Title

Do monkeys use sex toys? Evidence of stone tool-assisted masturbation in free-ranging long-tailed macaques

Running title

Tool-assisted masturbation in monkeys

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Graphical Abstract

Do monkeys use sex toys? Evidence of stone tool-assisted masturbation in free-ranging long-tailed macaques

Camilla Cenni*, Jessica B. A. Christie, Yanni Van der Pant, Noëlle Gunst, Paul L. Vasey, I Nengah Wandia & Jean-Baptiste Leca

- Genital-directed stone play actions are sexually motivated in male long-tailed macaques.
- Adult females show a higher level of selectivity for the texture of the stones they use to perform genital-directed stone play.
- Balinese long-tailed macaques can use stones as tools to masturbate.

Abstract

Recent reports on tool use in non-foraging contexts have led researchers to reconsider the proximate drivers of instrumental object manipulation. In this study, we explore the physiological and behavioral correlates of two stone-directed and seemingly playful actions, the repetitive tapping and rubbing of stones onto the genital and inguinal area, respectively, that may have been co-opted into self-directed tool-assisted masturbation in long-tailed macaques (i.e., "Sex Toy" hypothesis). We predicted that genital and inguinal stone-tapping and rubbing would be more closely temporally associated with physiological responses (e.g., estrus in females, penile erection in males) and behavior patterns (e.g., sexual mounts and other mating interactions) that are sexually motivated than other stone-directed play. We also predicted that the stones selected to perform genital and inguinal stone-tapping and rubbing actions would be less variable in number, size, and texture than the stones typically used during other stone-directed playful actions. Overall, our data partly supported the "Sex Toy" hypothesis indicating that stone-directed tapping and rubbing onto the genital and inguinal area are sexually motivated behaviors. Our research suggests that instrumental behaviors of questionably adaptive value may be maintained over evolutionary time through pleasurable/self-rewarding mechanisms, such as those underlying playful and sexual activities.

Keywords

Tool use; object play; sexual behavior; affordance learning; non-human primates.

1. Introduction

The instrumental use of objects (i.e., tool use) in non-human animals has been mostly reported in relation to foraging tasks and subsistence-related activities (Shumaker et al., 2011). As a result, tool use has been primarily discussed from a functional and an adaptive viewpoint (Bentley-Condit & Smith, 2010; Parker & Gibson, 1977). Thus, definitions of tool use pertaining to foraging/subsistence-related activities have focused on the *goal* of actions, describing the functional (both in terms of task-related function and evolutionary function) and possibly fitness-enhancing consequences of object-assisted behaviors (e.g., Shumaker et al., 2011; St Amant & Horton, 2008). However, this functional perspective on tool use comes with at least two caveats. First, unambiguously demonstrating the adaptive value of tool use is challenging; to our knowledge, there is no reported evidence that instrumental object manipulation increases an individual's survival rate or reproductive success (Biro et al., 2013). Second, this approach may have limited researchers' attention to object-assisted actions expressed within survival-dependent contexts. Even though reports of instrumental object manipulation outside the foraging domain abound – such as instances of tools used in agonistic displays (e.g., Leca et al., 2008a), courtship interactions (e.g., Falótico & Ottoni, 2013), and self-maintenance behaviors (e.g., Fayet et al., 2020) – their significance for our understanding of the function and evolution of tool use has been underrated. Additionally, identifying the immediate task-related function of such behaviors has been difficult because the end-goal of these object-assisted actions is unclear.

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

First, in Japanese macaques (*Macaca fuscata*), in which stone handling has been extensively studied for four decades (Leca et al., 2012), one of the 45 stone handling patterns, stone throwing, may have been co-opted into stone-tool use in a social context to increase the effect of agonistic displays (Leca et al., 2008a). Quantitative data on the contextual and behavioral correlates of stone throwing across 10 troops of monkeys indicated that (1) individuals were more likely to throw a stone under conditions of disturbance-related vigilance, such as intra-group aggressive interactions, than in playful situations, and (2) the performers displayed behavioral signs of excitement while throwing a stone (Leca et al., 2008a).

Additionally, detailed description of stone throwing actions revealed that the behavior was untargeted (i.e., stones were not thrown directionally), and the stones were more likely used to augment the social effect of behavioral displays in agonistic contexts than to hit a conspecific. Even though stone handling is a behavioral tradition in Japanese macaques (Huffman, 1984; Leca et al., 2007a,b; Nahallage & Huffman, 2007), the distribution of stone throwing across troops showed that this specific stone handling pattern had turned into stone tool use only in the group where stone throwing was commonly performed by several individuals. Longitudinal data showed that stone throwing had increasingly spread over time within the study group and across those individuals with strong social relationships (i.e., they spent more time in physical proximity; Leca et al., 2008a). Thus, quantitative data on the contextual and behavioral correlates of seemingly purposeless object-directed actions may provide insights into the instrumental nature of these actions.

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

Manual masturbation in males has been reported among several primate species (Dixson, 2012; Thomsen et al., 2003). Outside humans, however, manual masturbation seldom leads to ejaculation (Dixson, 2012). According to a study by Thomsen and colleagues (2003), male masturbation was documented in 34 species of non-human primates; however, it led to ejaculation in only 22 of them, and even so, it was occasional. Thus, definitions of manual masturbation in non-human primates do not typically include orgasm, such as ejaculation, as a necessary component of the behavior. Even in primate species in which masturbation leading to ejaculation has been associated with functional consequences, it remains occasional: in most instances, masturbation does not lead to orgasm (e.g., Japanese macaques: Thomsen & Soltis, 2004). Importantly, in non-human primates, functional explanations for masturbation

leading to orgasm have never been proposed nor investigated in females, for which masturbation is scarcely documented (but see Allen, 1977; Temerlin, 1975 for accounts of masturbation leading to orgasm in captive chimpanzees). Additionally, anecdotal evidence suggests that *object-assisted* masturbation is more common in females than in males (e.g., Ford & Beach, 1951; Kollar et al., 1968; Russon et al., 2009; Sinha, 1997). In the Balinese long-tailed macaques living in Ubud, males and females across age classes have been observed engaging in manual masturbation, but in line with findings from other non-human primate species, masturbation leading to orgasm seems to be rare (Cenni, personal observation).

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

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

2. Methods

2.1. Study population and site

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

2.2. Data collection and study subjects

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

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

2.3. Data analysis

For all four predictions, stone handling activity was scored using the same stone handling ethogram as in Pelletier et al. (2017) and Cenni et al. (2021, in review). During the scoring process, we detected new idiosyncratic variants of stone-assisted actions directed to the genital and inguinal regions, not described by Cenni and colleagues (2020) as genital stone-tapping and rubbing, which could be due to (a) the current study providing a broader description of the structure of the behavior, and (b) an additional focus on females, not previously included in Cenni et al. (2020). To explore the physiological and behavioral correlates of stone-assisted actions directed to the genital and inguinal regions, we created

a merged behavioral category which comprised “Tap on Groin” and “Rub on Groin” (as originally defined in Cenni et al., 2020), and novel behavioral variants directed to the genital and inguinal regions (see Supplementary Material S1 to distinguish what was considered genital and inguinal regions in males and females). Thus, the behavioral category *genital stone-tapping/rubbing* consisted of behaviors under the following operational definitions:

“Tap on groin” = to tap (a) stone(s) in a repeated sweeping gesture using the fingertips onto and around the genital area, including the inguinal region, while the individual is in a sitting posture. This stone handling pattern can be performed in combination with objects and body parts (i.e., to tap a stone against a stone that is in contact with the genital area) or may just involve the genital and inguinal regions. In both males and females, this pattern is performed with one or both hands. When it is expressed with one hand, the other hand is occasionally used to direct the stone(s) to the genital area.

“Rub on groin” = To slide or move (a) stone(s) back and forth onto and around the genital area, including the inguinal region, utilizing a power or precision grip, while the individual is in a sitting posture. Though this stone handling pattern may resemble “Roll,” the hand grip utilized in this activity is different. The stone(s) can slide, move back and forth, or in circular motion, with a power or precision grip. In males, the stone(s) is/are often rubbed with one or both hands on the penis (either erected or held stretched by one hand). In females, the stone(s) is/are often first rubbed on the ground in front of the individual, and then pushed under the lower belly, where the genitals are located.

“Pelvic thrusting” = To slide or move the pelvis back and forth onto a stone, which is stationary on the ground. This stone handling pattern is usually performed with large stones, and stones are generally not held against a body part.

“Roll on groin” = To move (a) stone(s) back and forth onto and around the genital area, including the inguinal region, in a rolling motion, performed with loose grips or open palms. This stone handling pattern resembles “Rub”; however, the hand grip utilized for this activity is different. In males, it is usually expressed with (a) stone(s) being rolled on the penis with both hands and loose grips or open palms.

Video references of genital stone-tapping/rubbing in males and females can be found in Supplementary Material S2. CC used *The Observer XT 15* (Noldus Information Technology, The Netherlands) to score the video-recorded stone handling sequences, with a precision to the second, and generate event-log files (i.e., series of consecutive stone handling patterns) for each subject. To assess reliability of video scoring, we calculated an inter-scorer reliability test for CC and JBL when transcribing the same samples of randomly selected stone handling video records, involving a total of 1892 stone handling patterns (i.e., average Cohen’s *k* across predictions = 0.97; range Cohen’s *k* across predictions = 0.92 – 1; Martin & Bateson, 1993).

To test Prediction #1 (i.e., penile erection should be more closely temporally associated with genital stone-tapping/rubbing than with any other stone handling patterns), for each subject, we selected all available one-minute stone handling sequences featuring the beginning of a fully rigid penile erection (Fig. 1B; cf. Hayes et al., 2016) exactly 30 seconds after the beginning of the sequence (i.e., penile erection occurred at mid-point within the stone handling sequence). Since Prediction #1 tested which behavior preceded the expression of penile erection, one-minute intervals provided a physiologically relevant time window. The selected stone handling sequences were truncated from longer stone handling sequences, and they were independent (i.e., they belonged to distinct stone handling sequences collected on different days). To be included in these analyses, penile erection should not have been attributed to external sex-related contextual factors (e.g., sexual inspection, sexual solicitation, sexual mounting behavior). Stone handling sequences had to be recorded under optimal visibility conditions, to ensure that all or most patterns performed were reliably identified. In the end, 38 stone handling sequences qualified for selection, belonging to 23 subjects (with an average of two sequences per subject), including 20 juvenile/subadult males and 3 adult males.

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

To test Prediction #2 (i.e., genital stone-tapping/rubbing should last longer in stone handling sequences featuring penile erection than in stone handling sequences without penile erection, whereas no such differences were expected for other stone handling patterns), for each subject, we selected two three-minute stone handling sequences, one featuring the beginning of a fully rigid penile erection (Fig. 1B; cf. Hayes et al., 2016) exactly 90 seconds after the beginning of the sequence (i.e., penile erection occurred at mid-point within the stone handling sequence), and one without penile erection. Since Prediction #2 tested whether certain stone handling patterns lasted longer when the performer was experiencing penile erection, three-minute intervals provided a good trade-off between a physiologically relevant time window and data availability. Occasionally, if penile erection did not reach full rigidity within the observed time period, we included instances of stone handling sequences featuring the beginning of a moderate increase in penile rigidity (Fig. 1A; cf. Hayes et al., 2016). The selected stone handling sequences were truncated from longer stone handling sequences, and they were independent (i.e., they belonged to distinct stone handling sequences collected on different days). For one subject, stone handling sequences with and without penile erection were truncated from the same stone handling sequence, but they did not overlap in time, being more than 10 minutes apart. For stone handling sequences featuring penile erection to be included in these analyses, penile erection should not have been attributed to external sex-related contextual factors (e.g., sexual inspection, sexual solicitation, sexual mounting behavior). For stone handling sequences without penile erection, the beginning of the truncated stone handling sequence was randomly selected with the use of a random time generator. Stone handling sequences had to be recorded under optimal visibility conditions, to ensure that all or most of the stone handling patterns performed were reliably identified. When multiple sequences could be selected, selection was made at random. In the end, we were able to select 18 subjects, including 16 juvenile/subadult males and 2 adult males.

To test Prediction #3 (i.e., genital stone-tapping/rubbing should be more often expressed in a sexual context than tapping/rubbing on body parts other than the genital region), for each subject, we selected two one-minute stone handling sequences, one featuring genital stone-tapping/rubbing exactly 30 seconds after the beginning of the sequence (i.e., genital stone-tapping/rubbing occurred at mid-point within the stone handling sequence), and one featuring either stone-tapping/rubbing on other body parts, the repetitive tapping and rubbing of stones on body parts other than the genital region, exactly 30 seconds after the beginning of the sequence (i.e., stone-tapping/rubbing on other body parts occurred at mid-point within the stone handling sequence). Since Prediction #3 tested for contextual differences

between the expression of genital stone-tapping/rubbing and the expression of stone-tapping/rubbing on body parts other than the genital region, one-minute intervals provided an environmentally relevant time window. Stone-tapping/rubbing on other body parts were used as a control to test for the contextual expression (see Table 1) of genital stone-tapping/rubbing, because (a) they are structurally similar to genital stone-tapping/rubbing, and (b) they also are directed to body parts, but not to the genital and inguinal area. Video references of stone-tapping/rubbing on other body parts in males and females can be found in Supplementary Material S4. To be selected, one-minute stone handling sequences with genital stone-tapping/rubbing at mid-point should not include stone-tapping/rubbing on other body parts and, vice versa, stone handling sequences with stone-tapping/rubbing on other body parts at mid-point should not include genital stone-tapping/rubbing. The selected stone handling sequences were truncated from longer stone handling sequences, and whenever possible they belonged to distinct stone handling sequences collected on different days. When they were truncated from the same stone handling sequences, they did not overlap in time. In the end, we were able to select 50 subjects, 18 juvenile/subadult males, 9 juvenile/subadult females, 9 adult males, and 14 adult females.

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

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

To determine whether the stones used in stone handling sequences with genital stone-tapping/rubbing were less variable than the stones used in stone handling sequences with stone-tapping/rubbing on other body parts, we used the coefficient of unalikeability (*u*; Kader & Perry, 2007).

The coefficient *u* ranges from 0 to 1; the higher the value, the more unalike the data set (i.e., the higher the variation in the data).

To explore the distribution of genital stone-tapping/rubbing across sex/age classes, we randomly selected, by drawing names from an online random generator, 56 subjects, including 14 juvenile/subadult males, 14 juvenile/subadult females, 14 adult males, and 14 adult females (Supplementary Material S3). Since (a) genital stone-tapping/rubbing has never been observed outside stone handling activity, and (b) stone handling activity represents a small proportion of the time budget of an individual in Ubud (Leca, unpublished data), we only examined the distribution of genital stone-tapping/rubbing across sex/age classes within the stone handling activity. For each of these 56 subjects, CC randomly selected, by drawing sequences from an online random generator, and scored on average 31 minutes of cumulative stone handling activity across multiple days. Whenever possible, to ensure a more comprehensive representation of an individual's stone handling activity, no more than 10 minutes of stone handling activity per day were scored. To do so, stone handling sequences longer than 10 minutes were randomly truncated with the use of a random time generator.

2.4. Statistics

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

2.5. Ethical statement

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

3. Results

Among all the stone handling patterns performed by juvenile/subadult and adult males, genital stone-tapping/rubbing was the only criterion behavior that significantly differed in its transitional probability to the target behavior "penile erection" (transitional probability = 0.22, adjusted residuals $z = 7.90$, $p < 0.001$, corrected $\alpha = 0.002$, Yule's $Q = 0.82$). No statistically significant differences were found in the transitional probabilities from other stone handling patterns to penile erection (Table 2). Prediction #1 was supported.

In juvenile/subadult and adult males, genital stone-tapping/rubbing lasted significantly longer in stone handling sequences featuring penile erection than in stone handling sequences without penile erection (Wilcoxon signed rank-test, $z = -3.07$, $p = 0.002$, corrected $\alpha = 0.005$; 12 ± 13 sec and 1 ± 2 sec, respectively; Fig. 3), whereas no statistically significant differences were found in the duration of any other stone handling patterns in the presence or absence of penile erection. Prediction #2 was supported.

In juvenile/subadult males, we found that genital stone-tapping/rubbing was performed significantly more often in a "sexual" context than stone-tapping/rubbing on other body parts (McNemar's test, $\chi 2$ (1, N = 18) = 10.08, $p < 0.001$, corrected $\alpha = 0.01$; Fig. 4), whereas no statistically significant differences were found in other contexts. No other statistically significant differences were found between genital stone-tapping/rubbing and stone-tapping/rubbing on other body parts in any contexts within age/sex classes. Prediction #3 was partly supported.

In terms of variability of stones used by different age/sex classes to perform genital stone-tapping/rubbing and to perform stone-tapping/rubbing on other body parts, we found that, in adult females, there was significantly less variation in texture in stones used to perform genital stone-tapping/rubbing than in stones used to perform stone-tapping/rubbing on other body parts (coefficient of unalikeability, $u = 0.26$ and $u = 0.36$, respectively; test statistic $C = -3.37$, $p < 0.001$, corrected $\alpha = 0.017$; Fig. 5). When performing genital stone-tapping/rubbing, adult females used more *angular/rough* stones than *non-angular/smooth* stones (113 and 21, respectively), whereas no statistically significant preference for stone texture was found when performing stone-tapping/rubbing on other body parts (91 and 28, respectively). No other statistically significant differences were found in other stone characteristics (i.e., number and size) within age/sex classes. Prediction #4 was partly supported.

We found a statistically significant difference in the distribution of genital stone-tapping/rubbing durations across age/sex classes (Kruskal-Wallis' test, $H_3 = 10.35$, $p = 0.016$; Fig. 6). Dunn's post-hoc tests revealed that juvenile/subadult males spent significantly more time performing genital stone-tapping/rubbing during their overall stone handling activity (3.53% ± 5.07) than adult males (0.24% ± 0.63; Dunn's post-hoc test, $z = 18.43$, $p = 0.002$, corrected $\alpha = 0.008$), whereas no statistically significant differences were found between juvenile/subadult males and both, juvenile/subadult females (0.92% ± 1.20; Dunn's post-hoc test, $z = -5.93$, $p = 0.323$, corrected $\alpha = 0.008$) and adult females (1.87% ± 5.01; Dunn's post-hoc test, $z = 11.64$, $p = 0.052$, corrected $\alpha = 0.008$). No other statistically significant differences were found between age/sex classes.

4. Discussion

Our results provide some support to the "Sex Toy" hypothesis, which holds that genital stone-tapping/rubbing comprise behavioral variants of self-directed stone tool-assisted masturbation in Balinese long-tailed macaques. Taken together, our results showed that genital stone-tapping/rubbing (a) immediately preceded the beginning of a fully fledge penile erection, (b) lasted longer when penile erection occurred compared to when penile erection was absent, (c) was expressed within a sexual context in juvenile males, and (d) bore some degree of selectivity in the stones used by females to perform these actions. Thus, it can be confidently concluded that these actions are not incidental (see also Supplementary Material S2, which shows how different variants of the category *genital stone-tapping/rubbing* are primarily directed towards the genitals, in both males and females). Lastly, we found

that young males spent on average more time performing genital stone-tapping/rubbing than other age/sex classes. However, this difference was significant only when comparing juvenile/subadult males and adult males. Thus, together with previous findings showing a higher temporal organization of stone handling sequences with genital stone-tapping/rubbing than that of stone handling sequences where those two actions were absent (Cenni et al., 2020), our study provides further support to the view that genital stone-tapping/rubbing comprise behavioral variants of tool-assisted self-directed masturbation in Balinese long-tailed macaques.

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

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

Several causes have been proposed to explain the proximate and evolutionary significance of masturbatory behavior patterns (Baker & Bellis, 1993; Dixson & Anderson, 2004; Dubuc et al., 2013; Inoue, 2012; Thomsen & Soltis, 2004; Waterman, 2010). In a questionnaire-based study, Thomsen and colleagues (2003) found a strong association between a primate species' mating system and the occurrence of male masturbation, with masturbation being more often displayed in species living in a multimale/multifemale organizational system, like macaques. In those species, males and females form short-term, and generally non-exclusive, sexual relationships that include courtship behaviors and a single, or a series of, mounting interaction(s) (Dixson, 2012). As a result, multimale/multifemale systems are characterized by high levels of intra-sexual competition, especially among males, for access to, and insemination of, females. Such intra-sexual competition can select for sexual traits in male anatomy, physiology and behaviors (i.e.,

sperm competition; Parker, 1970). Males living in these mating systems have relatively large testes, whose numerous Leydig cells produce high levels of testosterone necessary to maintain competitive levels of sexual arousal (Dixson, 2012; Dixson & Anderson, 2004). Therefore, a higher distribution in the performance of male masturbation in species living in multimale/multifemale systems, including macaques, may be proximately (i.e., physiologically) and ultimately (i.e., evolutionarily) explained by higher intra-sexual competition among males. In this regard, the expression of stone tool-assisted masturbation in Balinese long-tailed macaques could be a by-product of sexual arousal and serve as a form of sexual outlet for individuals with limited access to mating opportunities (cf. "sexual outlet" hypothesis; Dixson & Anderson, 2004). However, given that male masturbation events lead to ejaculation in a small proportion of the observed masturbation time, new hypotheses are needed to explain masturbation (Dubuc et al., 2003). The lack of ejaculation after genital stone-tapping/rubbing and the majority of manual masturbation instances may still be explained from a by-product perspective. The "sexual pleasure" hypothesis is a more holistic approach recently proposed to explain masturbation (Roth et al., 2022). In line with the neurobiology of sexual pleasure, this hypothesis holds that genital self-stimulation (with and without object) is maintained by sexually pleasurable feedback, thereby modulating the individual's emotional state. This could explain our results showing that younger males (which displayed early signs of sexual interest, as demonstrated by the genital inspection of females, mounting attempts directed to females, and self-directed manual masturbation; Cenni, personal observation) spent more time performing genital stone-tapping/rubbing than older males, who may be more successful in the competition for female mates. However, this hypothesis has not been fully tested yet, and it does not fully account for the time spent by females performing genital stone-tapping/rubbing in our study population.

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

It is important to acknowledge that our study subjects may represent a STRANGE population (as per Webster & Rutz, 2020), in which food provisioning relaxed selective pressures on foraging causing the part of the activity budget typically devoted to looking for natural foods to decrease (Brotcorne, 2014; Leca et al., 2008b). Such anthropogenic influences created spare time for the monkeys that may have been invested into less functionally constrained forms of behavior, including object-assisted masturbation. Indeed, in the *Macaca* genus, stone handling traditions have only been reported in provisioned groups (Leca et al., 2008b; Pelletier et al., 2017), whereas substance-related tool-assisted behaviors have been primarily reported in populations in which high selective pressure on foraging is high (Gumert et al., 2009).

Nonetheless, the phylogenetic closeness among macaque species and populations that handle stones, either playfully or instrumentally, suggests a general tendency to conditionally use stones in some environments, be it functional or non-functional (Tan, 2017).

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

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

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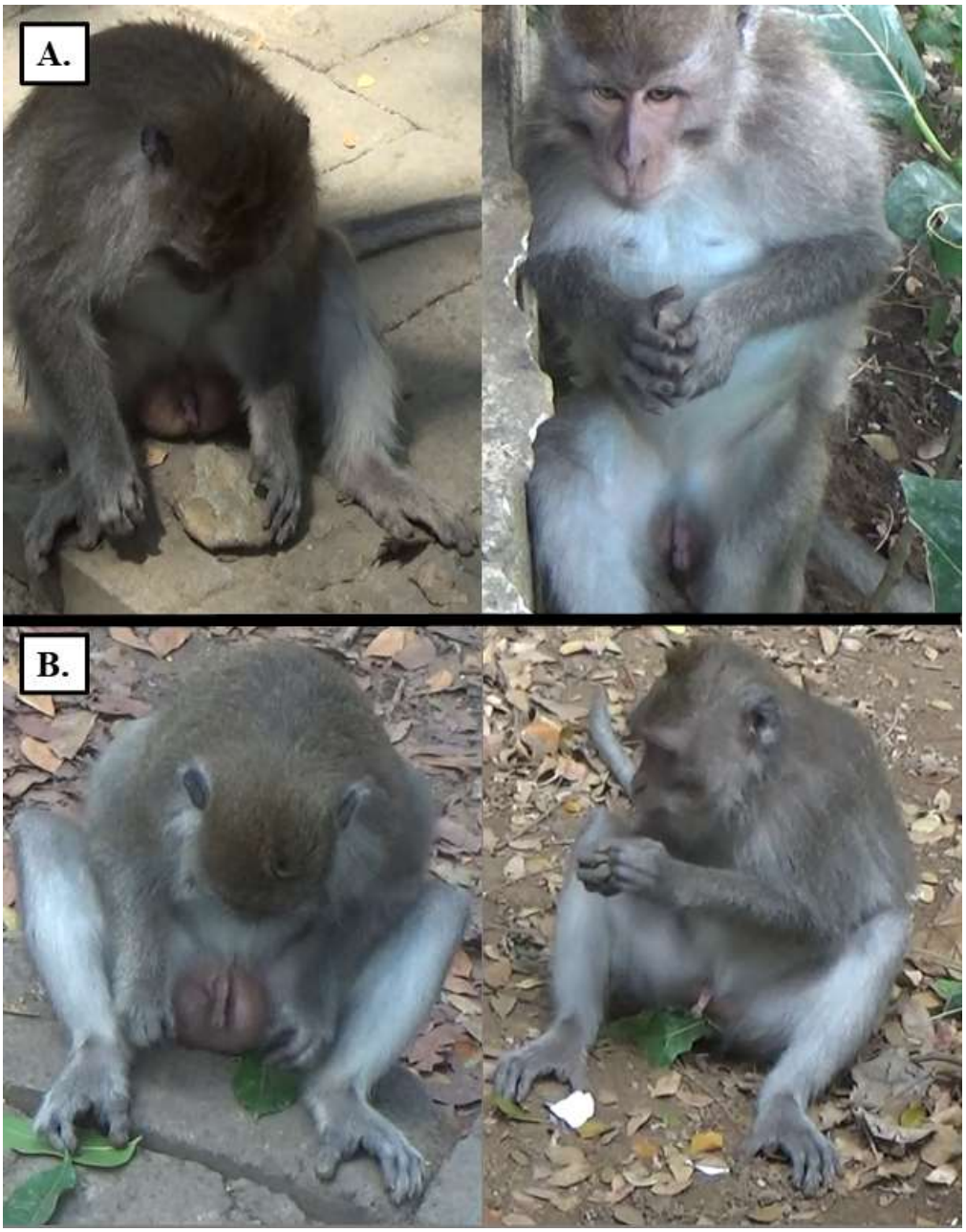


Fig. 1 – Two categories of erection based on perceived erection hardness (cf. Hayes et al., 2016) with (A.) moderate increase in penile rigidity, but not completely hard, with prepuce still visible, and (B.) completely hard and fully rigid penile erection, with prepuce fully visible.

Fig. 2 – Hypothetical sequence of stone handling patterns occurring within a T_0 – T_x observation period (top row). A lag +1 sequential analysis detects the temporal transitions from a criterion pattern to a target pattern occurring immediately after (bottom row).

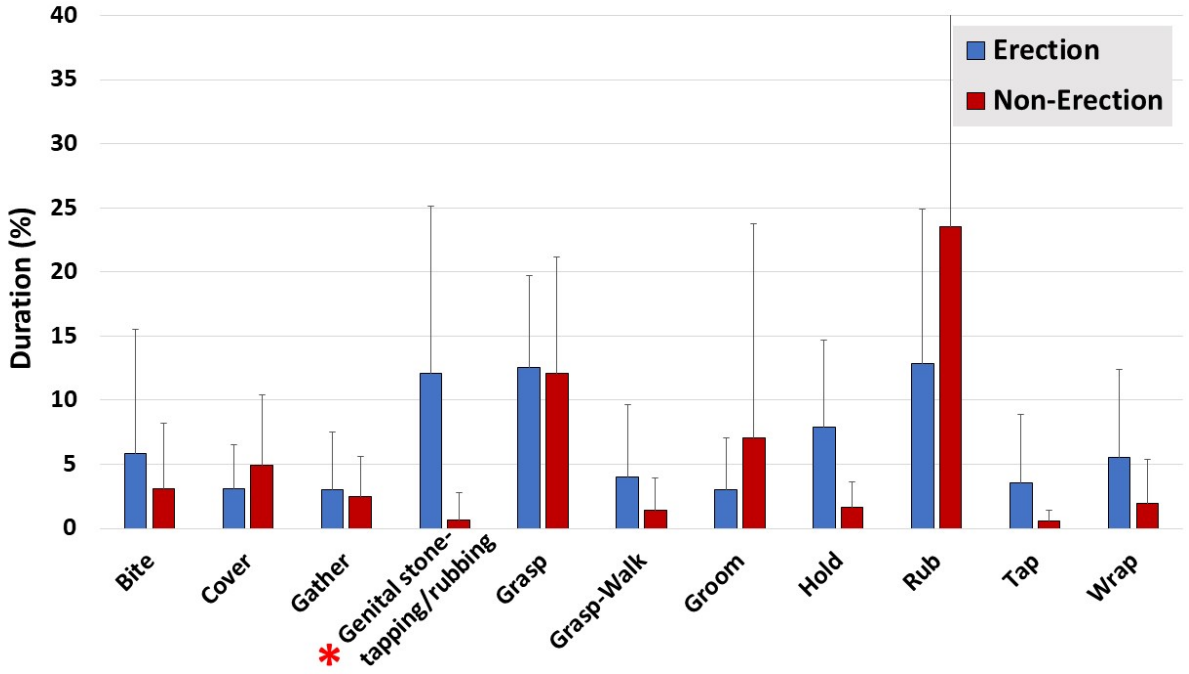


Fig. 3 – Average percentages of duration (± SD) of stone handling patterns performed by at least 50% of the sample in stone handling sequences with penile erection (blue bars) and in stone handling sequences without penile erection (red bars). *: corrected $p < 0.005$.

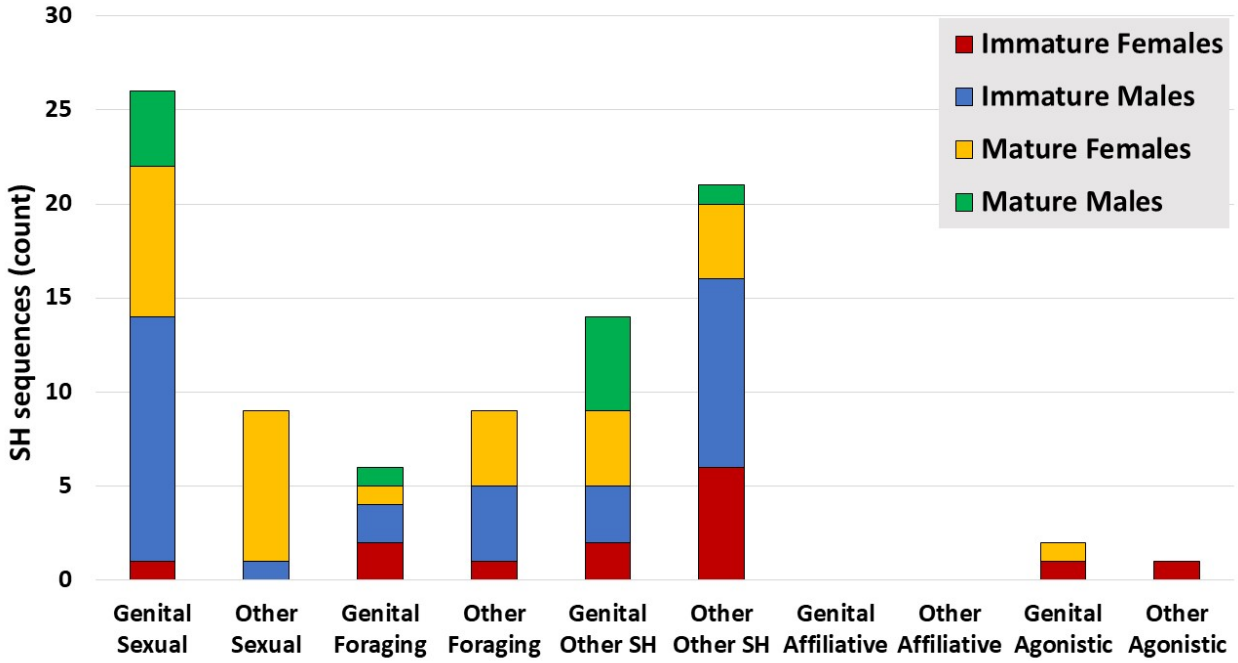


Fig. 4 – Number of stone handling sequences with genital stone-tapping/rubbing ("Genital") and tapping/rubbing on other body parts ("Other") performed in different contexts across age/sex classes. "SH" = stone handling.

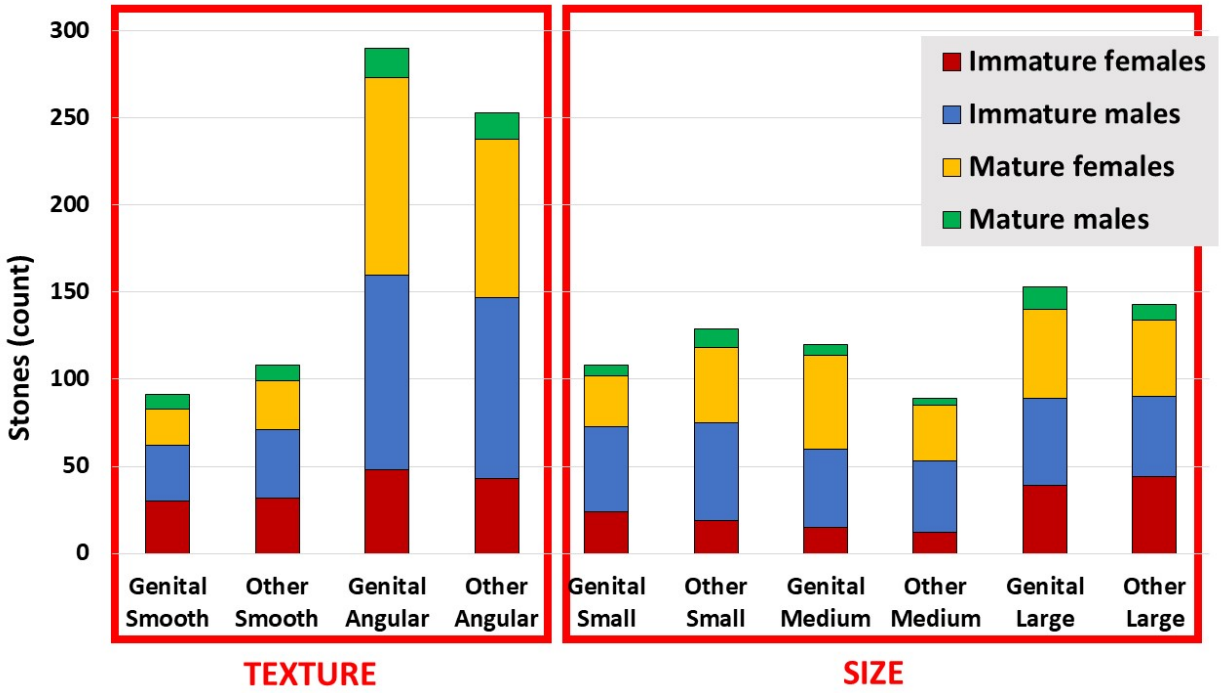


Fig. 5 – Number of stones, classified by texture, and relative size, used to perform genital stone-tapping/rubbing ("Genital") and to perform tapping/rubbing on other body parts ("Other") across age/sex classes.

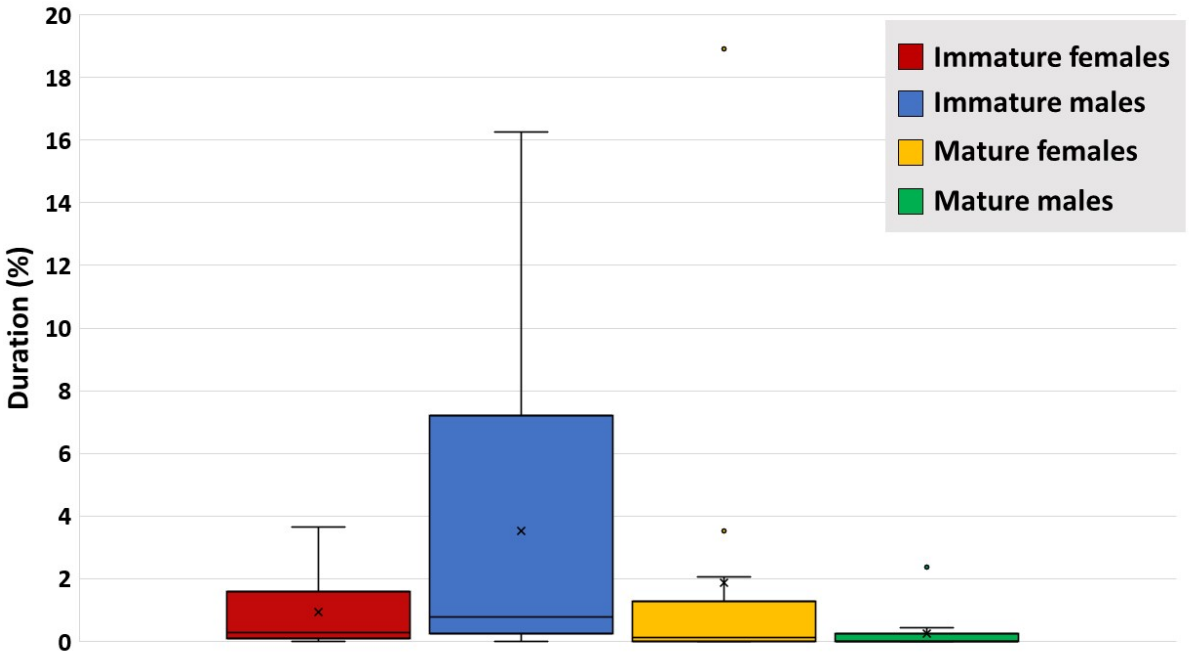


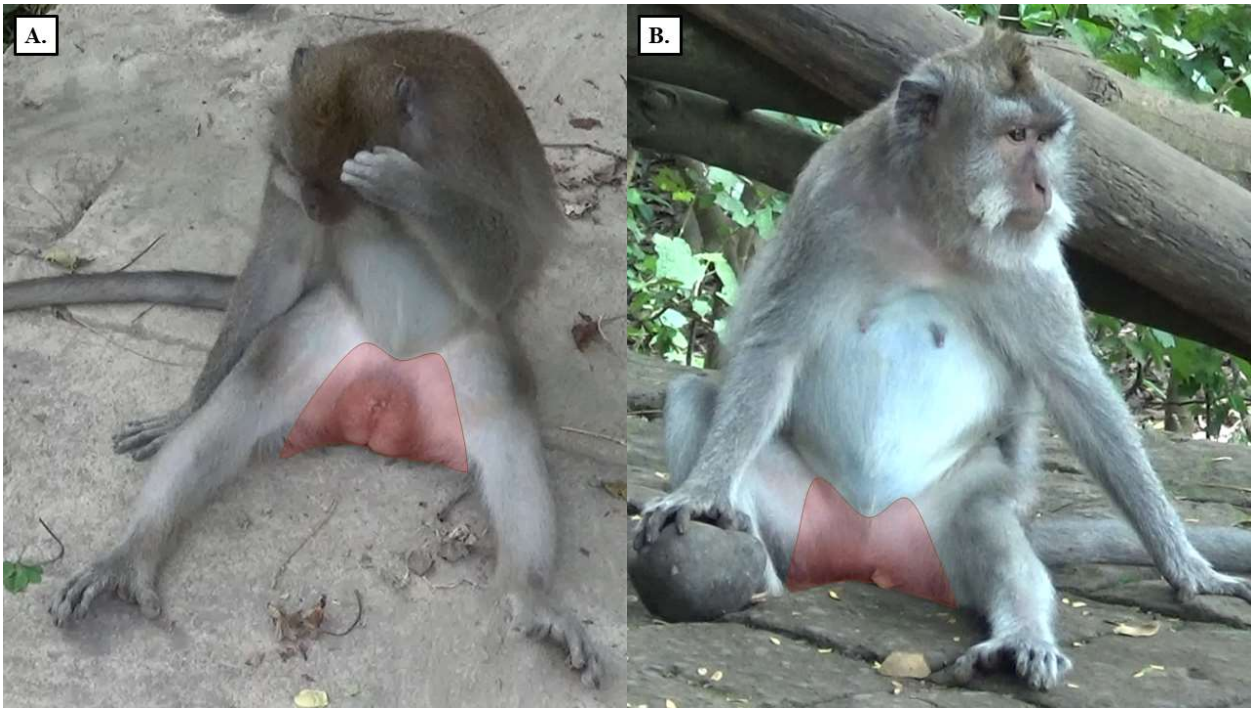
Fig. 6 – Distribution of percentages of duration (± SD) of genital stone-tapping/rubbing (TOG/ROG) in relation to total stone handling activity for each age/sex class.

Table 1 – Contexts and their definitions

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

Table 2 – Transitional probabilities of criterion behaviors to target behavior "penile erection", and respective adjusted residuals, p-values and Yule's Q. Boldface indicates statistically significant results.

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



Supplementary Material S1 – Genital and inguinal regions in (A.) males and (B.) females used to score the stone handling patterns belonging to the category *genital stone-tapping/rubbing*.

https://youtu.be/lAQJumWMrL0

Supplementary Material S2 – Examples of “Tap On Groin”, “Rub On Groin”, “Pelvic Thrusting”, and “Roll On Groin” in male and female Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

Table S1 – Number of days of data collection per subject, total duration (in minutes, and seconds) of stone handling (SH) recorded for each subject across multiple days, mean stone handling (SH) duration (± SD) per day and per subject.

Subject	Age	Sex	Obs day	Total SH (mm:ss)	μ SH (mm:ss)
Duchess	Young	Female	8	33:31	04:11 (± 02:55)
Encrenca	Young	Female	6	36:00	05:37 (± 04:51)
Fake Robin	Young	Female	9	25:59	02:53 (± 04:40)
Grinch	Young	Female	9	33:40	03:44 (± 03:43)
Kappa	Young	Female	8	30:16	03:47 (± 03:50)
Kyla	Young	Female	7	34:35	04:56 (± 03:40)
Lady Deadpool	Young	Female	9	23:13	02:35 (± 02:01)
Langur	Young	Female	3	30:09	06:02 (± 04:11)
Marilyn	Young	Female	10	32:33	03:15 (± 02:49)
Pirata	Young	Female	5	33:27	06:41 (± 03:55)
Robin	Young	Female	8	35:36	04:27 (± 03:15)
S3	Young	Female	8	39:34	04:57 (± 04:15)
Samanta	Young	Female	7	33:17	04:45 (± 04:01)
Wax	Young	Female	8	37:18	04:40 (± 03:52)
Bass	Young	Male	5	38:11	07:38 (± 03:42)
C-17	Young	Male	5	30:56	06:11 (± 03:53)
Carlo	Young	Male	7	30:28	04:21 (± 03:29)
Dome	Young	Male	5	30:17	06:03 (± 03:19)
Inmate	Young	Male	6	30:01	05:00 (± 03:43)
Lookout	Young	Male	7	30:27	04:21 (± 02:41)
Newby	Young	Male	5	30:43	06:09 (± 02:31)
Nyoman	Young	Male	10	30:09	03:01 (± 02:28)
Paggio	Young	Male	6	32:34	05:26 (± 02:21)
Paul	Young	Male	6	31:35	05:16 (± 03:32)
Scarface	Young	Male	4	34:52	08:43 (± 02:35)
Sick Boy	Young	Male	4	31:07	07:47 (± 02:27)
Sugar	Young	Male	7	31:54	04:34 (± 03:47)
Watson	Young	Male	5	30:26	06:05 (± 02:32)
Beardy	Adult	Female	7	30:01	04:17 (± 03:07)
Big Eyes	Adult	Female	6	30:36	05:06 (± 03:03)
Carmen	Adult	Female	9	34:27	03:50 (± 03:20)

Subject	Age	Sex	Obs day	Total SH (mm:ss)	μ SH (mm:ss)
Chifu	Adult	Female	5	31:43	06:21 (± 03:32)
Deadpool Lard	Adult	Female	7	30:37	04:22 (± 04:04)
Izma	Adult	Female	8	29:36	03:42 (± 02:26)
Musty	Adult	Female	6	30:01	05:00 (± 04:01)
Punk	Adult	Female	5	32:12	06:26 (± 02:57)
S12	Adult	Female	4	31:35	07:54 (± 03:12)
S9	Adult	Female	9	32:04	03:34 (± 02:46)
Selma	Adult	Female	8	32:40	04:05 (± 02:01)
Sorry	Adult	Female	7	37:01	05:17 (± 04:28)
T5	Adult	Female	10	32:06	03:13 (± 01:45)
Yetta	Adult	Female	7	31:12	04:27 (± 02:15)
Anvil	Adult	Male	4	31:20	07:50 (± 02:33)
Baggy	Adult	Male	8	30:54	03:52 (± 02:46)
Danger	Adult	Male	5	30:48	06:10 (± 07:19)
Lancelot	Adult	Male	8	30:50	03:51 (± 02:50)
Ned	Adult	Male	4	23:26	05:52 (± 06:53)
Nigel	Adult	Male	9	32:21	03:36 (± 03:07)
Obelix	Adult	Male	6	20:11	03:22 (± 01:49)
Pinocchio	Adult	Male	5	31:11	06:33 (± 03:46)
Ramsey	Adult	Male	7	31:07	04:27 (± 03:39)
Ronald	Adult	Male	4	34:38	08:39 (± 01:14)
Splash	Adult	Male	5	35:54	07:11 (± 03:30)
Temple Baggy	Adult	Male	3	30:00	10:00 (± 05:19)
White Eyebrows	Adult	Male	8	31:15	03:54 (± 02:01)
Zeus	Adult	Male	7	30:13	04:19 (± 04:10)

Supplementary Material S3 – Number of days of data collection per subject, total duration (in minutes and seconds) of stone handling (SH) recorded for each subject across multiple days, mean stone handling (SH) duration (± SD) per day and per subject.

https://youtu.be/c-Pp9WlGTUs

Supplementary Material S4 - Examples of “Tap On Other body parts”, and “Rub On Other body parts” in male and female Balinese long-tailed macaques (Ubud, Monkey Forest, Bali, Indonesia).

https://youtu.be/MlAziAla1SU

Supplementary Material S5 – Examples of twig-assisted masturbation in an adult female Balinese long-tailed macaque (Ubud, Monkey Forest, Bali, Indonesia).