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Stone Affordances as Potential for Action Expression in Object Play in Long-Tailed Macaques (*Macaca fascicularis*)

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Camilla Cenni[1], Sergio M. Pellis[2], I Nengah Wandia[3], and Jean-Baptiste Leca[1, 4]

[1] Department of Psychology, University of Lethbridge
[2] Department of Neuroscience, University of Lethbridge
[3] Primate Research Center, Udayana University
[4] School of Natural and Engineering Sciences, National Institute of Advanced Studies

Object affordances play a major role in action expression: (a) providing opportunities to generate potential solutions to instrumental problems and (b) shaping and constraining the motor actions available to an individual. The playful manipulation of objects can facilitate individual acquisition of functional object-assisted actions through affordance learning. We tested the "object affordance" hypothesis in free-ranging long-tailed macaques. This hypothesis holds that the physical properties associated with stone size afford different stone-directed actions, in the context of stone handling (SH) behavior, a form of culturally maintained stone play from which stone tool use can emerge. We predicted that higher SH *versatility* (i.e., total number of different SH behavioral elements expressed) and higher duration of the SH behavioral element "Pound" would be associated with the manipulation of medium-sized stones, followed by small stones, and then large stones. Our data partly supported these predictions. Both medium-sized and small-sized stones afforded the highest SH *versatility*, and a higher duration of "Pound" than large stones. As expected, duration of "Pound" was higher with medium than small stones, but the difference was not statistically significant. Our results were consistent with Newell's constraint model, which emphasizes the role of objects' physical properties in limiting and enhancing the expression of actions directed to these objects. The relaxed selective pressures acting on SH behavior may enhance the expression of a range of actions directed toward stones of different sizes that could facilitate the emergence of instrumental solutions and may contribute to explaining the evolution of lithic technology in early humans.

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Acting selectively on the basis of available information is an adaptive component of problem-solving and instrumental object manipulation (i.e., tool use; Shumaker et al., 2011) because it allows individuals to tailor effective behavioral responses to local environmental features (Fragaszy et al., 2010; Stephens & Krebs 1986). There are several extrinsic (e.g., ecological, social) and intrinsic (e.g., anatomical, motivational, cognitive) variables that affect selectivity in tool-assisted actions (Cenni & Leca, 2020a).

Camilla Cenni https://orcid.org/0000-0002-5990-8553
Jean-Baptiste Leca https://orcid.org/0000-0002-2371-671X

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Correspondence concerning this article should be addressed to Camilla Cenni, Department of Psychology, University of Lethbridge, 4401 University Drive West, Lethbridge, AB T1K3M4, Canada. Email: camilla.cenni@uleth.ca

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Among the ecological factors, object *affordances* (i.e., the physical properties of objects that determine their potential for manipulation; Gibson, 1979) play a major role in shaping and constraining the efficiency of instrumental object-directed actions. Indeed, affordances mediate motor acquisition and expression (a) by limiting the actions available to an individual, through the structural constraints associated with both the object and the user (Newell, 1986; Newell & Jordan, 2007; Newell et al., 1989); and (b) by creating opportunities to experience actions, enabling affordance learning (Bourgeois et al., 2005; Fontenelle et al., 2007; Lockman, 2000; Palmer, 1989).

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

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

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

To further explore the relationships between object affordances and action expression in instrumental object manipulation, one may investigate how the physical properties of objects influence noninstrumental forms of object manipulation, such as object play, often claimed to be proximately and ultimately linked with tool use (Lockman, 2000). In long-tailed macaques, Zou and colleagues (2017) examined the exploratory and noninstrumental behavior patterns directed toward novel objects of different sizes (i.e., a basketball ball and a tennis ball), to determine how the physical properties of novel objects mediate the expression of object-directed actions. Interestingly, they found no significant variation in the overall time spent manipulating these two objects across subjects, but marked interindividual differences emerged in the relative duration of several behavioral actions directed toward the objects, for example, a tennis ball was rolled, held and bitten more often than a basketball ball (Zou et al., 2017). Thus, meaningful differences caused by the physical properties of objects that can predict differential action expression in a population may not be found in the total time allocated to their noninstrumental handling (i.e., the overall duration of play with different objects), but in the qualitative structural components of object-directed playful handling (i.e., relative durations of differential manipulative actions expressed toward different objects). AQ: 14

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

To explore the role of object affordances in the expression of object-directed playful actions, we examined the various SH behavioral elements involving stones of different sizes in free-ranging Balinese long-tailed macaques. Our objective was to assess whether various stone sizes differentially afforded SH behavioral elements. We tested the "object affordance" hypothesis, whereby the expression of SH behavioral elements was mediated by the size of the stones being manipulated; in other words, the selection, diversity, and duration of the SH behavioral elements performed by the monkeys should covary with the size of the stones they playfully handle. To do so, we compared SH behavioral elements directed toward small, medium and large stones. From this hypothesis, in line with Newell's constraint model, we generated two predictions. First, we predicted that SH *versatility* (i.e., defined as the number of different SH behavioral elements displayed across subjects) would differ across stone sizes. Specifically, handling a medium-sized stone should be associated with the greatest SH *versatility*, followed by small stones and large stones (i.e., large stones should afford the smallest number of different SH behavioral elements; Prediction #1). Second, in line with previous findings in long-tailed macaques on grip patterns during the performance of instrumental stone-pounding (Gumert et al., 2009), we predicted that SH behavioral elements requiring power grip (i.e., Pound) should be preferentially performed with medium stones, followed by large stones and small stones. In other words, object-directed actions requiring all fingers and thumb to be expressed, as well as control over the object, should be more likely to be performed using medium stones, followed by large stones and small stones (Prediction #2). Finally, in line with previous findings about the different manual grips expressed in the SH repertoire of long-tailed macaques (cf. Pelletier et al., 2017) and in light of Newell's constraint model, which emphasizes how objects' physical properties affect the expression of actions directed to these objects, we discussed the distribution of different SH behavioral actions across stone sizes. To assess whether different SH behavioral elements are preferentially associated with specific stone sizes, we measured the relative durations of each SH behavioral element (in relation to the overall duration of SH activity) directed toward stones of different sizes.

Method

Study Population and Site

We observed a population of free-ranging, urban-dwelling, habituated and provisioned Balinese long-tailed macaques inhabiting the Sacred Monkey Forest Sanctuary in Ubud, central Bali, Indonesia. The area is forested and surrounded by human settlements and Hindu temples. In 2019, the population of long-tailed macaques living in Ubud totalled over 1000 individuals and was comprised of seven neighbouring groups with overlapping home range areas (Giraud, 2020). During the study period, the monkeys were provisioned at least three times per day with fruits and vegetables by the temple staff.

Data Collection and Study Subjects

Observations were conducted during the dry season, from May to August 2018 and 2019; between 08:00 and 17:00. SH behavior occurred in all seven groups of this primate population, and across all age and sex classes (Pelletier et al., 2017). In this study, we sampled 37 individually identified subjects, 15 females and 22 males, belonging to the same group, which counted around 200 individuals. Of the 37 sampled subjects, 13 were old juveniles (aged 2 to 3 in females and 2 to 4 in males), nine were subadults (adolescents individuals aged 3 to 4 in females and 4 to 6 in males), and 15 were adults (aged 4 or more in females, and 6 or more in males; Brotcorne et al., 2015). We selected individuals 2 years old or older because in Japanese macaques, a phylogenetically close species, within the same *fascicularis* subgenus group of *Macaca*, previous findings showed that at this age individuals already exhibit all SH behavioral elements (Nahallage & Huffman, 2007). No senile individuals were sampled, since previous findings showed that in aging individuals the complexity of the SH repertoire gradually decreases, possibly due to the degradation of their motor coordination (Nahallage & Huffman, 2007). All the SH sequences used in this study were video recorded with a digital camera (Sony Full HD Handycam Camcorder). SH sequences were collected by Camilla Cenni and two field research assistants using *ad libitum* sampling method (Altmann, 1974): the subject was filmed if performing SH, and the observation was extended for two minutes after the end of the SH activity (Huffman, 1996). Whenever possible, the subjects were filmed from the front or the side, within 3 to 5 m, and about 2 m^2 in frame, to ensure excellent visibility conditions and to obtain good quality videos.

For each subject, we collected the stones used by the monkeys to perform SH activity. To determine stone size, Camilla Cenni and two field research assistants measured the length along the longest line of the stone with the use of a caliper. Because our subjects varied in age and consequently in hand size, we used two measures to characterize stone size, (a) absolute stone length, expressed in cm and (b) relative stone size, inferred by comparing the size of the stone to the subject's palm. A *small* stone was defined as being smaller than the subject's palm of hand and characterized by a length < 3 cm ($M \pm SD$: 2.15 $\pm$ 0.47 cm, ranging from 0.70 to 2.90 cm). A *medium* stone was defined as being of similar size to the subject's palm with a length varying between 3 and 5 cm (3.99 $\pm$ 0.54 cm, ranging from 3.00 to 5.00 cm). A *large* stone was defined as being greater than the subject's palm and

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characterized by a length > 5 cm (7.92 ± 1.51 cm, ranging from 5.40 to 11.10 cm). After being collected and measured, all stones were video recorded, to allow for a later match between the stone and the corresponding SH bout.

Data Analysis and Statistics

For each of the sampled subjects, we selected three two-minute SH sequences, truncated from longer independent SH bouts (i.e., they belonged to distinct SH bouts collected on different days). Thus, a SH bout represented the display of SH activity with possible pauses for up to 120 s (Huffman, 1996; Leca et al., 2007a), whereas a SH sequence represented a truncated two-minute segment of a longer SH bout. For five subjects, two of the selected SH sequences were truncated from SH bouts collected on the same day, and for three out of these subjects, the selected SH sequences were truncated from the same SH bout, but they did not overlap in time (i.e., two SH sequences did not share any SH behavioral elements). In each of these SH sequences, the subject manipulated at least a *small* stone, a *medium* stone and a *large* stone, respectively, independent from each other: each stone was used in a single SH sequence (see three video examples of an individual manipulating a small, medium and large stone on different days in Video S1 in the online supplemental materials). Regarding the three subjects whose selected SH sequences were truncated from the same SH bout, two selected stones were present in both SH sequences. In addition, whenever possible, we ensured that the small, medium and large stones manipulated by one subject were not manipulated by another subject. In two cases, the same stone was manipulated by two subjects on two separate SH bouts recorded on the same day. Thus, in total, we selected 36 small, 37 medium, and 36 large stones. In the selected SH sequences, a subject could use more than one stone to perform SH within the same SH sequence, or the stone of interest could be combined with objects other than stones (e.g., locally available hard-shelled nuts, that are commonly manipulated but almost never consumed and usually discarded), but we only scored the SH behavioral elements directed to the selected stone (i.e., the selected small, medium and large stone, respectively). The SH behavioral elements that require at least two stones to be performed (e.g., Clack, Flint, Rub Together) were scored if the stone of interest was used together with other stones or objects to perform them. In the end, the selected SH sequences contained on average 1 min and 42 s (±25 s) of SH activity (i.e., the overall SH behavior displayed in a SH sequence) with the selected stone. SH sequences were chosen and truncated on the basis of optimal visibility conditions, to ensure that all the behavioral elements directed to the stone of interest could be reliably identified. For a SH sequence to be eligible, the stone used should be matched with the video-record available for the stone collected. If more than one SH sequence was eligible for selection, SH sequences were chosen at random, with the use of a random number generator. If a SH bout was longer than two minutes, the beginning of the truncated SH sequence was randomly selected with the use of a random time generator. In each video-recorded SH sequence, Camilla Cenni scored all the SH behavioral elements performed by the subject with the stone of interest, and used the same SH ethogram as in Pelletier and colleagues (2017) to generate event-log files (i.e., series of consecutive SH behavioral elements), by using *BORIS* software (Friard & Gamba, 2016). During the scoring process, we detected two stone-directed actions not previously described by Pelletier and colleagues (2017). Given that SH is a culturally-maintained form of object play, it is not surprising that the behavior may undergo transformation (Huffman & Quiatt, 1986; Leca et al., 2012). The two newly described SH behavioral elements were named "Push-Through" and "Slam." Operational definitions and video references of these two new SH behavioral elements can be found in Table S2 and Video S3 in the online supplemental materials. To assess reliability of video scoring, we calculated an interscorer reliability test for Camilla Cenni and Jean-Baptiste Leca when transcribing the same samples of SH video records, involving a total of 24 SH sequences (i.e., 22% of the sample; $k = 0.95$; Martin & Bateson, 1993).

To test Prediction #1, we used the "rarefaction analysis" to generate rarefaction curves, calculated through *EcoSim* software (Gotelli & Entsminger, 2001). Rarefaction analysis is a technique commonly used by ecologists to characterize the species composition of ecological samples, based on the cumulative number of individuals belonging to different species found in a sample, and to estimate the predicted number of species in a subsample of individuals (Gotelli & Colwell, 2001). By repeatedly resampling a large pool of N individuals, the expected number of species in a smaller collection of n individuals, drawn at random from N, can be generated (Simberloff, 1978). Rarefaction curves are plotted from the number of expected species found in smaller subsets, and they move from right to left, as the full dataset N increasingly rarefies. A rarefaction curve describes, on the y axis, species *versatility*, defined as the total number of different species found across a collection of individuals, providing confidence intervals that allow for statistical comparisons between samples. Rarefaction analysis has been previously used to characterize animal behavioral repertoires (Peshek & Blumstein, 2011). To apply the rarefaction analysis to estimate SH *versatility*, defined as the total number of different SH behavioral elements displayed across subjects, we treated SH behavioral elements (e.g., Bite, Pound, Wrap) within an individual's repertoire as species, and the total abundance of SH behavioral elements performed (e.g., the total number of Bite, Pound, Wrap, recorded; i.e., SH abundance) as individuals. As a result, SH *versatility* was calculated as a function of SH abundance (Figure 1). F1

We performed sample-based rarefaction analysis to compare SH *versatility* across small, medium and large stone sizes (cf. Gotelli & Colwell, 2001). A sample-based rarefaction preserves the heterogeneity that comes from comparing individuals differing in the SH *versatility* (i.e., performing a different number of SH behavioral elements than other individuals) associated to a stone size. In fact, although sample-based rarefaction computes the expected sample SH *versatility* as a function of SH abundance, it maintains the relationship between an individual's SH *versatility* and its SH abundance. Operationally, a sample-based rarefaction curve is generated by repeatedly resampling and pooling a smaller sample of individuals and computing the mean and variance for the SH *versatility* found across smaller subsets of individuals, depending on their relative SH abundance. The main function of this rarefaction analysis is that it allows for the comparison of rarefaction curves belonging to different stone sizes with different SH abundance, by calculating the expected SH *versatility* for smaller SH abundances. To do so, sample-based rarefaction curves representing SH *versatility* for different stone sizes can be compared at

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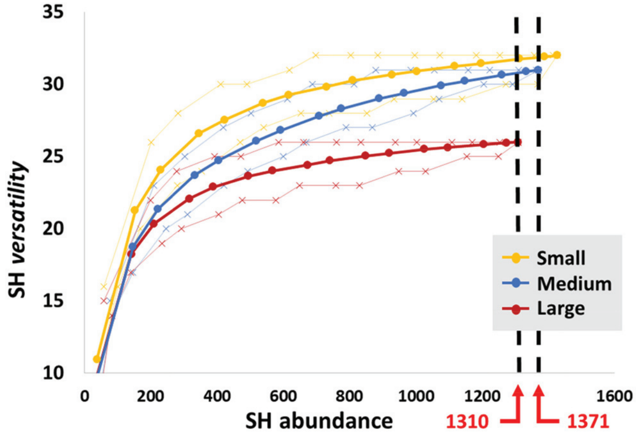
Figure 1
Rarefaction Curves for Small Stones (Solid Yellow Line), Medium Stones (Solid Blue Line), and Large Stones (Solid Red Line)



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

the maximum common abundance level available to the curves that are being compared (black dotted lines in Figure 1). Because we compared three rarefaction curves, we considered two maximum common SH abundance levels, one for the stone size associated with the smallest SH abundance (i.e., SH *versatility* associated to the curve with the smallest SH abundance was compared to SH *versatility* associated to the other two curves), and one for the stone size associated with the second smallest SH abundance (i.e., SH *versatility* associated to the curve with the second smallest SH abundance was compared to SH *versatility* associated to the curve with the highest SH abundance). At equal abundance level, the 95% confidence intervals (95% CI) allow for statistical comparisons between samples. Further details about the application of rarefaction analysis to behavioral repertoires can be found in Peshek and Blumstein (2011).

To test Prediction #2, we extracted for each subject the relative duration (i.e., in relation to the cumulative duration of SH activity) of Pound expressed with each stone size from the generated event-log files. In addition, we examined the relative duration of SH behavioral elements across stone sizes that comprised 1% or more of the overall sampled SH activity. To compare the duration of SH behavioral elements directed to stones of different sizes, we used a Friedman test with Dunn's posthoc tests for multiple pairwise comparisons and Bonferroni correction to control for type I errors (Siegel & Castellan, 1988).

Ethical Statement

This research was exclusively observational and noninvasive. 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).

Results

Rarefaction Analysis

At the maximum common SH abundance to large, medium and small stones (i.e., 1310), SH *versatility* significantly differed across stone sizes (i.e., the 95% CIs of the three rarefaction curves did not overlap). Handling small stones was associated with significantly higher SH *versatility* than handling large stones, and handling medium stones was associated with significantly higher SH *versatility* than handling large stones. Specifically, at SH abundance level = 1310; 32 different SH behavioral elements were exhibited with small stones (95% CI [30, 32]), 31 different SH behavioral elements were exhibited with medium stones (95% CI [30, 31]), and 26 different SH behavioral elements were exhibited with large stones (95% CI [26, 26]; Figure 1). At the maximum common SH abundance to medium and small stones (i.e., 1371), SH *versatility* did not significantly differ between small stones and medium stones. Handling small stones was associated, on average, with higher SH *versatility* than handling medium stones, but the difference was not statistically significant. Specifically, at SH abundance level = 1371; 32 different SH behavioral elements were exhibited with small stones (95% CI [30, 32]), and 31 different SH behavioral elements were exhibited with medium stones (95% CI [31, 31]; Figure 1). Therefore, SH *versatility* was significantly higher for medium and small stones than for large stones; Prediction #1 was partly supported.

Duration of SH Behavioral Elements

We found a statistically significant difference in the duration of Pound across stone sizes (χ^2 (2, $N = 37$) = 16.88, $p < .001$). Pound lasted longer when handling medium stones than when handling large stones ($z = -0.65$, $p = .005$). As expected, Pound lasted on average longer when handling medium stones than when handling small stones, but the difference was not statistically significant ($z = 0.00$, $p = 1.000$). Contrary to what we expected, Pound lasted longer when handling small stones than when handling large stones ($z = -0.65$, $p = .005$). The relative duration of Pound when handling small, medium and large stones constituted 6.72% (±10.85), 9.11% (±14.83), and 1.78% (±4.03) of the cumulative SH activity, respectively. Prediction #2 was partly supported.

Across stone sizes, we found statistically significant differences in the duration of some SH behavioral elements. In Table 1, we T1
reported the statistics of the Friedman's test and the posthoc pairwise comparisons of all SH behavioral elements that comprised 1% or more of the overall sampled SH activity across stone sizes. When handling different stone sizes, durations of SH behavioral elements differed for Cuddle, Hold, Roll, and Rub. Cuddle lasted longer when handling large stones than when handling small and medium stones. Hold lasted longer when handling small stones than when handling medium and large stones. Roll lasted longer when handling small stones than when handling medium and large stones. Rub lasted longer when handling medium and large stones than when handling small stones.

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Table 1

Friedman's Test χ^2 *and Dunn's Post Hoc Tests z for Multiple Pairwise Comparisons for the Duration of SH Behavioral Elements Across Stone Sizes and p Values, and Average Percentages* μ (± *SD*) *of SH Duration Within the Three Stone Size Categories*

SH behavioral element	Small vs medium vs large		Small vs medium		Small vs large		Medium vs large		Small	Medium	Large
	χ^2 (2, N = 37)	p value α = 0.003	z	p value α = 0.017	z	p value α = 0.017	z	p value α = 0.017	μ (± *SD*)	μ (± *SD*)	μ (± *SD*)
Bite	0.30	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	4.99% (± 9.00)	4.27% (± 9.11)	2.54% (± 4.17)
Carry	5.31	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	1.29% (± 2.76)	0.83% (± 1.85)	2.67% (± 5.89)
Cover	5.96	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	3.03% (± 4.64)	5.36% (± 5.47)	4.60% (± 4.39)
Cuddle	**23.19**	**< .001**	−0.08	n.s.	−0.65	**.005**	−0.57	**.015**	0.24% (± 1.44)	0.43% (± 1.57)	2.86% (± 5.78)
Gather	6.47	n.s.	−0.50	n.s.	−0.51	n.s.	−0.01	n.s.	6.81% (± 8.12)	2.52% (± 2.73)	3.45% (± 3.45)
Grasp	6.05	n.s.	−0.43	n.s.	−0.54	n.s.	−0.11	n.s.	17.47% (± 10.32)	29.20% (± 19.87)	33.46% (± 22.74)
Grasp-Walk	9.84	n.s.	−0.11	n.s.	−0.50	n.s.	−0.39	n.s.	2.79% (± 4.68)	1.72% (± 3.03)	0.30% (± 1.13)
Groom	1.94	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	2.26% (± 4.94)	2.29% (± 3.90)	4.00% (± 7.67)
Hold	**25.81**	**< .001**	−0.62	**.008**	−1.12	**< .001**	−0.50	n.s.	8.40% (± 7.88)	3.60% (± 4.62)	1.28% (± 2.37)
Pound	**16.88**	**< .001**	0.00	n.s.	−0.65	**.005**	−0.65	**.005**	6.72% (± 10.85)	9.11% (± 14.83)	1.78% (± 4.03)
Pound-Drag	3.29	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.40% (± 1.29)	2.03% (± 7.34)	1.03% (± 4.76)
Roll	**20.72**	**< .001**	−0.92	**< .001**	−0.70	**.003**	−0.22	n.s.	16.79% (± 19.33)	3.98% (± 8.96)	4.76% (± 8.58)
Roll with fingers	6.32	n.s.	−0.26	n.s.	−0.43	n.s.	−0.18	n.s.	2.66% (± 4.16)	2.13% (± 9.28)	0.66% (± 2.00)
Rub	**23.19**	**< .001**	−0.92	**< .001**	−0.91	**< .001**	−0.01	n.s.	5.24% (± 9.24)	19.47% (± 17.86)	20.42% (± 21.66)
Scatter	2.70	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	2.68% (± 6.06)	2.56% (± 5.18)	2.84% (± 3.36)
Slap	2.18	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	1.06% (± 1.67)	0.78% (± 1.35)	1.73% (± 3.45)
Tap	3.43	n.s.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	2.62% (± 6.83)	0.83% (± 1.50)	5.56% (± 14.14)
Wrap	8.03	n.s.	−0.34	n.s.	−0.14	n.s.	−0.47	n.s.	2.87% (± 5.81)	3.40% (± 5.13)	1.43% (± 3.55)

AQ: 12 *Note.* SH = stone handling; α = Bonferroni adjusted-*p*-value. n.s. = not statistically significant; n.a. = not applicable. Boldface indicates statistically significant results.

Discussion

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

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

Our results are in line with Newell's constraint model, which emphasizes the role of task constraints, such as the size of the

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

It is noteworthy that we did not find a statistically significant difference between medium and small stones in the expression of pounding actions, although on average medium stones were associated with longer Pound in relation to cumulative SH activity than small stones. In line with Newell's constraint model, only a few grip configurations (and therefore, actions) are commonly used toward specific objects differing in sizes, even though theoretically those objects could still be grasped and manipulated via a wider range of grip configurations (cf. Cesari & Newell, 1999; Newell et al., 1989). Thus, actions that generally require specific grip configurations to be expressed, such as Pound, may be performed using behavioral variants that are macrostructurally similar (i.e., the trajectory of the action is maintained, but a different grip configuration is adopted) and therefore qualify as the same SH behavioral element; however more data are needed to test this possibility. Furthermore, the potential variability of actions ("motor abundance"; Latash, 2000, 2012) associated with different objects is likely higher in object play than in tool use, which may favor the maintenance of a reservoir of solutions upon which selection can act to shape and refine functional responses to environmental problems (Bateson, 2014; Bruner, 1972). The relaxed selective pressures under which object play is expressed (Burghardt, 2005); together with the anthropogenic influences acting on this population of long-tailed macaques (i.e., food provisioning), may maintain a pool of playful actions directed toward stones of different physical characteristics (i.e., size, weight, texture) that could be coopted into stone tool use (cf. Huffman & Quiatt, 1986; Leca et al., 2007b; Leca, Gunst, et al., 2008; Leca, Nahallage, et al., 2008). In this view, the perception of relevant physical properties of stones by individuals during playful manipulation may later facilitate the functional use of stones during the expression of instrumental object-mediated actions, such as tool-assisted masturbation, a form of stone tool use documented in the long-tailed macaque population living in Ubud (Cenni et al., 2020), but more data are needed to test this prediction.

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

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

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

Fox et al., 1999). Therefore, understanding the interface between the expression of playful and instrumental object-directed actions and the role of affordances mediated by objects in their performance is essential to appreciate the emergence of flexible tool use solutions, lithic culture and primate intelligence.

References

Allison, M. L., Reed, R., Michels, E., & Boogert, N. J. (2020). The drivers and functions of rock juggling in otters. *Royal Society Open Science*, *7*(5), 200141. https://doi.org/10.1098/rsos.200141

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3), 227–267. https://doi.org/10.1163/156853974X00534

Bateson, P. (2014). Play, playfulness, creativity and innovation. *Animal Behavior and Cognition*, *1*(2), 99–112. https://doi.org/10.12966/abc.05.02.2014

Bourgeois, K. S., Khawar, A. W., Neal, A. S., & Lockman, J. J. (2005). Infant manual exploration of objects, surfaces, and their interrelations. *Infancy*, *8*(3), 233–252. https://doi.org/10.1207/s15327078in0803_3

Brotcorne, F., Fuentes, A., Wandia, I. N., Beudels-Jamar, R. C., & Huynen, M. C. (2015). Changes in activity patterns and intergroup relationships after a significant mortality event in commensal long-tailed macaques (Macaca fascicularis) in Bali, Indonesia. *International Journal of Primatology*, *36*(3), 548–566. https://doi.org/10.1007/s10764-015-9841-5 AQ: 3

Bruner, J. S. (1972). Nature and uses of immaturity. *American Psychologist*, *27*(8), 687–708. https://doi.org/10.1037/h0033144

Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. Bradford Books (MIT Press). https://doi.org/10.7551/mitpress/3229.001.0001

Cenni, C., & Leca, J.-B. (2020a). Technical intelligence hypothesis. In J. Vonk & T. Shettleworth (Eds.), *Encyclopedia of animal cognition and behavior*. Springer. https://doi.org/10.1007/978-3-319-47829-6_103-1 AQ: 5

Cenni, C., & Leca, J.-B. (2020b). Tool use. In J. Vonk & T. Shettleworth (Eds.), *Encyclopedia of animal cognition and behavior*. Springer. https://doi.org/10.1007/978-3-319-47829-6_1541-1 AQ: 4

Cenni, C., Casarrubea, M., Gunst, N., Vasey, P. L., Pellis, S. M., Wandia, I. N., & Leca, J.-B. (2020). Inferring tool use behavior patterns from the temporal structure of object play sequences in a non-human primate species. *Physiology & Behavior*, *222*, 112938. https://doi.org/10.1016/j.physbeh.2020.112938 AQ: 6

Cesari, P., & Newell, K. M. (1999). The scaling of human grip configurations. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 927–935. https://doi.org/10.1037/0096-1523.25.4.927

Fontenelle, S. A., Alexander Kahrs, B., Ashley Neal, S., Taylor Newton, A., & Lockman, J. J. (2007). Infant manual exploration of composite substrates. *Journal of Experimental Child Psychology*, *98*(3), 153–167. https://doi.org/10.1016/j.jecp.2007.07.001

Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The mentality of gorillas and orangutans* (pp. 99–116). Cambridge University Press. https://doi.org/10.1017/CBO9780511542305.005

Fragaszy, D. M., & Visalberghi, E. (1989). Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (Cebus apella). *Journal of Comparative Psychology*, *103*(2), 159–170. https://doi.org/10.1037/0735-7036.103.2.159

Fragaszy, D. M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Visalberghi, E. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *368*(1630), 20120410. https://doi.org/10.1098/rstb.2012.0410

Fragaszy, D. M., Greenberg, R., Visalberghi, E., Ottoni, E. B., Izar, P., & Liu, Q. (2010). How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Animal Behaviour*, *80*(2), 205–214. https://doi.org/10.1016/j.anbehav.2010.04.018

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

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

Giraud, G. (2020). *Potential side-effects of sterilization on socio-ecology of female long-tailed macaques (Macaca fascicularis) in Bali (Indonesia)*. Progress Report, RISTEK—Ministry of Research and Technology of the Republic of Indonesia.

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*(4), 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x AQ: 7

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

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*(7), 594–608. https://doi.org/10.1002/ajp.20694

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

Hiscock, P. (2014). Learning in lithic landscapes: A reconsideration of the hominid "toolmaking" niche. *Biological Theory*, *9*(1), 27–41. https://doi.org/10.1007/s13752-013-0158-3 AQ: 8

Huffman, M. A. (1984). Stone-play of Macaca fuscata in Arashiyama B troop: Transmission of a non-adaptive behavior. *Journal of Human Evolution*, *13*(8), 725–735. https://doi.org/10.1016/S0047-2484(84)80022-6

Huffman, M. A. (1996). Acquisition of innovative cultural behaviors in nonhuman 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). Academic Press. https://doi.org/10.1016/B978-012273965-1/50014-5

Huffman, M. A., & Quiatt, D. (1986). Stone handling by Japanese macaques (Macaca fuscata): Implications for tool use of stone. *Primates*, *27*(4), 413–423. https://doi.org/10.1007/BF02381887

Kenward, B., Rutz, C., Weir, A. A. S., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour*, *72*(6), 1329–1343. https://doi.org/10.1016/j.anbehav.2006.04.007

Latash, M. (2000). There is no motor redundancy in human movements. There is motor abundance. *Motor Control*, *4*(3), 259–260. https://doi.org/10.1123/mcj.4.3.259

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

Leca, J.-B., Gunst, N., & Huffman, M. A. (2007a). Age-related differences in the performance, diffusion, and maintenance of stone handling, a behavioral tradition in Japanese macaques. *Journal of Human Evolution*, *53*(6), 691–708. https://doi.org/10.1016/j.jhevol.2007.05.009

Leca, J.-B., Gunst, N., & Huffman, M. A. (2007b). Japanese macaque cultures: Inter- and intra-troop behavioural variability of stone handling patterns across 10 troops. *Behaviour*, *144*(3), 251–281. https://doi.org/10.1163/156853907780425712

Leca, J.-B., Gunst, N., & Huffman, M. A. (2008). Food provisioning and stone handling tradition in Japanese macaques: A comparative study of ten troops. *American Journal of Primatology*, *70*(8), 803–813. https://doi.org/10.1002/ajp.20551

Leca, J.-B., Gunst, N., & Huffman, M. A. (2010a). Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, Macaca fuscata. *Animal Behaviour*, *79*(1), 117–126. https://doi.org/10.1016/j.anbehav.2009.09.035

Leca, J.-B., Gunst, N., & Huffman, M. A. (2010b). Principles and levels of laterality in unimanual and bimanual stone handling patterns by Japanese macaques. *Journal of Human Evolution*, *58*(2), 155–165. https://doi.org/10.1016/j.jhevol.2009.09.005

Leca, J.-B., Gunst, N., & Huffman, M. (2011). Complexity in object manipulation by Japanese macaques (Macaca fuscata): A cross-sectional analysis of manual coordination in stone handling patterns. *Journal of Comparative Psychology*, *125*(1), 61–71. https://doi.org/10.1037/a0020868

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

Leca, J.-B., Nahallage, C. A. D., Gunst, N., & Huffman, M. A. (2008). Stone-throwing by Japanese macaques: Form and functional aspects of a group-specific behavioral tradition. *Journal of Human Evolution*, *55*(6), 989–998. https://doi.org/10.1016/j.jhevol.2008.06.004

Lockman, J. J. (2000). A perception—Action perspective on tool use development. *Child Development*, *71*(1), 137–144. https://doi.org/10.1111/1467-8624.00127

Lonsdorf, E. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, Pan troglodytes schweinfurthii, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683. https://doi.org/10.1016/j.anbehav.2004.12.014

Martin, P., & Bateson, P. P. G. (1993). *Measuring behaviour: An introductory guide*. Cambridge University Press. https://doi.org/10.1017/CBO9781139168342

Nahallage, C. A. D., & Huffman, M. A. (2007). Acquisition and development of stone handling behavior in infant Japanese macaques. *Behaviour*, *144*(10), 1193–1215. https://doi.org/10.1163/156853907781890959

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*(6-7), 845–869. https://doi.org/10.1163/1568539X-00003361

Napier, J. R. (1956). The prehensile movements of the human hand. *The Journal of Bone and Joint Surgery*, *38-B*(4), 902–913. https://doi.org/10.1302/0301-620X.38B4.902

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

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

Newell, K. M., McDonald, P. V., & Baillargeon, R. (1993). Body scale and infant grip configurations. *Developmental Psychobiology*, *26*(4), 195–205. https://doi.org/10.1002/dev.420260403

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

Palmer, C. F. (1989). The discrimination nature of infants: Exploratory actions. *Developmental Psychology*, *25*(6), 885–893. https://doi.org/10.1037/0012-1649.25.6.885

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

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

Peshek, K. R., & Blumstein, D. T. (2011). Can rarefaction be used to estimate song repertoire size in birds? *Current Zoology*, *57*(3), 300–306. https://doi.org/10.1093/czoolo/57.3.300

Pouydebat, E., Gorce, P., Coppens, Y., & Bels, V. (2009). Biomechanical study of grasping according to the volume of the object: Human versus non-human primates. *Journal of Biomechanics*, *42*(3), 266–272. https://doi.org/10.1016/j.jbiomech.2008.10.026

Randerath, J., Goldenberg, G., Spijkers, W., Li, Y., & Hermsdörfer, J. (2011). From pantomime to actual use: How affordances can facilitate actual tool-use. *Neuropsychologia*, *49*(9), 2410–2416. https://doi.org/10.1016/j.neuropsychologia.2011.04.017 AQ: 13

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

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

Simberloff, D. (1978). Use of rarefaction and related methods in ecology. In K. L. Dickson, J. Cairns Jr., & R. J. Livingston (Eds.). *Biological data in water pollution assessment: Quantitative and statistical analyses* (pp. 150–165). American Society for Testing and Materials. https://doi.org/10.1520/STP35663S

Sirianni, G., Wittig, R. M., Gratton, P., Mundry, R., Schüler, A., & Boesch, C. (2018). Do chimpanzees anticipate an object's weight? A field experiment on the kinematics of hammer-lifting movements in the nut-cracking Taï chimpanzees. *Animal Cognition*, *21*(1), 109–118. https://doi.org/10.1007/s10071-017-1144-0 AQ: 10

Stephens, J., & Krebs, D. (1986). *Foraging theory*. Princeton University Press.

Torigoe, T. (1987). Further report on object manipulation in non-human primates: A comparison within 13 species of the genus Macaca. *Primates*, *28*(4), 533–538. https://doi.org/10.1007/BF02380867 AQ: 11

van Elk, M., van Schie, H. T., & Bekkering, H. (2009). Action semantic knowledge about objects is supported by functional motor activation. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(4), 1118–1128. https://doi.org/10.1037/a0015024

Zou, H., Liu, M., Luan, Y., Xie, Q., Cheng, Z., Zhao, G., Jin, M., Guo, N., Jin, G. J., & Yu, L. (2017). Pattern of novel object exploration in cynomolgus monkey *Macaca fascicularis*. *Journal of Medical Primatology*, *46*(2), 19–24. https://doi.org/10.1111/jmp.12251

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AQ11—Author: Please provide issue number.

AQ12—Author: Please explain the use of boldface in Table 1.

AQ13—Author: Randerath et al. 2011:is not cited in your text. Please cite the text or delete the references.

AQ14—Author: Zou and colleagues (2017): is not cited in your text. Please check.

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