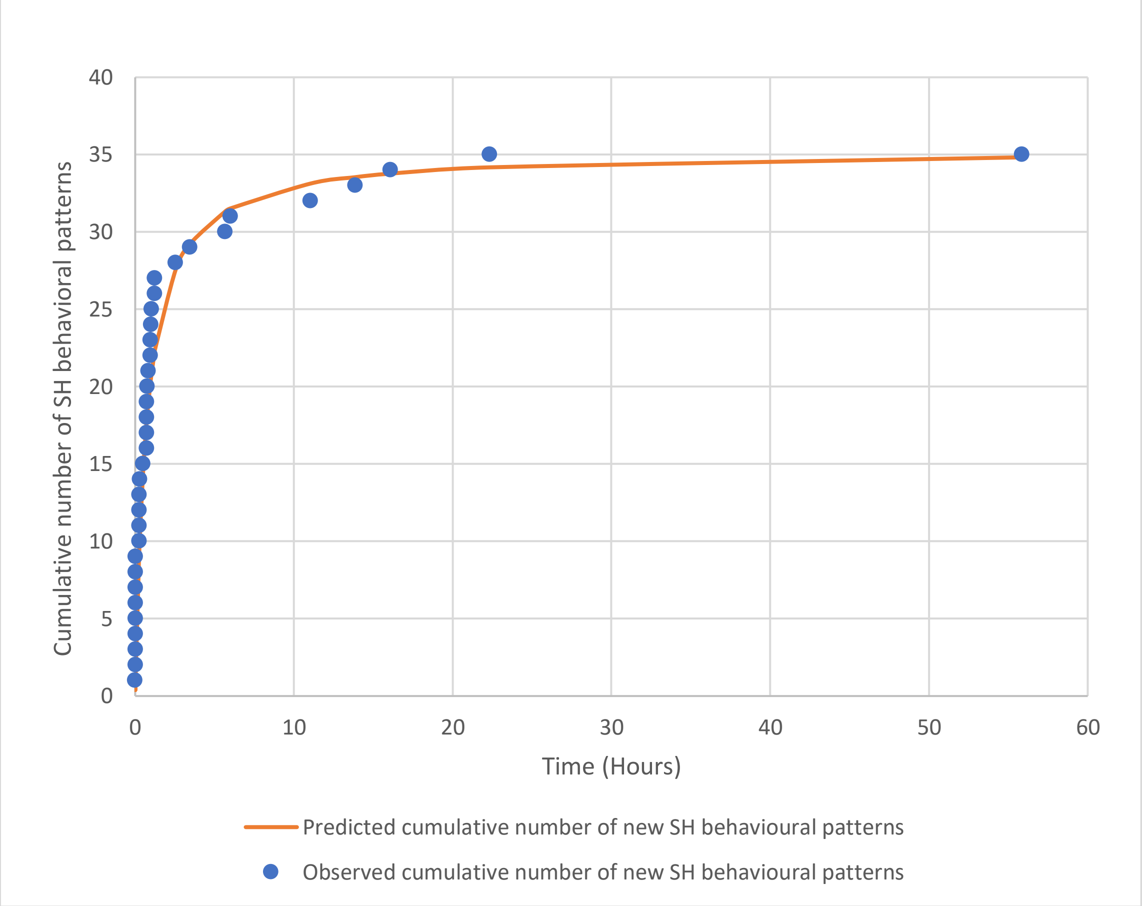

Figure 2.1. Behavior discovery curve representing the observed and predicted cumulative numbers of SH patterns obtained from focal data as a function of observation time.

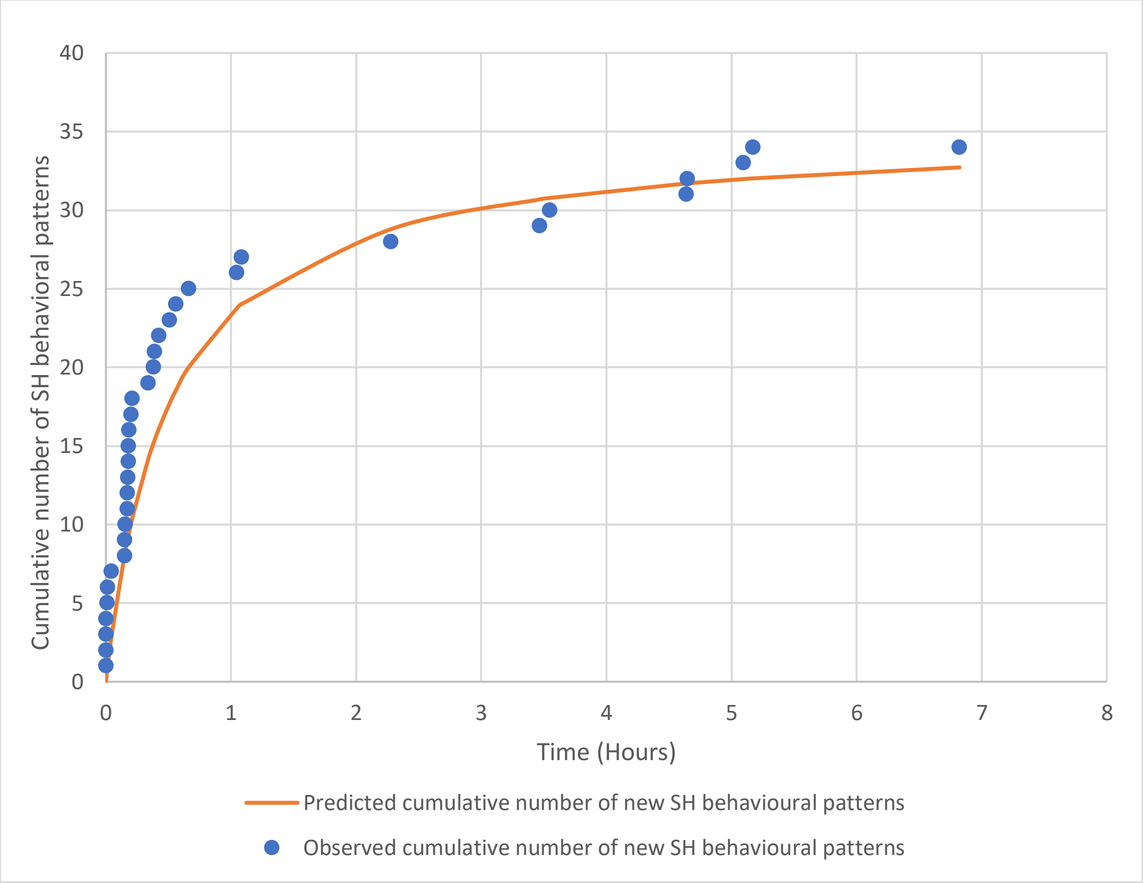

Figure 2.2. Behavior discovery curve representing the observed and predicted cumulative numbers of SH patterns obtained from ad libitum data, as a function of observation time.

Figure 2.3. Examples of stone handling (SH) patterns by Balinese long-tailed macaques at Ubud, Bali, Indonesia. (1) Roll In Hands, (2) Pound, (3) Sniff, (4) Cover, (5) Roll, (6) Flint (in mouth), (7) Grasp, (8) Carry, (9) Gather, (10) Move And Push, (11) Rub Together, (12) Wrap, (13) Cuddle, (14) Hold. (Photos by J.-B. Leca).

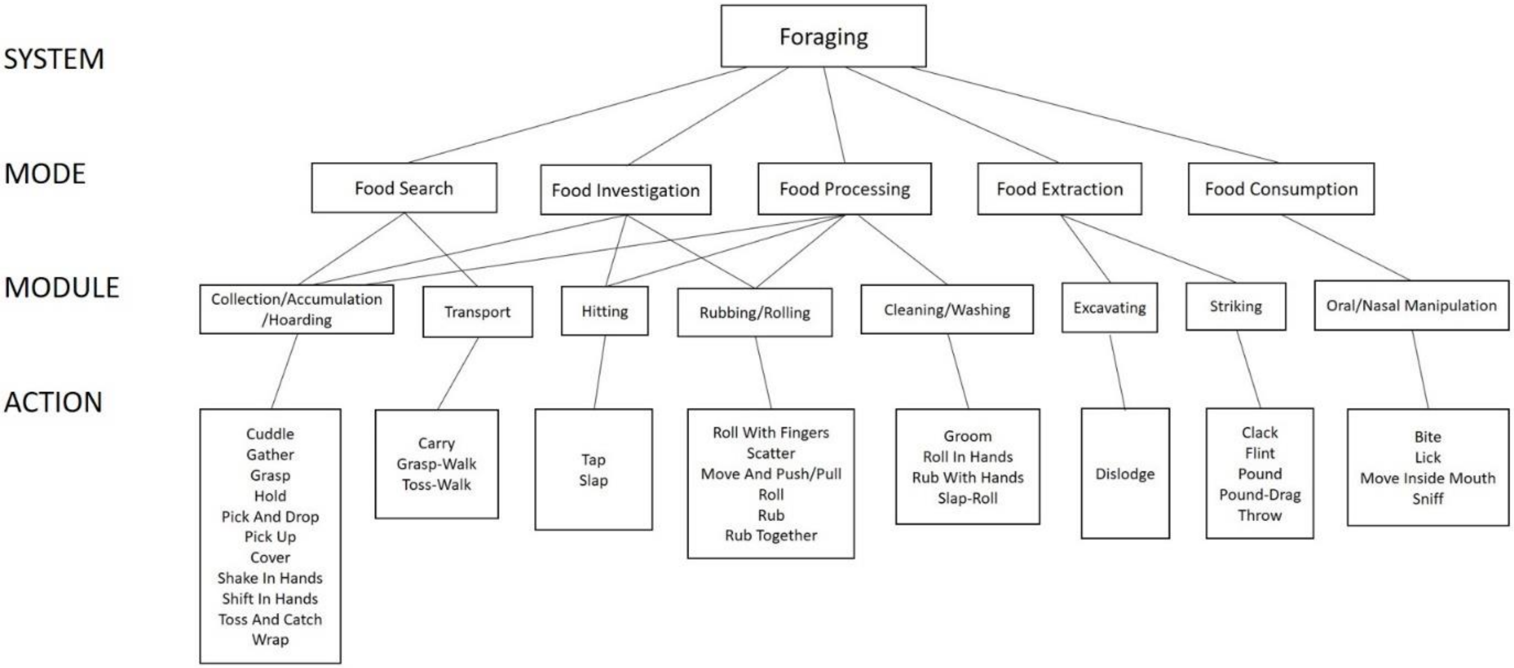

Figure 2.4. Behavior systems diagram representing the foraging behavior system in which the 36 SH patterns displayed by Balinese long-tailed macaques can most reliably be grouped.

CHAPTER THREE

Is Object Play Motivationally Linked to Extractive Foraging? Structural Analysis of Two Percussive Actions in Macaques[2]

Abstract

Most studies of play come with a major caveat: because play is primarily observed in young individuals, it is unclear whether structural differences (i.e., exaggeration, variability, and incompleteness) between so-called playful behaviours and their functional counterparts can really be attributed to playfulness, or may be due to poor behavioural execution due to reduced sensorimotor coordination in immature subjects. This is the first study to examine the proposed motivational links between object play and complex foraging, while controlling for the confounding effect of "immaturity." First, we compared in free-ranging *adult* Balinese long-tailed macaques (*Macaca fascicularis*) – whose sensorimotor systems are mature enough – the detailed structure of the same behavioural pattern (i.e., pounding action) when performed in an unambiguously functional context (i.e., nut pounding) versus in a seemingly playful context (i.e., stone pounding). Second, we compared the detailed structure of stone pounding in adults and juveniles to test potential age differences in the organization of stone pounding. Our results suggest 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 are indeed properties of play behaviour.

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Keywords: object play, extractive foraging, percussive actions, motivation, Eshkol-Wachman movement notation, kinematics, macaque

Introduction

In their outward appearance, most play behaviours are reminiscent of functional ones. For example, social play includes predatory actions, locomotor play includes anti-predatory actions, and object play includes foraging actions (Fagen, 1981; Power, 2000). Yet, we generally identify these behaviours as playful, as they also show structural differences when compared to their functional (or "more serious") counterparts, namely, exaggeration, variability, and incompleteness (Burghardt, 2005). However, most studies of play come with a major caveat: because so-called play behaviours are primarily observed in young individuals, it is unclear whether these structural differences can really be attributed to playfulness, or may be due to these immature subjects' reduced sensorimotor coordination causing poor behavioural execution (Fentress, 1983). This is the first study to control for the confounding effect of "immaturity" by comparing, in *adult* individuals (whose sensorimotor systems are mature enough), the detailed structure of the same behavioural pattern when performed in a functional context versus in a seemingly playful context. To our knowledge, we thus conducted the first direct test of some of Burghardt's (2005) definitional criteria of play (i.e., exaggeration, variability, and incompleteness).

Stone handling (SH), defined as the solitary and playful manipulation of stones (e.g. clacking two stones together, rubbing or pounding stones on a substrate, or wrapping a stone in a leaf; Leca et al., 2012; Pelletier et al., 2017a), is an excellent candidate behaviour to address this problem and investigate the possible motivational links between object play and complex foraging. This is the case for multiple reasons. SH is one of the few forms of object play that is routinely performed throughout the lifespan in several macaque species. In free-ranging Japanese macaques (*Macaca fuscata*), SH has been temporally linked to foraging activities, as this behaviour is mainly performed after food provisioning (Leca et al., 2008a). In free-ranging long-tailed macaques (*Macaca fascicularis*), SH consists of performing foraging-like actions on non-edible objects, and we hypothesized that all 36 SH patterns could be reliably categorized in a foraging behaviour system (Pelletier et al., 2017b). Finally, SH closely resembles nut handling (NH), an extractive foraging technique in long-tailed macaques that involves directing combinatorial actions to hard shelled nuts (e.g., pound, rub, wrap, water-soak, and bite) in order to weaken and break open the shell and feed on the nutritious seeds inside (Pelletier et al., 2017a).

In this study, we aimed to further examine the proposed motivational links between object play and complex foraging (e.g., Hall & Bradshaw, 1998; Pellis, 1991; or lack thereof: Ahloy Dallaire, & Mason, 2016; Gamble & Cristol, 2002). To do so, we compared the kinematic structural characteristics of pounding actions involving a stone (i.e., stone pounding or SP) with that involving a nut (i.e., nut pounding or NP). Adult males are generally successful in gaining access to the content of the nuts, whereas adult females and juveniles are not. Consequently, for the adult males, the same action (i.e., pounding) could be compared in an unambiguously foraging context – a nut was manipulated until the contents were exposed and eaten – and an unambiguously non-foraging context – an inedible stone was manipulated (Leca et al., 2016).

Pounding actions were chosen specifically because (1) they are complex and constrained enough to allow us to distinguish between immaturity and playfulness, (2) they are characteristic of this species' extractive foraging techniques in the form of stone pound-hammering and stone axe-hammering (Gumert et al., 2009; Tan, Tan, Vyas, Malaivijitnond, & Gumert, 2015), (3) they are performed from a relatively standard and stable position, making them amenable to a movement notation analysis, and (4) they are more prevalent, more frequent, and more diverse in long-tailed macaques when compared to other macaque species (Pelletier et al., 2017b).

First, we tested a series of predictions generated from two alternative hypotheses about the motivation to perform SP in adults (Table 3.1). If SP and NP are motivationally linked, we should expect a number of structural similarities between these two types of pounding actions (e.g., there should be no significant differences in the speed, height, and variability of the pounding actions, and no significant differences in the basic structural organization). As such, SP could be considered a form of misdirected NP toward stones, as a foraging substitute, where individuals would perform foraging-like percussive actions on non-edible objects (Hypothesis 1: “SP as pseudo-foraging”: Pelletier et al., 2017b). If SP and NP are motivationally distinct, we should expect major structural differences between these two types of pounding actions (e.g., SP should be more exaggerated in speed, height, and variability of the pounding actions, and major differences between SP and NP should be present in the basic structural organization). In this case, SP could be identified as a form of purposeless object play that is exaggerated, variable, and incomplete in its execution, and less functionally constrained when compared to NP, its functional counterpart in an extractive foraging context (Hypothesis 2: “SP as object play”).

Second, we tested another series of predictions generated from three alternative hypotheses about potential age differences in the motivation to perform SP (Table 3.2). If SP is a form of pseudo-foraging that improves with age, physical maturation and practice, then its execution should be more constrained in juveniles than in adults, due to reduced sensori-motor coordination (Hypothesis 3: “SP as needing-to-learn”; after Ross & Jones, 1999). If SP is a form of object play that enables the adaptive expenditure of excess metabolic energy, then its execution should be more variable and exaggerated (in intensity, form, duration) in juveniles, and more fixed in adults (Hypothesis 4: “SP as surplus energy”; after Barber, 1991). Alternatively, if SP is a form object play that reveals the playful nature of SH throughout the lifespan, then its execution should not differ between juveniles and adults (Hypothesis 5: “Lifetime playfulness”).

Methods

Study Population, Site, and Objects

We studied a population of free-ranging, habituated and provisioned Balinese long-tailed macaques (*Macaca fascicularis fascicularis*), living in and around the Sacred Monkey Forest Sanctuary in Ubud (also known as Ubud Monkey Forest, UMF), central Bali, Indonesia. The study population totalled approximately 700 individuals, and was comprised of six neighbouring groups with overlapping home range areas (Kluzinski, 2016). The monkeys were provisioned twice per day with fruits and vegetables by the temple staff. The two objects of interest in this study (namely, stones and nuts) were readily accessible to the monkeys across several areas of the study site. Stones naturally occur throughout the UMF. Among the different types of nuts locally handled by the monkeys, we focused on Pangi nuts (*Pangium edule*, from the Achariaceae family, known as “picung” in Balinese and “keluak” in Indonesian), because they were comparable in size and shape to most handled stones (i.e., between 3 and 5 cm in length/width). The fruit of *Pangium edule* is composed of a hard shell containing a seed kernel, rich in lipids (Andarwulan, Fardiaz, Wattimena, & Shetty, 1999). Wild Balinese long-tailed macaques forage on Pangi nuts in several forested areas throughout the island, including West Bali National Park (Leca, personal observation). There are *Pangium edule* trees in UMF, but their fruits seldom reach maturity because they are eaten by the monkeys at an earlier stage of their development (M. Nama, personal communication). Pangi nuts are introduced into the UMF by local villagers as part of food offerings used in religious ceremonies held at the UMF temples. After these events, food remains are discarded in dump areas, where the monkeys forage and find the Pangi nuts. To get access to the encased seed, the monkeys use a variety of foraging techniques aimed to weaken and break open the hard-shelled nut, such as pounding, rubbing, water-soaking, and biting (Pelletier et al., 2017a).

Data Collection and Study Subjects

Three observers (i.e., SS, EN, and JBL) used continuous focal-animal sampling (cf. Altmann, 1974) to video-record behavioural data, including SP and NP over a six-month period from May to October 2016, between 08:00 and 18:00. Data were primarily collected from two main groups (i.e., Temple group and New Forest group), and occasionally supplemented with data from the remaining four groups. Individually identified focal subjects were randomly selected, independently of their activities, and the individuals from the age and sex classes with the least cumulative data were given priority. In order to maximize the number of NP samples, naturally occurring NP bouts were supplemented by experimentally-induced NP bouts with minimal environmental disturbance to the animals. When a prospective focal subject spontaneously approached a dump area, the observer discreetly placed a Pangi nut on the ground, within five meters of the monkey and without it noticing, and started a focal observation on this subject. Therefore, the situation resembled that when a monkey would naturally find a Pangi nut on its own in this typical area. If the subject started to manipulate the nut, it was then continuously video recorded by following Huffman's (1996) protocol, which previously determined that the optimal duration to record a complete object manipulation sequence from a randomly selected macaque focal subject was 15 minutes. If the focal subject performed SH (including SP) or NH (including NP) activity during the last five minutes of this 15-minute period, the observation was extended for another five minutes before ending, unless SH or NH was still in progress.

For all the video recordings, we used Sony digital video cameras (CX675 32GB HD). Visibility conditions were excellent overall, allowing for good quality video to be obtained. Whenever possible, the subjects were filmed from the front or side, within 3-5 meters, and about two-meter square in-frame. A total of 95.0 hours of SH and 30.1 hours of NH were collected from a total of 8 adult males, 8 adult females, 8 juvenile males, and 8 juvenile females.

Data Analysis

This study examined a total of 14 subjects. Five adult males were selected for SH bouts containing SP, and six adult males for NH bouts containing NP (one individual named Danger was present in both the SP and NP samples, yielding a total of ten unique adult males). Three juvenile males and one juvenile female were selected for SH bouts containing SP. Males were considered to belong to the adult age class if they were over six years of age. Individuals, both male and female, were considered to belong to the juvenile age class if they were between the ages of two and four years (Brotcorne, 2014).

Pound selection. A total of 52 NH pounds and 46 SH pounds were analyzed for the adult male sample, and 51 SH pounds were analyzed in the juvenile sample. Both SH and NH pounds were selected if they were observed in a bout that included a minimum of three pounds, and pounds were selected randomly throughout the SH/NH bout whenever possible (i.e., pounds randomly selected from beginning, middle, and end). Table 3.3

outlines the number of pounds selected for each individual. To be included in the analysis, NH sequences including NP should have been terminated by the nut being cracked open and the seed eaten.

Between September 2016 and April 2017, the first author (ANP) used the Eshkol-Wachman Movement Notation (EWMN) system to analyze pounding actions in these SP and NP samples. The EWMN is a system of description that allows for the tracing of movement by individual limb segments using a spherical coordinate system (Eshkol & Wachman, 1958). The surface of the sphere is divided at 45° intervals, yielding locations with a vertical and horizontal coordinate. For greater resolution, the sphere could be divided at 22.5°, yielding more coordinates. Even greater resolution could be achieved by noting if the movement was half a unit in either the vertical or horizontal dimension (i.e., designated as an *h*). The type, direction, and magnitude of the movement of each body segment are then notated, with the proximal end of the segment anchored at the center of the sphere and the distal end tracing a trajectory on the surface of the sphere. Body segments are defined anatomically. For example, the lower arm is defined as the section of the arm between the elbow and wrist, and the upper torso as the segment of the torso above the midpoint of the abdomen. Movements are notated on a horizontally ruled page, where each frame of movement, lasting approximately 30 ms, was accounted for by moving along the row horizontally. The name of each body segment, is identified on the far left-hand side of the page at the beginning of the row, with the heaviest limb segments (i.e., the weight bearing parts of the body) at the bottom of the page, and the notation moves from left to right (Figures 3.1 and 3.2). An advantage of the EWMN system is that the same movements by a body segment can be notated in relationship to neighbouring body segments, to some fixed location in space or to a moving location in space, such as a social partner. Juxtaposing these different frames of reference can be very helpful in identifying the regularities in the organization of functional sequences of behaviour (Golani, 1976). EWMN has been successfully used to describe the organization of both solitary and social behaviour in a variety of animals (e.g., Eilam & Golani, 1988; Moran, Fentress, & Golani, 1981; Ottenheimer Carrier et al., 2015; Whishaw & Pellis, 1990).

For notation purposes, the beginning frame of a pounding sequence was defined as the frame immediately prior to the first movement made by the wrist during the upswing. The ending frame was defined as the frame in which the hand holding the object was resting on the ground again after the downswing. The median number of frames was 12.5 (range: 6-24) for SP performed by adult males, 14.0 (range: 7-27) for NP performed by adult males, and 9.0 (range: 5-17) for SP performed by juveniles.

Distance and speed measurements. As pounding actions were filmed from varying vantage points, a method to standardize the various movements of different body parts was employed to allow comparisons both among body parts and across individuals. This involved calculating ratios between distances from body parts to a fixed location on the ground. To determine the amount of head movement during a pound, the distance of the head to ground was measured at three points of the hand's trajectory as described in the EWMN scores: the frame at the beginning of the sequence immediately before movement commences (A), at the apex of the upswing and so the frame in which the hand grasping the object reached the highest distance from the ground, prior to the onset of the downswing (B), and the end frame when the hand/object is resting on the ground (C) (Figure 3.3). ANP measured the head-to-ground distance (i.e., $D_{h\text{-}g}$) from the lowest point of the head to the ground at all three points in hand position. To compare the amount of head movement between each of the three points across pounds, we used the following ratios: $D_{h\text{-}g(C)}$/ $D_{h\text{-}g(A)}$ was the head-to-ground distance ratio during total head movement from beginning to end; $D_{h\text{-}g(B)}$/ $D_{h\text{-}g(A)}$ was the head-to-ground distance ratio during head movement from beginning to apex; $D_{h\text{-}g(C)}$/ $D_{h\text{-}g(B)}$= was the head-to-ground distance ratio during head movement from apex to end.

An additional structural variable that we compared across pounds was the distance between the head and the object held by the hand at the apex (point B). We defined head-to-object distance by using the following ratio: $D_{o\text{-}g(B)}/D_{h\text{-}g(B)}$, where $D_{o\text{-}g(B)}$ was the object-to-ground distance at the apex, measured from the base of the object (held in hand at point B) to the ground. These measurements were determined by using a standardized method to compare between pounds for both objects: ANP measured the length of the monkey subject's head (i.e., mh) with a standard ruler, and used it as a unit of measurement to determine the distance from the lowest point of the object to the ground (e.g., 1.2 mh; with a precision down to one decimal).

Upswing and downswing speeds (*V* in mh/s) were calculated by dividing $D_{o\text{-}g(B)}$ by the duration (estimated by the number of video frames) of the hand movement between point A and point B, and between point B and point C, respectively.

Variability assessment. In order to compare the amount of variability in continuous variables (i.e., distances, duration of phases, and speed in SP and NP), we used the coefficient of variation (CV), which is calculated as follows: $CV = (SD/\bar{X}) \times 100$, where SD is the standard deviation and $\bar{X}$ is the mean. To determine whether differences in CV were statistically significant or not, we used the test statistic *C* (Lehner, 1996) calculated as follows: $C = (CV1 – CV2)/ \sqrt{}(Scv_1^2 + Scv_2^2)$, where $Scv= CV/\sqrt{}2N$.

In order to compare the amount of variability in nominal dichotomous variables that were scored as either "yes" or "no" (e.g., "forward-facing torso immediately before upswing", "ground-directed gaze immediately before downswing"), we used Kader & Perry's (2007) method to calculate the coefficients of 'unalikeability' (u). To test whether two coefficients of unalikeability were statistically significantly different, we used a modified version of the Levene's test for homogeneity of variance, as part of a one-way ANOVA.

Statistics

For descriptive purposes, the findings for most variables are reported as mean values ± the standard deviation (*SD*). For statistical analysis, when our raw and transformed data violated parametric assumptions, we conducted non-parametric tests. Where possible parametric statistics were used. To test for correlations between (1) head-to-ground distance ratios and head-to-object distance, and (2) duration and speed of upswing and downswing and object-to-ground distance at the apex, for both types of pounds and age classes, we used Pearson correlation coefficient tests. To compare speed of upswing and downswing, object-to-ground distance, head-to-object distance at the apex, for both types of pounds and age classes, we used Mann-Whitney *U* tests. To compare torso positions before the upswing as well as gaze directions before the downswing, for both types of pounds and age classes, we used chi-square tests for independence. Data were analyzed using IBM SPSS statistics 24 with a significance level set at $\alpha = 0.05$.

Ethical note

This research 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 our federally mandated institutional Animal Welfare Committee at the University of Lethbridge (Protocol #1430).

Results

Comparative Structure of SP and NP in Adult Males

Basic structural organization. The pounds executed in both SP and NP performed by adults were similarly divided into three consecutive phases; upswing, adjustment, and downswing (Figure 3.4). For *both* SP and NP, the upswing phase started with the subject in a seated position, orienting its body to a particular location, typically with the front of the torso facing directly forward, preparing for the beginning of the pounding actions. The subject then lifted the object using both the upper and lower arm segments to a particular location in space, and its gaze was generally directed towards a location on the ground, predicting the location of contact following the downswing. The adjustment phase consisted of wrist and/or upper arm movement resulting in the palm of the hand holding the object facing downwards immediately before the downswing. The downswing then consisted of the downward trajectory, combining movements of the upper and lower arm segments ending with the hand holding the object resting on the ground.

In terms of variability in the duration of phases, we found no significant differences between SP and NP for the upswing (mean duration = 147 ± 72 ms and 182 ± 62 ms, respectively; $CV_{SP} = 49.1\%$, $CV_{NP} = 33.8\%$; $C = 1.30$, df = 60, $P > 0.05$) and downswing (mean duration = 94 ± 34 ms and 94 ± 29 ms, respectively; $CV_{SP} = 36.0\%$, $CV_{NP} = 30.9\%$; $C = 1.06$, $P > 0.05$). The duration of the adjustment phase did reveal a difference between SP and NP (mean duration = 23 ± 28 ms and 25 ± 18 ms, respectively), with SP being significantly more variable than the NP ($CV_{SP} = 124.4\%$, $CV_{NP} = 71.7\%$; $C = 3.56$, $P < 0.05$). Overall, these results support prediction 1a (Table 3.1).

Detailed structural organization. The upswing speed was significantly greater during NP than during SP (mean $V_{SP} = 5.7 \pm 3.1$ mh/s and mean $V_{NP} = 6.6 \pm 2.3$ mh/s; Mann-Whitney U test, $N_{SP} = 46$, $N_{NP} = 52$, $U = 910.0$, $P = 0.040$). Therefore, prediction 2b was supported. The downswing speed was also significantly greater during NP than during SP ($V_{SP} = 8.8 \pm 5.0$ mh/s and $V_{NP} = 13.0 \pm 5.2$ mh/s; $U = 664.5$, $P < 0.001$). Therefore, prediction 2c was supported (Table 3.1).

Object-to-ground distance at the apex was significantly greater during NP than during SP (mean $D_{o\text{-}g(B)}$ for SP = 0.8 ± 0.5 mh and mean $D_{o\text{-}g(B)}$ for NP = 1.1 ± 0.3 mh, $U = 863.5$, $P = 0.017$). Therefore, prediction 2d was supported. The head-to-hand distance at the apex was significantly smaller during NP than during SP ($D_{o\text{-}g(B)}/D_{h\text{-}g(B)} = 1.0 \pm 0.3$ and $D_{o\text{-}g(B)}/D_{h\text{-}g(B)} = 0.8 \pm 0.5$, respectively; $U = 874.0$, $P = 0.022$). Since these distance values were calculated using a ratio, the mean value can be interpreted as follows: the larger the value, the smaller the distance. Therefore, prediction 2e was supported (Table 3.1).

Moreover, there was no significant correlation between the head-to-hand distance and the amount of head movement during the upswing for either SP (Pearson correlation test, $N = 46$, $r = -0.268$, $P = 0.072$) or NP ($N = 52$, $r = -0.051$, $P = 0.719$). This indicates that adult males keep the distance between the head and the hand holding the object relatively stable during the upswing for both types of pounding. No significant correlation was found between $D_{o\text{-}g(B)}$ and the amount of head and upper torso movement from beginning to apex for SP ($r = 0.259$, $P = 0.718$). However, we found a significant positive correlation between $D_{o\text{-}g(B)}$ and the amount of head movement from beginning to apex for NP ($r = 0.376$, $P = 0.006$). This suggests that the more upward movement of the head during the upswing, the higher the subjects bring the nut.

There was no significant difference between NP and SP in the frequency of the torso facing forward immediately before the upswing (93.5% of SP and 94.2% of NP, Pearson chi-square test, $N_{\mathrm{SP}} = 46$, $N_{\mathrm{NP}} = 52$, $\chi^2 = 0.024$, $P = 0.877$). In both types of pounding, a frontward facing torso position was utilized most frequently. Therefore, prediction 1f was supported. The frequency of ground-directed gaze immediately before the downswing was significantly higher during NP than during SP (94.2% of NP and 80.4% of SP, $\chi^2 = 4.323$, $P = 0.038$). Therefore, prediction 2h was supported (Table 3.1).

Variability. There was statistically greater variability during SP than during NP in the upswing speed ($\mathrm{CV}_{\mathrm{SP}} = 54.9\%$, $\mathrm{CV}_{\mathrm{NP}} = 34.8\%$; $C = 3.00$, df = 60, $P < 0.05$), downswing speed ($\mathrm{CV}_{\mathrm{SP}} = 56.8\%$, $\mathrm{CV}_{\mathrm{NP}} = 39.9\%$; $C = 2.39$, $P < 0.05$), object-to-ground distance at apex ($\mathrm{CV}_{\mathrm{SP}} = 62.3\%$, $\mathrm{CV}_{\mathrm{NP}} = 31.6\%$; $C = 4.26$, $P < 0.05$), head-to-hand distance at apex ($\mathrm{CV}_{\mathrm{SP}} = 62.9\%$, $\mathrm{CV}_{\mathrm{NP}} = 34.3\%$; $C = 3.84$, $P < 0.05$), and frequency of ground-directed gaze immediately before the downswing ($u = 0.161$ and 0.055, respectively, $F_{1,85} = 15.65$, $P < 0.001$). These results support predictions 2h, 2i, 2j, 2k, and 2m, respectively (Table 3.1). There was no significant difference between SP and NP in the variability in the frequency of forward-facing torso immediately before the upswing ($u = 0.062$ and 0.055, respectively, $F_{1,96} = 0.083$, $P = 0.774$). Therefore, prediction 1l was supported (Table 3.1).

Comparative Structure of SP in Adults and Juveniles

Basic structural organization. In overall appearance, the pounding of stones by juveniles resembled that observed in adults, in that both could be divided into the same three consecutive phases (i.e., upswing, adjustment and downswing phases) as shown in Figure 3.4. The detailed execution of the components was examined to determine whether they more resembled adult SP (see Table 3.2).

In terms of variability in the duration of these phases, we found no significant differences between juveniles and adults for the upswing ($CV_{juv} = 48.9\%$, $CV_{adult} = 49.1\%$; $C = 0.01$, df = 60, $P > 0.05$), downswing ($CV_{juv} = 33.0\%$, $CV_{adult} = 36.0\%$; $C = 0.62$, $P > 0.05$), and adjustment phase ($CV_{juv} = 107.0\%$, $CV_{adult} = 124.4\%$; C = 1.05, $P > 0.05$). Therefore, prediction 5a was supported (Table 3.2).

Detailed structural organization. There was greater variability in SP performed by adults than by juveniles in terms of the upswing speed ($CV_{juv} = 25.7\%$, $CV_{adult} = 54.9\%$; $C = 4.68$, df = 60, $P < 0.05$), and downswing speed ($CV_{juv} = 40.5\%$, $CV_{adult} = 56.8\%$; $C = 2.28$, $P < 0.05$). Therefore, predictions 4b and 4c were not supported. There were no significant age differences in variability in object-to-ground distance at the apex ($CV_{juv} = 50.9\%$, $CV_{adult} = 62.3\%$; $C = 1.40$, $P > 0.05$) and head-to-hand distance at the apex ($CV_{juv} = 56.0\%$, $CV_{adult} = 62.9\%$; $C = 0.80$, $P > 0.05$). Therefore, predictions 4d and 4e were not supported.

We found no significant differences between juveniles and adults in the upswing speed (mean $V_{juv} = 5.8 \pm 1.5$ mh/s and mean $V_{adult} = 5.7 \pm 3.1$ mh/s; Mann-Whitney U test, $N_{juv} = 51$, $N_{adult} = 46$, $U = 1100.0$, $P = 0.592$), downswing speed (mean $V_{juv} = 8.3 \pm 3.4$ mh/s and mean $V_{adult} = 8.8 \pm 5.0$ mh/s; $U = 1139.0$, $P = 0.805$), and object-to-ground distance at apex (mean $D_{o\text{-}g(B)}$ for juveniles = 0.6 ± 0.3 mh and mean $D_{o\text{-}g(B)}$ for adults = 0.8 ± 0.5 mh, $U = 905.0$, $P = 0.052$). These results support prediction 5b, 5c, and 5d, respectively (Table 3.2).

There was no significant correlation between the head-to-hand distance and the amount of head movement during the SP upswing in both juveniles (Pearson correlation test, $N = 51$, $r = -0.132$, $P = 0.355$) and adults ($N = 46$, $r = -0.268$, $P = 0.072$). This indicates that both juveniles and adults keep the distance between the head and the hand holding the stone relatively stable during the SP upswing. However, we found significantly higher ratios for head-to-hand distance at the apex in adults than in juveniles ($D_{o\text{-}g(B)}/D_{h\text{-}g(B)}$ for juveniles = 0.3 ± 0.1 and $D_{o\text{-}g(B)}/D_{h\text{-}g(B)}$ for adults = 0.7 ± 0.5, Mann-Whitney *U* test, $N_{juv} = 51$, $N_{adult} = 46$, $U = 774.5$, $P = 0.004$), indicating longer head-to-hand distance at the apex in juveniles. Therefore, this result supported prediction 3e (Table 3.2).

Compared to adults, the frequency of forward-facing torso immediately before the SP upswing in juveniles was significantly lower (93.5% in adults and 70.6% in juveniles, Pearson chi-square test, $N_{juv} = 51$, $N_{adult} = 46$, $\chi^2 = 8.385$, $P = 0.004$) and more variable ($u = 0.212$ and 0.062, respectively, $F_{1,95} = 33.28$, $P < 0.001$). Therefore, predictions 3f and 4f were concurrently supported (Table 3.2). There was no significant difference between juveniles and adults in the variability in frequency of ground-directed gaze immediately before the downswing ($u = 0.145$ and 0.161, respectively, $F_{1,85} = 0.227$, $P = 0.635$). Therefore, Prediction 4g was not supported. There was no significant difference between juveniles and adults in the frequency of ground-directed gaze immediately before the downswing (74.5% in juveniles and 80.4% in adults, Pearson chi-square test, $N_{juv} = 51$, $N_{adult} = 46$, $\chi^2 = 0.484$, $P = 0.487$). Therefore, prediction 3g was supported.

Discussion

The present paper provides a unique study design to disentangle the effects of ‘immaturity’ on the organization of playful pounding actions, thus enabling us to test some of the hypotheses about the underlying motivational processes of presumed playful behaviour. To do so, we first conducted a fine-grained comparative structural analysis of pounding actions involving stones (i.e., a non-food item used in a non-functional/playful context) with those involving nuts (i.e., a food item used in a functional/foraging context) by *adult* male long-tailed macaques. Second, we compared the detailed structure of SP in adult and juvenile monkeys.

Adult Pounding of Nuts and Stones

Two mutually exclusive hypotheses were tested using the adult males (Table 3.1). The pounding involving stones could arise as a result of pseudo-foraging behaviour (e.g., Hall & Bradshaw, 1998; Pellis, 1991) or as a distinctly motivated playful action (e.g., Ahloy Dallaire & Mason, 2016; Giljov, Karenina & Kochev, 2017). As adults are involved, differences between similar actions performed with stones and nuts, with the latter being eaten if opened, cannot be accounted for as being due to immaturity of sensorimotor ability. The results show that 10 of the 13 predictions for the "object play" hypothesis were supported (Table 3.1), suggesting that the pounding of stones is not pseudo-foraging, but playful behaviour.

SP and NP actions differed both in their detailed structural organization and in the variability in the execution of these actions. Both the upswing and downswing (i.e., strike) were performed faster during NP than during SP. Nuts were lifted higher and brought closer to the head at the apex than stones. During NP actions, the position of the head dictated the position of the hand during the upswing, and the direction of the gaze predicted the position of the strike. This was not the case during SP actions, suggesting that adult males perform pounding behaviour in a more functional way when directed at a food item than when directed at a stone. Moreover, the execution of SP was significantly more variable than the execution of NP, in terms of upswing and strike speed, object height at the apex, distance between the object and the head at the apex, and how often individuals gazed at the ground prior to the strike. Taken together, these results indicate that, among adult males, SP can be considered a form of object play, motivationally distinct from foraging activity, and as such, is less functionally constrained, more exaggerated, and more variable in its execution than NP.

It is noteworthy that partial support was found for the "pseudo-foraging" hypothesis, with three behavioural components showing no significant differences between SP and NP. The basic structural organization did not differ significantly between these two percussive actions. Both types of pound were found to be performed in three consecutive phases (i.e., upswing, adjustment, and strike), showing no *major* differences in variability. The only significant difference was in the amount of variability in the duration of the adjustment phase, with SP showing more variability. Since we did not break down this prediction to include the individual phases (i.e., prediction 1a/2a in Table 3.1), it was fairly inclusive overall, and therefore the significant difference in the adjustment phase was not reflected in our conclusion. It is possible that the duration of both the upswing and strike are relatively fixed, due to sensorimotor constraints inherent to the kinematics and forces applied to lifting up and striking down limb motions, whereas the more stationary nature of the adjustment phase may allow for more variability to occur during less functional actions, for example in terms of slight rotatory movements of the wrist at the apex when performing SP. Since NP actions aim to crack open hard-shelled nuts, a relatively fixed duration in the adjustment phase of this type of percussive behaviour could be functionally explained by the need to maintain some consistency in the execution of a pounding task in a foraging context, in order to maximize the number of strikes needed to extract the seed from the nut. This interpretation is congruent with findings from kinematic and energetic studies of stone-tool-assisted nut-cracking behaviour in capuchin monkeys and chimpanzees, maintaining similar pounding actions for similar hammer stones and nuts, and only adjusting their movements to modulate the kinetic energy of each strike according to the weight of the stones or the resistance of the nuts (Günther & Boesch, 1993; Sirianni, Wittig, & Boesch, 2015; Visalberghi, Sirianni, Fragaszy, & Boesch, 2015).

No significant differences were found in the frequency of, and variability in, torso orientation between SP and NP in adult male long-tailed macaques. Both pounding activities were preferentially performed while showing similar sitting postures, with the torso oriented towards the front. These results suggest that an optimal torso position is needed in order to perform pounding actions in both a functional and playful way. Adult males could utilize the stability of this body position to engage core strength and give both more power and speed to NP actions, and alternately, while being able to adjust some of these movements and be more variable in the execution of SP actions.

Juvenile Pounding Versus Adult Pounding of Stones

The comparison of how SP was executed in adults and juveniles enabled us to test three hypotheses accounting for these actions among juveniles (Table 3.2). Differences between juvenile and adult long-tailed macaques in the execution of SP could be explained in terms of either poorer sensorimotor coordination in the immature monkeys (i.e., “Needing-to-learn” hypothesis), or if the limb movements of juveniles are more variable and exaggerated in the younger animals, then SP may function as a form of energy dissipation (i.e., “Surplus energy” hypothesis). If pounding stones does not differ between juveniles and adults, then this would be consistent with play being distinct at all ages (i.e., “Lifetime playfulness” hypothesis). Given that juvenile and adult monkeys did not differ in either the basic structural organization of pounding, in the variability of the duration of any of the three phases of the SP action pattern, in the upswing and strike speed, in stone height at the apex, or in the gaze direction before the strike, the present data mostly support the Lifetime play hypothesis. That is, when playing with stones, adults and juveniles execute their movements in a similar manner.

The only age differences in *variability* were found in upswing and strike speed, and torso orientation. Indeed, contrary to what was predicted in the “surplus energy” hypothesis, adults were more variable than juveniles in their upswing and strike speed. Such a result could be explained because the juveniles lack the sensorimotor coordination required to adjust the speed of limb movements during the acceleration and deceleration parts of the upswing and strike phases. In contrast, adults may be able to slow down their arm movement during the last part of the upswing phase to avoid losing balance, and during the last part of the strike phase, possibly to avoid hurting their wrist after hitting the ground too hard with a stone held in hand. We also found that juveniles were more variable than adults in their torso orientation before the upswing, and more likely to deviate from this adult-typical forward-facing torso position (supporting both the “surplus energy” hypothesis and “needing-to-learn” hypothesis, respectively). These results could suggest that a stable forward-facing torso position is necessary for, or at least facilitates, the higher variability in upswing and strike speed found in adults. Again, juveniles may lack the sensorimotor coordination to adjust their arm movement speed while maintaining a stable torso position.

The last age difference in the execution of SP consisted in juveniles keeping a longer distance between the stone and the head at the apex. It could be argued that a longer distance is due to greater playfulness in juveniles. However, this explanation is unlikely, because if juveniles were keeping a longer head-to-hand distance due to being more playful than adults, they should also exhibit greater variability in maintaining this distance, which was not the case. A more likely explanation for juveniles displaying a longer distance between the stone and the head at the apex, is that juveniles do not have the necessary sensorimotor control to maintain this smaller distance, a skill that probably requires time, practice, and physical maturation (cf. the "needing-to-learn" hypothesis; Table 3.2). The more variable torso orientation displayed by juveniles during SP may also impact this capability, as it may require greater balance and more developed sensorimotor coordination to achieve this smaller distance. In contrast, adults have the capacity to shorten this distance (as is also present in NP), but may choose not to when engaging in a playful activity like SP.

Foraging and its Relationship to Object Play

Previous studies have shown a motivational link between object play and foraging activities in some species, both temporally and in the actions performed. In captive oriental small-clawed otters, object play was considered a form of pseudo-feeding because it was observed to occur most frequently prior to food provisioning, and the behavioural patterns performed closely resembled those observed in a foraging context (Pellis, 1991). Similar results have also been observed in other predatory species. In domestic cats, Hall and Bradshaw (1998) demonstrated that hunger influenced the rate of object play observed, and the actions performed were reminiscent of predatory behaviour. Additionally, SH in free-ranging and frequently provisioned groups of Japanese macaques has been temporally linked to foraging activities (Leca et al., 2008a).

Pelletier et al. (2017b) used a behaviour systems approach to explore the motivational processes underlying SH in long-tailed macaques, and hypothesized that all 36 SH patterns could be ascribed to a foraging behaviour system. This paper aimed to begin testing this hypothesis, focusing on the kinematic structure of one type of percussive SH pattern, more specifically pounding actions. Our results indicate that while actions such as pounding during SH may be derived from foraging behaviour, the execution of SP in long-tailed macaques can be considered a playful activity that is motivationally distinct from foraging. Additionally, we demonstrated that SP is performed in a similar manner in both adults and juveniles. This latter finding is important because the execution of actions during play are defined by having properties such as exaggeration, variability, and incompleteness (Burghardt, 2005). Given that most play occurs in young individuals (Fagen, 1981), clumsiness in their actions may be attributed to immaturity in sensorimotor development (Fentress, 1983) rather than playfulness. However, our finding that when playing, adults exhibit the same deviation in the execution of actions from functional contexts as do juveniles, substantiates that exaggeration, variability and incompleteness are indeed properties of play.

Even though SP appears to be motivationally distinct from foraging in adult male and juvenile Balinese long-tailed macaques, more research is needed to investigate the psychological mechanisms underlying the expression of SH behaviour. Future studies should examine the sequential organization of SP patterns within a SH bout, in combination with daily activity budgets, in order to assess whether SH could be temporally connected to foraging or feeding activities. If the frequency of SP increases around feeding time, or if the other behavioural patterns performed near feeding time closely resemble those performed at the end of a foraging sequence, this could indicate that SH and foraging share a common underlying motivation. Thus, future work should combine a kinematic analysis and a sequential analysis on the remaining 35 SH patterns. These investigations should also be expanded to additional age and sex classes, while controlling for independence in the data points (i.e., the same individuals performing similar actions in both playful and a functional contexts) and individual variability. This would allow us to test whether a seemingly playful activity, such as stone handling, could serve as preparation for more functional behaviour, like nut handling, and other complex foraging actions, like stone-tool-assisted extractive techniques, which could have implications for the evolution of lithic technology in early humans.

Table 3.1

Two alternative hypotheses and 13 related predictions about the motivational processes underlying SP in adults (assuming that NP is a functional food processing technique aiming to weaken and break open the hard-shelled nut). SP: stone pounding, NP: nut pounding; n.s.: no statistically significant difference is expected; ^{1}: because object play is more exaggerated in its execution than foraging; ^{2}: because foraging is more functionally constrained than object play. The predictions supported by the data are in bold and underlined.

		SP and NP are motivationally…	
		Linked	Distinct
Hypotheses: Motivation to perform SP in adult males		**Hypothesis 1. "Pseudo-foraging"**: SP is misdirected NP toward stones, as a foraging substitute	**Hypothesis 2. "Object play":** SP is purposeless object play, exaggerated in its execution
Predictions: Differences between SP and NP in:	a. Basic structural organization (upswing, adjustment, and downswing phases)	**n.s.**	Major (e.g., variability in the duration of all phases; SP > NP[1])
	b. Upswing speed	n.s.	SP > NP[1] or **NP > SP[2]**
	c. Downswing speed	n.s.	SP > NP[1] or **NP > SP[2]**
	d. Object-to-ground distance at apex	n.s.	SP > NP[1] or **NP > SP[2]**
	e. Head-to-hand-distance at apex	n.s.	**NP < SP[2]**
	f. Frequency of forward-facing torso immediately before upswing	**n.s.**	NP > SP[2]
	g. Frequency of ground-directed gaze immediately before downswing	n.s.	**NP > SP[2]**
… *variability* in:	h. Upswing speed	n.s.	**NP < SP[2]**
	i. Downswing speed	n.s.	**NP < SP[2]**
	j. Object-to-ground distance at apex	n.s.	**NP < SP[2]**
	k. Head-to-hand-distance at apex	n.s.	**NP < SP[2]**
	l. Frequency of forward-facing torso immediately before upswing	**n.s.**	NP < SP[2]
	m. Frequency of ground-directed gaze immediately before downswing	n.s.	**NP < SP[2]**

Table 3.2

Three alternative hypotheses and seven related predictions about potential age differences in the motivation to perform SP. SP: stone pounding. The predictions supported by the data are in bold and underlined.

		SP structure *differs* between juveniles and adults due to…		SP structure is *similar* in juveniles and adults due to…
Hypotheses: Motivation to perform SP in juveniles		Hypothesis 3. "Needing-to-learn": The execution of SP is constrained by reduced sensori-motor coordination characteristic of juveniles, and improves with age, physical maturation and practice	Hypothesis 4. "Surplus energy": The execution of SP is more variable and exaggerated (in intensity, form, duration) in juveniles, and more fixed in adults	Hypothesis 5. “Lifetime playfulness”: The execution of SP in juveniles and adults is similar because the motivation to perform SP is similar throughout the lifespan: general playfulness in stone-directed percussive actions
Predictions: Compared to adults, SP performance in juveniles should be…	a. Basic structural organization (upswing, adjustment, and downswing phases)	Incomplete (e.g., missing phases)	More variable (duration of phases)	**Similar**
	b. Upswing speed	Lower	More variable	**Similar**
	c. Downswing speed	Lower	More variable	**Similar**
	d. Object-to-ground distance at apex	Lower	More variable	**Similar**
	e. Head-to-hand-distance at apex	**Longer**	More variable	Similar
	f. Frequency of forward-facing torso immediately before upswing	**Lower**	**More variable**	Similar
	g. Frequency of ground-directed gaze immediately before downswing	Lower	More variable	**Similar**

Table 3.3

Individual identification for each subject, age class, and number of pounding actions analyzed for each percussive activity. SP: Stone pounding, NP: nut pounding.

Subject	Age/Sex	Activity	Number of pounds
Eric	AM	SP	7
Danger	AM	SP and NP	18 and 9
Daniel	AM	SP	15
Wrapper	AM	SP	3
Linus	AM	SP	3
Marc	AM	NP	7
Gerry	AM	NP	8
Hare	AM	NP	9
Ronald	AM	NP	12
Kelapamuda	AM	NP	7
Tim	JM	SP	11
Bob	JM	SP	20
Carl	JM	SP	10
Tina	JF	SP	10

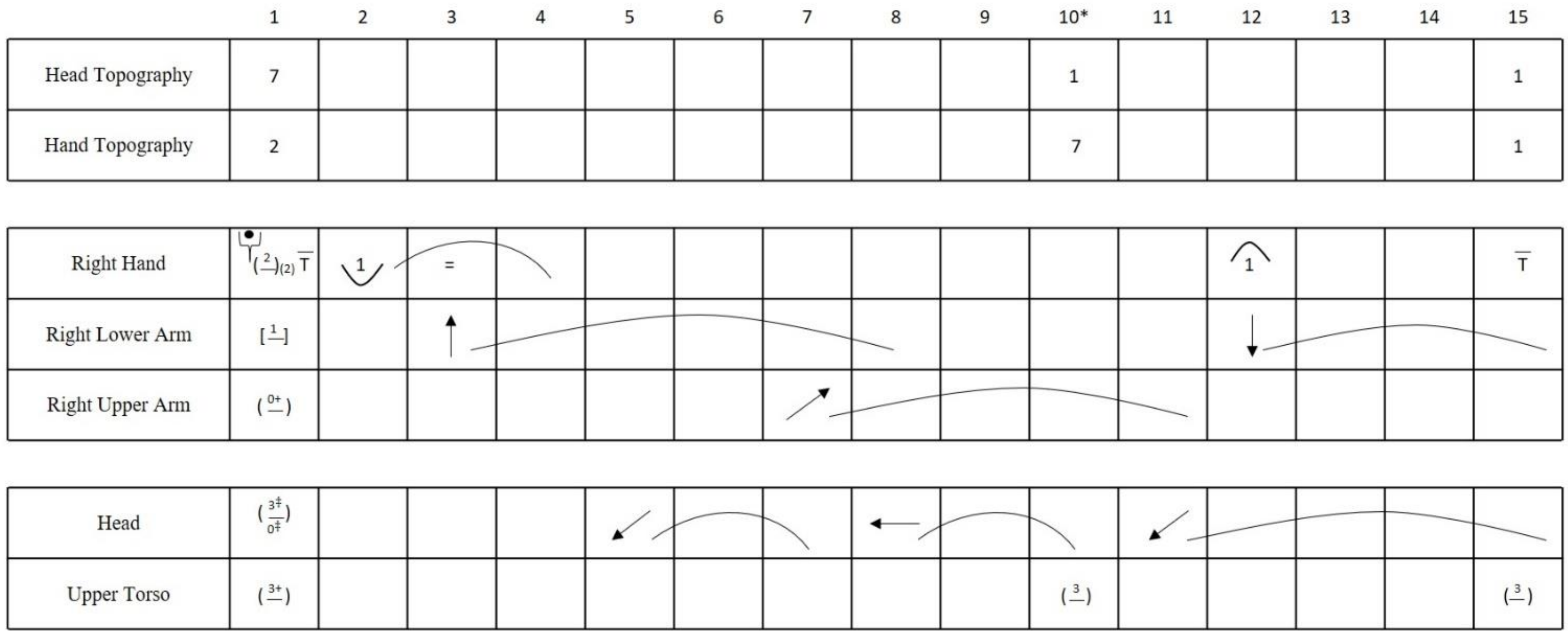

Figure 3.1. An Eshkol-Wachman Movement Notation (EWMN) score is shown for a SP action performed by an adult male. The score is read from left to right with the numbers along the top of the score sheet denoting the video frames. Frame 1 characterizes the starting position for each limb segment. Body-wise positions are indicated in [] referring to the position of the limb segment in relationship to its neighbouring limb segment, and absolute positions are indicated in () referring the position of the limb segment to an unmoving reference point in space. Arrows indicate the direction of movement, while the curved lines, arcing across columns show the duration of the movement. The T with the bar over top indicates that the limb is in contact with the ground, while = indicates that the limb is no longer in contact with the ground. The ⨃ symbol at the top left corner of frame one in the Right Hand row indicates that an object is being grasped. The ∪ in frame four indicates a negative rotation of the hand around its long axis, while the ∩ in frame eight indicates a positive rotation, and the number above and below indicates the amount of movement achieved in that rotation. The * indicates when the highest point at the apex has been reached.

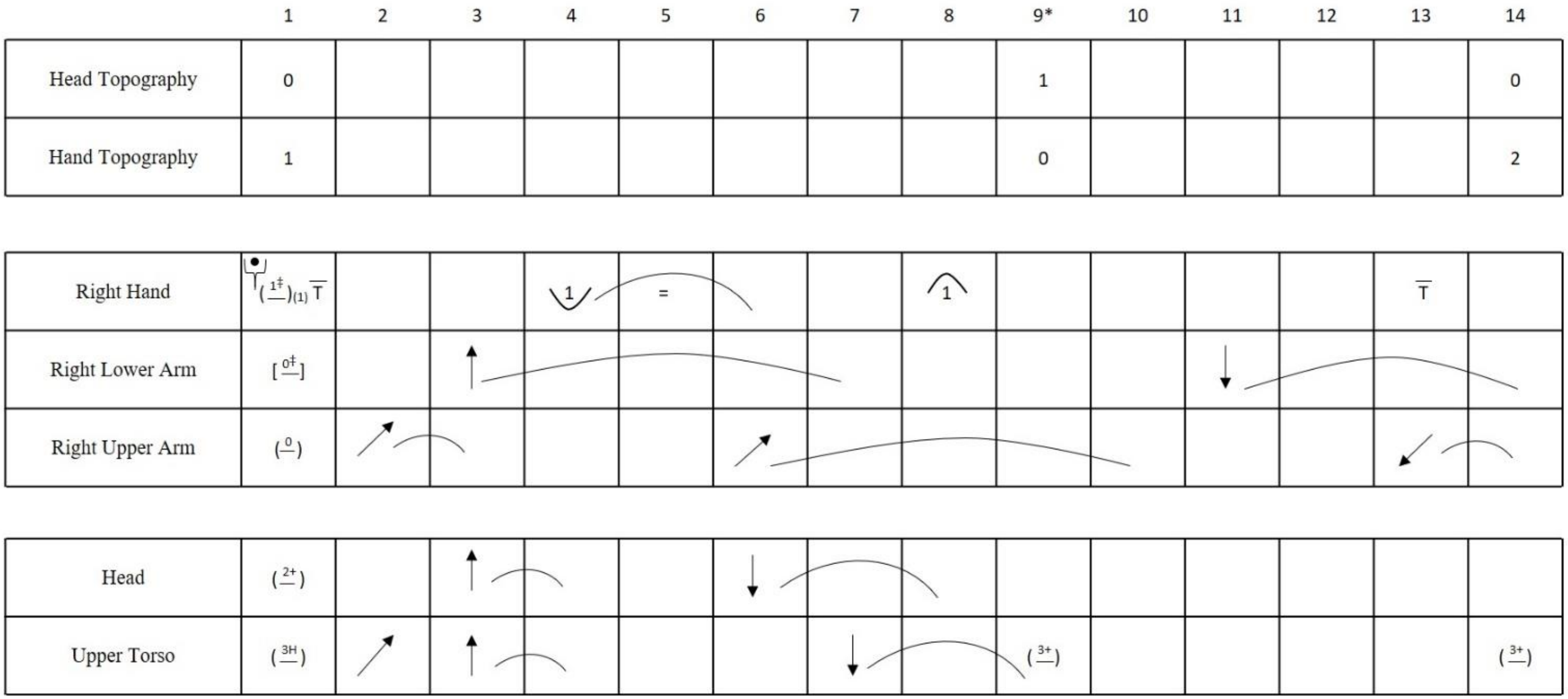

Figure 3.2. An Eshkol-Wachman Movement Notation (EWMN) score is shown for a NP action performed by an adult male. The score is read from left to right with the numbers along the top of the score sheet denoting the video frames. Frame 1 characterizes the starting position for each limb segment. Body-wise positions are indicated in [] referring to the position of the limb segment in relationship to its neighbouring limb segment, and absolute positions are indicated in () referring the position of the limb segment to an unmoving reference point in space. Arrows indicate the direction of movement, while the curved lines, arcing across columns show the duration of the movement. The T with the bar over top indicates that the limb is in contact with the ground, while = indicates that the limb is no longer in contact with the ground. The ⊍ symbol at the top left corner of frame one in the Right Hand row indicates that an object is being grasped. The ∪ in frame four indicates a negative rotation of the hand around its long axis, while the ∩ in frame eight indicates a positive rotation, and the number above and below indicates the amount of movement achieved in that rotation. The * indicates when the highest point at the apex has been reached.

Figure 3.3. Photographs depicting elements from the three phases (namely upswing, adjustment, and downswing) of a nut handling pound performed by an adult male long-tailed macaque. Frame 1 illustrates the starting position (point A), frame 2 illustrates the apex position (point B), and frame 3 illustrates the end position (point C).

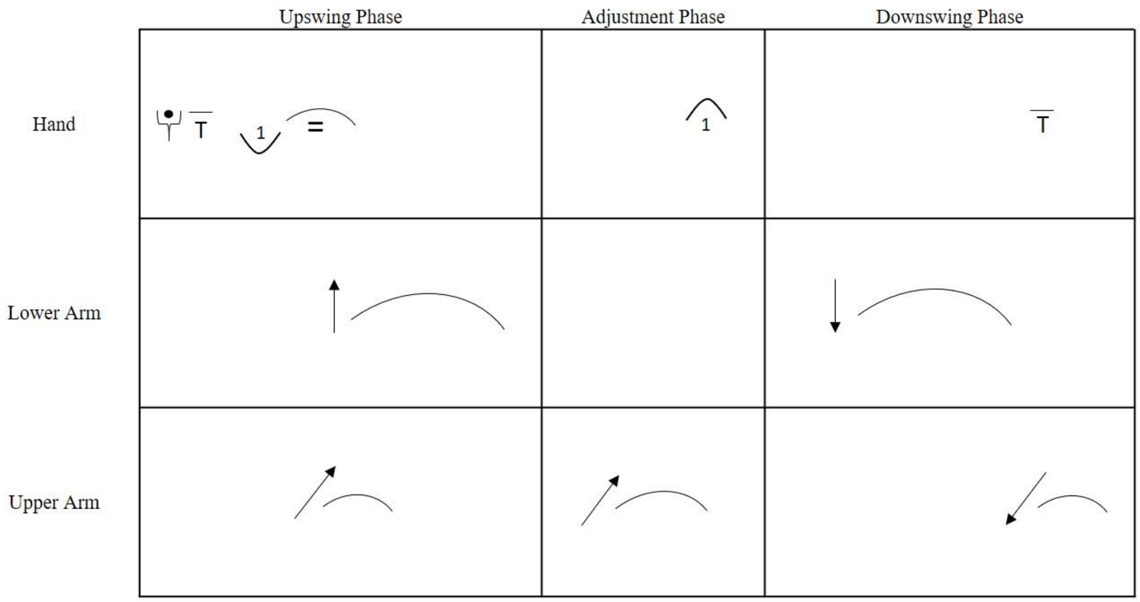

Figure 3.4. A simplified EWMN score (following Whishaw & Pellis, 1990) highlights the three consecutive phases of a pounding action. The upswing phase begins with the hand resting on the substrate with light contact holding the object (⊍; T). The wrist begins to rotate outward (∪) while the upper arm begins to move in an upward and out motion away from the body (↗), causing the hand to lose contact with the substrate (=). The lower arm then moves upwards in a vertical movement (↑) until the hand reaches the highest point at the apex. During the adjustment phase, the upper arm continues to move in an upward and out movement (↗), which partly rotates the wrist, while the wrist completes the remainder of the rotation (∩), moving back to a flat position with the palm facing downwards. The downswing phase begins when the lower arm moves in a downward vertical motion (↓), stopping when the object comes back into contact with the substrate (T), and the upper arm moves in a downwards motion back towards the body (↙). Arrows indicate the direction of movement, while arcs indicate the relative durations for each movement.

CHAPTER FOUR

Discussion

For a behaviour to be considered playful, a set of five criteria must be met. These criteria state that when compared with its more “serious” (i.e., functional) behavioural counterpart(s), play behaviour should be functionally incomplete, intrinsically pleasurable, structurally distinct, non-stereotypically repeated, and performed in the absence of severe stress (Burghardt, 2005). The main objective of this MSc thesis was to explore the third criterion by examining the behavioural structure of stone handling (SH) in Balinese long-tailed macaques and compare it with a foraging activity. On the basis of Burghardt’s (2005) third criterion, we argued that, to qualify as a form of object play behaviour, SH must display some structural *differences* from the functional activity it most commonly resembles (i.e., foraging). However, some proximate-level theories (e.g., Hutt, 1985; Mitchell, 1990; Verenikina et al., 2003) and empirical studies (e.g., Hall & Bradshaw, 1998; Leca et al., 2008a; Pellis, 1991) suggest that object play may have originated from foraging behaviour, and thus, both activities could share a common underlying motivation. From this perspective, object play is also expected to display some structural *similarities* with foraging behaviour. This thesis addressed the following questions: *Can SH be considered an object play activity (at least on the basis of Burghardt’s third criterion, 2005)? Are structural components of play (e.g., exaggeration, variability, and incompleteness), intrinsic features of play behaviour, or are they constrained by the immaturity of the performer? Is SH motivationally linked to foraging?*

Chapter One of this thesis outlined the theoretical and empirical importance of establishing species-specific ethograms, in combination with hierarchically organized models, as a first step in better defining, describing, and understanding the motivational underpinnings of seemingly playful activities.

In Chapter Two, I provided the first ethogram of SH behaviour performed by the Balinese long-tailed macaques of Ubud, and used a particular hierarchically organized model, the behaviour systems framework, to *hypothesize* that SH is motivationally linked to foraging-related activities, as a foraging-substitute. I completed a preliminary comparison of the SH repertoires of three species in the *Macaca* genus, namely *M. fascicularis, M. fuscata,* and *M. mulatta*. This comparison showed that long-tailed macaques displayed the highest diversity in SH patterns among the three macaque species. The percussive behavioural profile of Balinese long-tailed macaques was also unique in that their stone-directed actions were more diverse, more frequent, and lasted longer than those performed by Japanese macaques.

In Chapter Three, I began testing the pseudo-foraging hypothesis for SH, proposed in Chapter Two, by conducting a kinematic analysis on the structure of percussive pounding actions in adult male long-tailed macaques, in both a seemingly playful context (i.e., stone handling) and a functional foraging context (i.e., nut handling). Contrary to what previous research on the motivational basis of other forms of object play has suggested (cf. Hall & Bradshaw, 1998; Pellis, 1991), I found that the kinematic structure of stone pounding actions (i.e., SP) was significantly different from that of nut pounding actions (i.e., NP). Therefore, my data did not support the pseudo-foraging hypothesis for SP, suggesting that SP appears to be a playful behaviour that is motivationally distinct from NP.

In the second part of Chapter Three, I conducted the first test of the confounding effect of immaturity on the performance of object play. According to this effect, some well-recognizable structural components of play behavior performed before adulthood (e.g., increased variability in the form or duration of the execution of playful actions, exaggeration of body movement during play bouts, and incompleteness in the basic temporal organization of a play sequence) could simply be due to juvenile individuals lacking fine-tuned sensori-motor coordination. With SH being one of the very few examples of a seemingly playful (or at least non-functional) object-directed behaviour whose performance continues well into adulthood, I was able to compare the detailed structure of a specific percussive SH pattern (i.e., SP) in both juvenile monkeys and adult monkeys (whose sensorimotor systems are mature enough). To the best of my knowledge, this is the first study design controlling for the "immaturity confounder" in the performance of a play behaviour in a non-human animal species.

My results demonstrated that juvenile and adult Balinese long-tailed macaques did not significantly differ in their performance of SP actions. This indicates that some of the defining structural characteristics of play (i.e., variability, exaggeration, and incompleteness) are not simply a consequence of immaturity, but indeed inherent components of playful actions. Therefore, my findings highlight the playful nature of SP, a percussive SH pattern, regardless of the age of the performer. By virtue of the behavior systems approach and a systematic kinematic analysis, this research allowed me to provide the first pieces of data-based evidence that SH can be operationally defined as a form of object play. Even though SH has long been assumed to be a playful activity in Japanese, Taiwanese, rhesus, and long-tailed macaques (e.g., Huffman, 1984; Leca et al., 2012; Nahallage & Huffman, 2008; Nahallage et al., 2012), none of the five definitional criteria established by Burghardt (2005) had been applied to any of the SH behavioural patterns performed by any macaque species until now. As the results provided in Chapter

Three did not support the pseudo-foraging hypothesis proposed in Chapter Two, they should be discussed further.

Explaining Motivational Differences in the Expression of Object Play

As outlined in Chapter One of this thesis, previous research has suggested that object play and foraging share a common underlying motivation. Pellis (1991) found that object play in oriental small-clawed otters was motivationally linked to foraging, as a pseudo-feeding behaviour. In this species, the frequency of solitary object play increased prior to feeding time and decreased after satiation, and the behavioural patterns performed during the object play bouts resembled those typically performed in a foraging context (Pellis, 1991). Such temporal and structural connections between object play and foraging suggest that these two activities are underlain by common motivational processes. Hall & Bradshaw (1998) found similar results in domestic cats, as the intensity of object play increased as individuals' hunger levels increased, and play behavioural patterns resembling more predatory actions were most frequently observed during this pre-feeding period. Leca et al. (2008a) found a temporal connection between SH and foraging activities in several free-ranging provisioned groups of Japanese macaques: SH occurred most frequently within the 20-minute period following food provisioning, while the monkeys chewed the food they had stored in their check pouches, after quickly collecting it from the feeding area. Taken together, these results suggest that, in some species, some forms of object play are motivationally linked to foraging activities both temporally and in the actions performed.

However, other studies of object play do not support this interpretation. For example, Ahloy Dallaire & Mason (2015) did not find any significant temporal associations between object play and feeding events in American mink (*Neovison vison*).

Likewise, Kuba et al. (2006) found that hunger did not significantly influence the onset and frequency of object play in common octopi (*Octopus vulgaris*). The general timing of expression of SH behaviour in the Balinese long-tailed macaques of Ubud appears to be consistent with these studies: SH in this macaque population can be observed throughout the day (i.e., not only immediately before or after food provisioning) and the vast majority of SH bouts are performed by individuals who are not simultaneously chewing food or involved in a food-seeking activity (Leca et al., 2016). Along with my results from Chapter Three (focusing on the kinematic structure) failing to find the expected structural similarities between SP and NP, these findings do not support the pseudo-foraging hypothesis for the expression of this form of percussive SH in Balinese long-tailed macaques.

There are at least two possible explanations for these discrepancies in the literature. First, differences in study objectives and designs could account for these seemingly conflicting results. Most studies investigating the possible motivational links between object play and foraging simply set out to examine the temporal connection between these two activities (but see Hall & Bradshaw, 1998; Pellis, 1991, for notable exceptions). Chapter Three was the first study to systematically compare the kinematic structure of the same type of behavioural pattern in both a play context (i.e., SP) and a foraging context (i.e., NP). It is possible that a detailed examination of the kinematic structure of both object play and foraging actions in oriental small-clawed otters and domestic cats would show results consistent with what was found in Balinese long-tailed macaques (i.e., more structural differences than similarities, therefore supporting the hypothesis that object play is motivationally distinct from foraging). Conversely, among the studies that did not find a temporal association between object play and foraging (e.g., Ahloy Dallaire & Mason, 2015; Kuba et al., 2006), a comparative kinematic examination of both activities could show more structural similarities than differences, therefore supporting the hypothesis that object play and foraging share a common motivational basis. Therefore, in order to fully explore the motivational processes underlying the expression object play and any functional activities it could derive from or lead to (e.g., foraging, communicating, escaping predators), it is necessary to systematically compare their structural organization (i.e., both kinematic and sequential) and investigate the potential temporal connections between them. Second, these conflicting results could simply be due to species differences in the motivational basis of object play (Ahloy Dallaire & Mason, 2015). For example, there may be inter-species differences in foraging styles (e.g., predatory species vs omnivorous species vs frugivorous species), which may affect the motivational processes involved in object play activities. Additionally, different species or group-specific activity levels, (e.g., such as an increase in general activity, particularly around feeding time), might lead to differences (e.g., increase) in object play activity for some species (Ahloy Dallaire & Mason, 2015).

Limitations of the Present Studies and Future Research Directions

Even though Chapter Three was the first study to systematically examine the kinematic structure of percussive object play patterns using Burghardt's (2005) third criteria, it is noteworthy that I focused on one of the 36 behavioural patterns (i.e., "pound") present in the SH repertoire of Balinese long-tailed macaques. Therefore, these results are likely not representative of the entire SH repertoire. A similar comparative kinematic analysis of other percussive patterns (e.g., "pound-drag", "clack") or other SH patterns that are reminiscent of food-processing techniques (e.g., "rub", "roll"; cf. Chapter Two) might yield different results, showing no significant differences in the performance of SH and NH behavioural patterns (e.g., clacking two stones together versus clacking two nuts together, or rubbing a stone on the ground versus rubbing a nut on the ground). This would suggest that only *some* SH patterns (but not the SH activity as a whole) could be underlain by the same motivational processes as some food-processing patterns. *Other* SH patterns (e.g., pounding actions) could be distinctly motivated: they could either be underlain by motivational processes associated with other functional (but non-food-related) activities, or have their own play-specific motivational basis (cf. Panksepp, 1998; Rasa, 1984).

Additionally, because Chapter Three aimed to present the first test of the pseudo-foraging hypothesis, I did not examine the temporal connection between SH and foraging activities. The expression of SH patterns within a SH sequence can show varying degrees of repetition, from SH sequences containing a few recurring SH patterns being performed over and over, to SH sequences comprised of many different SH patterns performed in a less predictable way. A future study that would combine a sequential analysis of SH patterns within a given SH bout and the general activity of the individual within a representative period of time before and after engaging in SH, could provide further insights into the motivational processes underlying SH in Balinese long-tailed macaques. For example, it could be the case that certain SH patterns associated with certain modules of the foraging behaviour system are performed closer to feeding time (e.g., the SH pattern “Rub” from the Rubbing/Rolling module occurring most frequently prior to or immediately following feeding/foraging).

In sum, the results from Chapter Three do not necessarily undermine the pseudo-foraging hypothesis, as complementary analyses may yield different results. The findings obtained in Chapter Three do highlight the importance of multiple types of analyses to develop a more complete understanding of the motivational underpinnings of object play. From an evolutionary perspective, it is also crucial to consider inter-species differences in foraging styles (e.g., predatory species vs omnivorous species vs frugivorous species), as they may affect the motivational processes of object play.

Chapter Three also aimed to assess whether SH can be considered a form of object play. I provided the first direct test of some of the structural aspects of Burghardt's criteria of play (2005) to address the possible immaturity confounder. Though my results suggest that SP can be considered a playful activity that is motivationally distinct from NP, it is important to note that not all of Burghardt's criteria were tested. In order to fully consider SH a playful activity, all five of Burghardt's criteria must be met. Future work should address Burghardt's other four criteria, as well as compare the levels of exaggeration, variability, and incompleteness present in some of the other SH patterns that are strongly reminiscent of foraging actions in Balinese long-tailed macaques.

This thesis aimed at testing whether object play could be motivationally linked to the foraging behaviour system specifically. However, Burghardt's (2005) work suggests that play behaviour (including object play) might involve specific actions and motivational processes associated with repertoires of other functional behaviours, including fighting, anti-predator responses, nest building, courtship, and sexual behaviour. Therefore, it is important to note that behaviour systems other than the foraging behaviour system may also underlie the expression of the SH repertoire. For example, the SH pattern "throw" could be part of a defense behaviour system (see results on Japanese macaques: Leca et al., 2008b), or the SH pattern "tap," when performed on the genital area, could be considered a form of tool-assisted masturbation, and as such, be part of a sexual behaviour system. It has been demonstrated that some primate species are able to compile actions from numerous behaviour systems into a sequence of play (Pellis & Burghardt, 2017). For example, Japanese macaques combine different behavioural patterns, such as playful mounting and biting (i.e., socio-sexual and aggressive actions, respectfully), into their play sequences (VanderLaan, Pellis, & Vasey, 2012). Since SH patterns are performed in a sequence, it could be argued that numerous behaviour systems are activated within or between SH bouts. Future work should conduct an analysis on all 36 SH patterns, in order to test whether they can be reliably grouped into consistent behavioural categories, or appropriate behaviour systems, based on shared sequential structural characteristics.

Importantly, the integration of different types of actions into a single play sequence is not shown in all species. Therefore, in the species that do display this integration, play could be considered to have transformed from primary, to secondary or tertiary process play (Burghardt, 2005; Pellis & Burghardt, 2017). As discussed in the first chapter of this thesis, SH is a cultural behaviour, and as such, is seen to undergo transformational phases that make the behaviour more diverse and complex. Over time, individuals may experiment with additional objects and contexts, expanding the SH repertoire. A SH pattern such as “tap” could have originated as part of one behaviour system (e.g., foraging), and once diversified to additional contexts, could have developed a separate motivation, and thus a different behaviour system could then be activated (e.g., tap on groin as part of the sexual/reproductive behaviour system). Additionally, the activation of certain behaviour systems could change with age if the motivational systems involved change (e.g., the incorporation of percussive foraging-like actions into object play as individuals mature; Bateson, 2014; Hall, 1998), and thus differences may be seen within the sequence of SH throughout an individual’s lifespan (i.e., frequency, duration, and timing; Burghardt, Albright, & Davis, 2016; Nahallage & Huffman, 2007a).

Results from Chapter Two demonstrated that though the SH repertoire size did not appear to differ significantly between Japanese macaques and long-tailed macaques, there were significant differences present between rhesus macaques and both Japanese macaques and long-tailed macaques. Since SH is seen to go through periods of transformation, differences in the SH profile of rhesus macaques could be due to SH being a relatively new tradition in this group at the time of study (Nahallage & Huffman, 2008). With time, their SH profile could more closely resemble what is seen in both the Japanese macaques and long-tailed macaques. Additionally, it is important to note that the results on the repertoire size of Japanese macaques used in Chapter Two were a combined result taken from the behavioural patterns displayed by ten troops, who vary in their SH profiles (cf. Leca et al., 2007).

In line with the transformational model of play, it is possible that some forms of play could have transformed in some species, due to additional factors (e.g., environment), and added new combinations (Burghardt, 2005). Therefore, depending on the environmental pressures experienced, there could be major inter-species differences in the expression of, and underlying motivation for SH. Environmental pressures could cause similar behaviour to be performed differently, and as such, should be considered when utilizing the behaviour systems approach to object play (Burghardt & Bowers 2017). Chapter Two indicated that long-tailed macaques, when compared to Japanese macaques, show significant differences in percussive SH patterns, as they displayed a higher diversity in percussive patterns (i.e., perform seven of the eight percussive patterns identified), and their performance was significantly more frequent, with longer durations, and a higher prevalence rate among individuals (i.e., 74.7% of sampled individuals). It is possible that the transformation of behaviour due to environmental pressures could account for these differences. Therefore, future research should acknowledge that the categorization of SH patterns into particular behaviour systems could differ across species. Additionally, in line with both the affordance learning theory (Gibson, 1979; Parker & Gibson, 1977), and the transformational model of play (Burghardt, 2005; Pellis & Burghardt, 2017), investigation on the integration of SH patterns into new contexts could aid in the understanding of the development of complex percussive actions, such as stone-tool use.

Conclusion

Understanding the proximate mechanisms, such as motivation, underlying object play activities can provide insight into the potential benefits of play behaviour, especially for those forms of object play that are performed throughout the lifespan. Hierarchically organized models, such as the behaviour systems framework, offers hypotheses for future structural and kinematic analyses investigating the underlying motivations of SH. Future work comparing SH in numerous species could help to foster our understanding of both the development and possible transformation of complex playful actions into more functional behaviour, such as percussive stone-tool use in a foraging context.

REFERENCES

Ahloy Dallaire, J., & Mason, G. J. (2016). Play in juvenile mink: Litter effects, stability over time, and motivational heterogeneity. *Developmental Psychobiology*, *58*, 945-957.

Altmann J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*, 227-267.

Andarwulan, N., Fardiaz, D., Wattimena, G. A., & Shetty, K. (1999). Antioxidant activity associated with lipid and phenolic mobilization during seed germination of *Pangium edule* Reinw. *Journal of Agricultural and Food Chemistry, 47*, 3158-3163.

Ansuini, C., Giosa, L., Turella, L., Altoè, G., & Castielle, U. (2008). An object for an action, the same object for other actions: effects on hand shaping. *Experimental Brain Research, 185*, 111-119.

Barber, N. (1991). Play and energy regulation in mammals. *The Quarterly Review of Biology*, *66*, 129-147.

Bateson, P. (2014). Play, playfulness, creativity and innovation. *Animal Behavior and Cognition*, *1*, 99-112.

Bateson, P., & Young, M. (1979). The influence of male kittens on the object play of their female siblings. *Behavioral and Neural Biology, 27*, 379-378.

Bjorklund, D. F., & Gardiner, A. K. (2011). Object-oriented play and tool use: Developmental and evolutionary perspectives. In A. D. Pellegrini (Ed.), *The Oxford handbook of the development of play* (pp. 153-171). New York: Oxford University Press.

Bjorklund, D. F., & Pellegrini, A. D. (2002). *The origins of human nature: Evolutionary developmental psychology*. Washington, DC: American Psychological Association.

Brotcorne, F. (2014). *Behavioral ecology of commensal long-tailed macaque (*Macaca fascicularis*) populations in Bali, Indonesia: Impact of anthropic factors*. (Unpublished doctoral dissertation). University of Liège, Liège, Belgium.

Brownlee, A. (1954). Play in domestic cattle in Britain: An analysis of its nature. *British Veterinary Journal, 110,* 48-68.

Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. Cambridge, MA: Bradford Books (MIT Press).

Burghardt, G. M., Albright, J. D., & Davis, K. M. (2016). Motivation, development and object play: Comparative perspectives with lessons from dogs. *Behaviour, 153*, 767-793.

Burghardt, G. M., & Bowers, R. I. (2017). From instinct to behavior systems: an integrated approach to ethological psychology. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowden, & T. Zentall (Eds.), *APA handbook of comparative psychology: Vol 1. Basic concepts, methods, neural substrate, and behavior* (pp. 333-364). Washington, DC: American Psychological Association. http://dx.doi.org/10.1037/0000011-000

Cappiello, B. M. (2017). Solitary and social object play in the bottlenose dolphin *(Tursiops truncatus)*. (Unpublished Master's Theses). University of Southern Mississippi, Mississippi. Retrieved September 10, 2017 from http://aquila.usm.edu/masters_theses/304

Caro, T. M. (1995). Short-term costs and correlates of play in cheetahs. *Animal Behaviour, 49*, 333-345.

Cohen, R. G., & Rosenbaum, D., A. (2004). Where grasps are made reveals how grasps are planned: generation and recall of motor plans. *Experimental Brain Research, 157*, 486-495.

Comins, J. A., Russ, B. E., Humbert, K. A., & Hauser, M. D. (2011). Innovative coconut-opening in a semi-free ranging rhesus monkey (*Macaca mulatta*): A case report on behavioral propensities. *Journal of Ethology, 29*, 187-189.

Dias, P. A. D., Rangel-Negrín, A., Coyohua-Fuentes, A., & Canales-Espinosa, D. (2009). Behaviour accumulation curves: A method to study the completeness of behavioural repertoires. *Animal Behaviour, 77*, 1551-1553.

Eilam, D. (2015). The cognitive roles of behavioral variability: Idiosyncratic acts as the foundation of identity and as transitional, preparatory, and confirmatory phases. *Neuroscience and Biobehavioral Reviews, 49*, 55-70.

Eilam, D., & Golani, I. (1988). The ontogeny of exploratory behavior in the house rat (*Rattus rattus*): The mobility gradient. *Developmental Psychobiology, 21*, 679-710.

Eilam, D., Zor, R., Szechtman, H., & Hermesh, H. (2006). Rituals, stereotypy and compulsive behavior in animals and humans. *Neuroscience and Biobehavioral Reviews, 30*, 456-471.

Eshkol, N., & Wachman, A. (1958). *Movement Notation.* London: Weidenfeld and Nicholson.

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

Fentress, J. C. (1983). A view of ontogeny. In J. F. Eisenberg & D. G. Kleiman (Eds.), *Advances in the study of mammalian behavior*: *Special publication No. 7* (pp. 24-64). Shippensberg, PA: The American Society of Mammalogists.

Fragaszy, D., & Perry, S. (2003). Towards a biology of traditions. In D. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 1-32). Cambridge, UK: Cambridge University Press.

Gamble, J.R., & Cristol, D.A. (2002). Drop-catch behaviour is play in herring gulls, *Larus argentatus*. *Animal Behaviour, 63*, 339-345.

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton-Mifflin.

Giljov, A., Karenina, K., & Kochev, A. (2017). Prey or play: interactions between walruses and seabirds. *Acta Ethologica*, *20*, 47-57.

Golani, I. (1976). Homeostatic motor processes in mammalian interactions: A choreography of display. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethologyol. 2* (pp. 69-134). New York: Plenum.

Greene, W. E., Mellilo-Sweeting, K., & Dudzinski, K. M. (2011). Comparing object play in captive and wild dolphins. *International Journal of Comparative Psychology*, *24*, 292-306.

Günther, M., & Boesch, C. (1993). Energetic cost of nut-cracking behavior in wild chimpanzees. In H. Preuschoft, & D. Chivers (Eds.), *Hands of the primates* (pp. 109-129). Vienna, Austria: Springer.

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.

Gumert, M., & Malaivijitnond, S. (2012). Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *American Journal of Physical Anthropology, 149*, 447-457.

Hall, S. (1998). Object play by adult animals. In M. Bekoff & J. A. Byers (Eds.), *Animal play: Evolutionary*, *comparative, and ecological perspectives* (pp. 45-60). Cambridge, UK: Cambridge University Press.

Hall, S. L., & Bradshaw, J. W. S. (1998). The influence of hunger on object play by adult domestic cats. *Applied Animal Behaviour Science, 58*, 143-150.

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.

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.

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 B. Galef, Jr. & C. Heyes (Eds.), *Social learning in animals: The roots of culture* (pp. 267-289). Orlando, FL: Academic Press.

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

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

Jensen, M. B. (1999). Effects of confinement on rebounds of locomotor behaviour of calves and heifers, and the spatial preferences of calves. *Applied Animal Behaviour Science, 62*, 43-56.

Jule, K. R., Lea, S. E. G., & Leaver, L. A. (2009). Using a behaviour discovery curve to predict optimal observation time. *Behaviour, 146*, 1531-1542.

Kader, G. D., *&* Perry, M. *(*2007). Variability for categorical variables. *Journal of Statistics Education, 15*, 1-16.

Kahrs, B. A., & Lockman, J. J. (2014). Building tool use from object manipulation: A perception-action perspective. *Ecological Psychology, 26*, 88-97.

Kuba, M. J., Byrne, R. A., Meisel, D. V., & Mather, J. A. (2006). When do octopuses play? Effects of repeated testing, object type, age, and food deprivation on object play in *Octopus vulgaris*. *Journal of Comparative Psychology, 120*, 184-190.

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 thesis (in French), Université de Liège.

Lacreuse, A., Woods, C. E., & Herndon, J. G. (2007). Effects of aging and hormonal status on bimanual motor coordination in the rhesus monkey. *Neurobiology of Aging, 28*, 186-193.

Leca, J. B., Brotcorne, F., Gunst, N., Holzner, A., Pelletier, A. N., Nahallage, C. A. D., Huffman, M. A., Rompis, A., & Wandia, I. N. (2016, August). *Two forms of material culture in Balinese long-tailed macaques: The stone handling and token exchange traditions.* Paper session presented at the Joint Meeting of the International Primatological Society and the American Society of Primatologists, Lincoln Park Zoo's Lester Fisher Center for the Study and Conservation of Apes, Chicago, USA.

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

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

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.

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, UK: Cambridge University Press.

Leca, J.-B., Nahallage, C. A. D., Gunst, N., Huffman, M. A. (2008b). Stone-throwing by Japanese macaques: Form and functional aspects of a group-specific behavioral tradition. *Journal of Human Evolution, 55*, 989-998.

Lehner, P. N. (1996). *Handbook of ethological methods* (2nd ed.). New York: Cambridge University Press.

Martins, E. P. (1996). *Phylogenies and the comparative method in animal behavior*. New York, USA: Oxford University Press.

Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge, UK: Cambridge University Press.

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.

Miller, G. A., Galanter, E., & Pribram, K. H. (1960). *Plans and the Structure of Behavior.* New York: Holt, Rinehart & Winston.

Mitchell, R. W. (1990). A theory of play. In M. Bekoff & D. Jamieson (Eds.), *Interpretation and explanation in the study of animal behavior, vol. 1: Interpretation, intentionality, and communication* (pp. 197-227). Boulder, Colorado: Westview Press.

Mook, D. G. (1996), *Motivation: The organization of action* (2nd ed.). New York, NY: W. W. Norton & Company.

Moran, G., Fentress, J.C., & Golani, I. (1981). A description of relational patterns of movement during ‘ritualized fighting’ in wolves. *Animal Behaviour, 29*, 1146-1165.

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

Nahallage, C. A. D., & Huffman, M. A. (2007b). Acquisition and development of stone handling behavior in infant Japanese macaques. *Behaviour*, *144*, 1193-1215.

Nahallage, C. A. D., & Huffman, M. A. (2008). Comparison of stone handling behaviour in two macaque species: Implications for the role of phylogeny and environment in primate cultural variation. *American Journal of Primatology*, *70*, 1124-1132.

Nahallage, C. A. D., & Huffman, M. A. (2012). Stone handling behavior in rhesus macaques (*Macaca mulatta*), a behavioral propensity for solitary object play shared with Japanese macaques. *Primates*, *53*, 71–78.

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.

Ottenheimer Carrier, L., Leca, J. B., Pellis, S. M., & Vasey, P. L. (2015). A structural comparison of female-male and female-female mounting in Japanese macaques (*Macaca fuscata*). *Behavioural Processes, 119*, 70-75.

Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions.* New York: Oxford University Press.

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.

Pellegrini, A. D. (2009). *The role of play in human development.* Oxford: Oxford University Press.

Pellegrini, A., & Gustafson, K. (2005). Boys’ and girls’ uses of objects for exploration, play, and tools in early childhood. In A. Pellegrini & P. Smith (Eds.), *The nature of play: Great apes and humans* (pp. 113-135). New York, NY: Guilford Press.

Pelletier, A. N., Huffman, M. A., Nahallage, C. A. D., Gunst, N., & Leca, J.-B. (2016, February). *Comparing stone play in two macaque species*. Poster session presented at the Prairie University Biology Symposium, University of Lethbridge, Lethbridge, Canada.

Pelletier, A. N., Sita, S., Neugebauer, E., Gunst, N, Pellis, S. M., & Leca, J.-B. (2017a, June). *Comparative analysis of two object-manipulation activities in Balinese long-tailed macaques*. Paper session presented at the meeting of the Animal Behavior Society, University of Toronto Scarborough, Toronto, Canada.

Pelletier, A. N., Kaufmann, T., Mohak, S., Milan, R., Nahallage, C. A. D., Huffman, M. A., Gunst, N. Rompis, A., Wandia, I. N., Arta Putra, I. G. A., Pellis, S. M., & Leca, J-B. (2017b). 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.

Pellis, S. M. (1983). The frequency and pattern of play behaviour. *Mammalia, 47*, 272-274.

Pellis, S. M. (1991). How motivationally distinct is play? A preliminary case study. *Animal Behaviour, 42*, 851-853.

Pellis, S. M., & Burghardt, G. M. (2017) Play and exploration. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowden, & T. Zentall (Eds.), *APA handbook of comparative psychology: Vol 1. Basic concepts, methods, neural substrate, and behavior* (pp. 699-722). Washington, DC: American Psychological Association. http://dx.doi.org/10.1037/0000011-000

Pellis, S. M., Burghardt, G. M., Palagi, E., & Mangel, M. (2015). Modeling play: Distinguishing between origins and current functions. *Adaptive Behaviour, 23*, 331-339.

Pellis, S. M., & Pellis, V. C. (2009). *The playful brain: Venturing to the limits of neuroscience.* Oxford: Oneworld Press.

Pellis, S. M., Pellis, V. C., & Bell, H. C. (2010). The function of play in the development of the social brain. *American Journal of Play, 2,* 278-96.

Power, T. G. (2000). *Play and exploration in children and animals.* Mahwah, NJ: Erlbaum.

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

Rasa, O. A. E. (1984). A motivational analysis of object play in juvenile dwarf mongooses (*Helogale undulata rufula). Animal Behaviour, 32,* 579-589.

Ross, C., & Jones, K. (1999). Socioecology and the evolution of primate reproductive rates. In Lee, P. (Ed.) *Comparative primate socioecology* (pp. 73-110). Cambridge: Cambridge University Press.

Saracho, O. N., & Spodec, B. (1995). Children's play and early childhood education: Insights from history and theory. *The Journal of Education, 177*, 129-148.

Sirianni, G., Wittig, R. M., & Boesch, C. (2015). Do chimpanzees anticipate an object's weight? A field experiment on the kinematics of hammer-lifting movements in the nut-cracking Tai chimpanzees. *Folia Primatologica, 86,* 360-361.

Smith, P. K. (1982). Does play matter? Functional and evolutionary aspects of animal and human play. *The Behavioral and Brain Sciences, 5*, 139-184.

Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: Can training for the unexpected be fun? *The Quarterly Review of Biology, 76*, 141-68.

Soberón, J. M., & Llorente, J. B. (1993). The use of species accumulation functions for the prediction of species richness. *Conservation Biology, 7*, 480-488.

Sutton-Smith, B. (2006). Play and ambiguity. In K. Salen & E. Zimmerman (Eds.), *The game design reader: A rules of play anthology* (pp. 296-313). Cambridge, Mass: MIT Press.

Tan, A. W. Y. (2016). Behavioral processes and social influences on the development of stone-tool use in long-tailed macaques. (Unpublished PhD Dissertation). Nanyang Technological University, Singapore.

Tan, A. W. Y. (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.

Tan, A. W. Y., Tan, S.H., Vyas, D., Malaivijitnond, S., & Gumert, M. (2015). There is more than one way to crack an oyster: Identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. *PLOS ONE, 10,* doi.org/10.1371/journal.pone.0124733

Timberlake, W. (1993). Behavior systems and reinforcement: An integrative approach. *Journal of the Experimental Analysis of Behavior, 60*, 105-128.

Timberlake, W. (2001). Motivational modes in behavior systems. In R. R. Mowrer & S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 155-210). San Francisco, CA: Erlbaum.

Torigoe, T. (1985). Comparison of object manipulation among 74 species of non-human primates. *Primates, 26*, 182-194.

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.

VanderLaan, D. P., Pellis, S. M., & Vasey, P. L. (2012). A theoretical model of the development and evolution of non-conceptive mounting behaviour in Japanese macaques. 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. 186-203). Cambridge, England: Cambridge University Press.

Verenikina, I., Harris, P., & Lysaght, P. (2003). Child's play: Computer games, theories of play and children's development. In J. Wright, A. McDougall, J. Murnane, & J. Lowe, (Eds.). *Proceedings Young Children and Learning Technologies, Selected papers from the International Federation for Information Processing Working Group 3.5 Open Conference* (pp. 99-106). Melbourne, Australia. CRPIT, 34. Retrieved September 20, 2017, from http://crpit.com/abstracts/CRPITV34Verenikina.html

Visalberghi, E., Sirianni, G., Fragaszy, D., & Boesch, C. (2015). Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: A comparison. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *370*, 20140351.

Watson, D. M. (1992). Object play in a laughing kookaburra *Dacelo novaeguineae*. *EMU, 92*, 106-108.

Whishaw, I. Q., & Pellis, S. M. (1990). The structure of skilled forelimb reaching in the rat: A proximally driven movement with a single distal rotatory component. *Behavioural Brain Research*, *41*, 49-59.

Appendix A

Ethogram comprised of 36 stone handling patterns performed by the Balinese long-tailed macaques of Ubud (Bali, Indonesia)

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.

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., 2007).

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.

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 of 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 a stone placed in front of or beside oneself, on the ground.

> Comments: This pattern can be performed by both the hands or the feet, with a power grip, either tightly or loosely. 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.

> 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.

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.

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.

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.

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.

Roll (ROL): To move a stone back and forth on a substrate 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 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, such as on the fur of the individual performing the action (i.e., rub on fur). When a stone is rubbed on the individual performing the action, the duration is typically very short, and the stone is most frequently rubbed along the lower arms. Stones may also be used to groom other individuals. 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.

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).

Toss And Catch (TAC): To lightly throw a stone upwards and catch it with one or both hands.

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.

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.

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, 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; Pelletier et al., 2016).