Nut-cracking behaviour in wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference, hand grips and efficiency

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Short title: Nut-cracking in wild-born, rehabilitated bonobos (*Pan paniscus*)

Abstract

There has been an enduring interest in primate tool-use and manipulative abilities, most often with the goal of providing insight into the evolution of human manual dexterity, right-hand preference, and what behaviours make humans unique. Chimpanzees (*Pan troglodytes*) are arguably the most well-studied tool-users among non-human primates, and are particularly well-known for their complex nut-cracking behaviour, which has been documented in several West African populations. However, their sister-taxon, the bonobos (*Pan paniscus*), rarely engage in even simple tool-use and are not known to nut-crack in the wild. Only a few studies have reported tool-use in captive bonobos, including their ability to crack nuts, but details of this complex tool-use behaviour have not been documented before. Here, we fill this gap with the first comprehensive analysis of bonobo nut-cracking in a natural environment at the Lola ya Bonobo sanctuary, Democratic Republic of the Congo. Eighteen bonobos were studied as they cracked oil palm nuts using stone hammers. Individual bonobos showed exclusive laterality for using the hammerstone and there was a significant group-level right-hand bias. The study revealed 15 hand grips for holding differently sized and weighted hammerstones, 10 of which had not been previously described in the literature. Our findings also demonstrated that bonobos select the most effective hammerstones when nut-cracking. Bonobos are efficient nut-crackers and not that different from the renowned nut-cracking chimpanzees of Bossou, Guinea, which also crack oil palm nuts using stones.

Key words: manual dexterity; hand grips; laterality; nut-cracking; tool-use

Introduction

Tool use and the selective manipulation of objects are widespread across the animal kingdom [Beck, 1980; Bentley-Condit and Smith, 2010] but only a few species of primates use a variety of tools for multiple purposes and show a wide range of different manipulative behaviours in the wild. Wild bearded capuchins and long-tailed macaques are well-known for their regular tool-use, involving highly controlled sequences of percussive actions [e.g., Spagnoletti et al., 2011; Gumert and Malaivijitnond, 2013; Visalberghi et al., 2015]. Orangutans and, to a lesser extent, western lowland gorillas also have been reported to use tools in the wild [Breuer et al., 2005; Meulman and Van Schaik, 2013]. However, among primates, chimpanzees are commonly regarded as the most skilled tool-users in the wild [McGrew, 1992] and their tool-use skills have been studied extensively since the 1960s [e.g., Goodall, 1964; Sugiyama, 1981; Boesch and Boesch, 1983; Inoue-Nakamura and Matsuzawa, 1997; Sanz and Morgan, 2013]. Chimpanzees are particularly well-known for their nut-cracking tool-use behaviour, with different populations across West Africa using a variety of methods and materials (e.g. wood vs. stone hammers) [e.g., Boesch and Boesch, 1983; Hanna and McGrew, 1987; Biro et al., 2006].

In contrast to the relatively ubiquitous and culturally diverse tool-use behaviours of wild chimpanzees (*Pan troglodytes*), it is particularly interesting that their sister taxon, the bonobos (*Pan paniscus*), rarely use tools in the wild. Only a few observations of bonobo tool use have been made in the wild [e.g., Kano, 1982; Ingmanson, 1996; Hashimoto et al., 1998; Hohmann and Fruth, 2003] and most of these are rarely-documented instances of simple and occasional tool-use actions [Hohmann and Fruth, 2003; Furuichi et al., 2014]. Unlike their chimpanzee cousins, nut-cracking, the most complex primate tool-use behaviour [Matsuzawa, 1994] ever recorded in the wild, has to date never been reported among wild bonobos. The simple tool-use actions in wild bonobos such as dragging branches, aimed stick throwing, leaf sponging or the use of leafy twigs to shield from rain [Kano, 1982; Hohmann and Fruth, 2003; Furuichi et al, 2014], involve the use of one hand rather than two hands [MacNeilage et al., 1987; Hopkins, 1995], few sequential stages to realize the task [Marchant and McGrew, 1991] and a low level of precision of the required motor acts [e.g., Morris et al., 1993]. In contrast, the nut-cracking behaviour in wild chimpanzees requires precise role-differentiated manipulation by both hands [Kano, 1982; Humle, 2003; Biro et al., 2006], the interface of three external objects (hammer, anvil and nut) at the same time, and a high level of motor control and cognitive ability [Matsuzawa, 1994].

Despite the general absence of tool-use in the wild, bonobos in captivity demonstrate an equally diverse and highly complex repertoire of tool-use behaviours compared with captive chimpanzees [Jordan, 1982; Takeshita and Walraven, 1996; Gruber et al., 2010; Roffman et al., 2015]. The bonobo "Kanzi" is the best example illustrating this species' capability to develop highly skilled tool-making and tool-using behaviours [e.g., Toth et al., 1993]. Kanzi is able to produce stone flakes and selectively choose tools that are more useful than others [Schick et al., 1999]. These findings suggest that bonobos have the same understanding of the functional properties of tools as other great apes [Hermann et al., 2008] and a cognitive ability for tool-related behaviours [Jordan, 1982; Gruber et al., 2010]. Gruber et al. (2010) reported the nut-cracking ability in the bonobos of Lola ya Bonobo sanctuary, but details of this complex tool-use behaviour have not yet been documented. In addition, their shared hand and upper limb anatomy with chimpanzees [Susman, 1979; Diogo and Wood, 2011] suggests that bonobos have the same physical capability to perform equivalent manipulative tasks as seen in chimpanzees.

Several hypotheses have been put forth, such as variation in ecological constraints [Furuichi et al., 2014] or inherent differences between the species [Koops et al., 2015], which might explain the relative rarity of tool-use in wild bonobos. Alternatively, tool-use may be more common among bonobos but due to their small numbers in the wild and the limited number of habituated groups compared with chimpanzees, primatologists simply may not have yet witnessed their full tool-use repertoire. For example, data for chimpanzees comes from several field sites [Whiten et al., 2001], whereas long-term studies of bonobos are restricted to two populations (Wamba and Lomako, DRC) and the number of individuals observed at both sites is relatively small (i.e., < 25 individuals) [Hashimoto et al., 1998; Hohmann and Fruth, 2003]. Moreover, some chimpanzee groups rarely use tools in the wild [Reynolds, 2005; Watts, 2008]. Thus, the lack of data on bonobos may exaggerate their reported differences with chimpanzees. Nevertheless, the relative rarity of simple tool-use and the absence of complex tool-use in wild bonobos are in stark contrast to the well-documented and frequent complex tool-use observed among captive and wild chimpanzees [e.g., Boesch and Boesch, 1983, 1993; Biro et al., 2006; Hirata et al., 2008; Schrauf et al., 2012].

Many studies of primate tool-use and manipulative abilities aim to provide insights into the evolution of human manipulation, human hand-preference, and what gripping abilities make humans unique compared with other primates. Of the non-human primates that have been studied, most show dominant use of one hand at an individual-level for specific tasks [e.g., Collel et al., 1995; McGrew and Marchant, 1997; Papademetriou et al., 2005; Cashmore et al., 2008]. A group-level bias has been occasionally reported in some non-human primate populations [e.g., Corps & Byrne, 2004; Spinozzi et al., 2004; Vauclair et al., 2005; Hopkins et al., 2007], but none has ever demonstrated species-wide consistency in hand-preference (i.e. ~90% right-handed) typical of humans [e.g., Annett, 1972; Raymond and Pontier, 2004; McManus, 2009]. Hand preference or laterality has been investigated in bonobos but almost exclusively in captive groups, and primarily involving unnatural objects and simple tasks such as reaching for food, gesturing or scratching [e.g., De Vleeschouwer et al., 1995; Hopkins and de Waal, 1995; Colell et al., 1995; Harrison and Nystrom, 2008]. In all of these studies, most bonobo individuals were non-lateralized (i.e., used both hands interchangeably) for most of the actions studied. However, task complexity has been shown to be an important factor influencing manual laterality in primates [McGrew and Marchant, 1997a, 1999]. The nut-cracking behaviour of chimpanzees is a particularly good example of a complex manual behaviour as the chimpanzee individuals exhibit more pronounced laterality of the dominant hand compared with simple unimanual tasks [Boesch, 1991; Sugiyama et al., 1993; Humle and Matsuzawa, 2009]. Similar findings have been made for other tool use actions in wild chimpanzees or captive capuchin monkeys [Westergaard et al., 1998; McGrew and Marchant, 1997b; McGrew et al., 1999; Londsdorf and Hopkins, 2005]. When bonobos are faced with artificial complex bimanual manipulative tasks, they show strong laterality at an individual-level but not at a group-level or population-level [Chapelain et al., 2011; Hopkins et al. 2011; Bardo et al., 2015]. However, apart from these few studies, there are no published data on laterality during a natural complex bimanual task performance in bonobos.

Similarly little is known about the diversity of hand grips used by bonobos, especially when manipulating natural objects. Studies of bonobo (and chimpanzee) hand grips are done almost exclusively in captivity [Christel, 1993; Marzke and Wullstein, 1996; Christel et al., 1998; Pouydebat et al., 2011]. These studies show that they are capable of precision grasping between the thumb and finger(s). However, because of their shorter thumb and smaller musculature [Marzke et al., 1999] they are generally considered to not be able to perform these grips as forcefully as humans [Marzke, 1997, 2013]. Nevertheless, a recent study of wild chimpanzees suggests the use of forceful precision pinch grips - an ability traditional thought to be unique to humans [Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke et al., 1998] - during food-processing [Marzke et al., 2015]. Long-tailed macaques show a similar ability during stone tool-use [Gumert and Malaivijitnond, 2009], suggesting more research on primate manipulative abilities is needed particularly in natural environments.

Here, we present the first detailed analysis of bonobo cracking oil palm nuts with stone hammers in the Lola ya Bonobo sanctuary, which is in a natural environment in the Democratic Republic of the Congo. The bonobos are known to show nut-cracking behaviour since the first nursery sanctuary was established in 1995. The rescued, wild-born bonobos are integrated into a social group where they can observe nut-cracking behaviour of more experienced individuals. The infants born there have ample opportunity to observe their mothers. This sanctuary population offers a unique opportunity to investigate a natural complex tool-use behaviour in bonobos and how this behaviour compares to the pervasive nut-cracking behaviour practiced by wild chimpanzees.

The aims of this study were to (1) investigate bonobo hand-preference (i.e., laterality) during a complex tool-use behaviour, (2) identify the full range of hand grips during nut-cracking using various hammer stone weights, shapes, thicknesses and sizes, and (3) analyse the efficiency of bonobo nut-cracking relative to a chimpanzee population (Bossou, Guinea) using similar materials (i.e., oil palm nuts and stone hammers). Based on shared anatomy and results from studies in captivity, we predicted that bonobos would use a similar diversity of hand grips as documented during complex manipulative tasks in chimpanzees. However, given that wild populations of bonobos are not known to nut-crack and since this behaviour was only recently shown and disseminated among adult members of the first nursery sanctuary in 1995, we predicted that they would be less efficient (i.e., require more hits to crack a nut, crack fewer nuts per minute) than their wild chimpanzee counterparts.

Methods

Species and study site

Lola ya Bonobo is a sanctuary, founded in 1995, for orphan bonobos rescued from the bush meat and pet trade. Unlike in zoos, the sanctuary enclosures include a natural and complex environment, including high canopy forest areas with oil palm trees, swampy areas, freshwater ponds or river streams. The social groups are divided into three enclosures, which include a semi-natural forested environment in which the bonobos are allowed to range freely throughout the day. All three enclosures allow for nut-cracking behaviour of oil-palm nuts (*Elaeis guineensis*) and the bonobos can be heard nut-cracking regularly in the forest. Nut-cracking in the open non-forested areas (i.e.: near the sanctuary housing and feeding areas) is facilitated by the placement of anvil stones by humans that are embedded in the ground. Palm oil nuts attached to their branches were supplied by humans in the non-forested areas every morning, but there is also natural supply in forest enclosure. Hammerstones of different sizes and shapes (see below) were placed near the anvils and individuals were free to engage in nut-cracking when and as they wished.

Data collection

Data were collected at the 'Lola ya Bonobo' sanctuary in Kinshasa (DRC) during April and May 2015. The research protocols reported in this manuscript were reviewed and approved by the 'Les Amis des Bonobos du Congo' Scientific Committee and its Scientific Coordinator and by the Ethics Committee of the School of Anthropology and Conservation at the University of Kent, UK. The methods used in this research adhered to the American Society of Primatologists principles for the ethical treatment of primates. High-definition video was recorded *ad libitum* at close range from multiple angles during nut-cracking on a sample of 18 individuals across all three bonobo groups, including 12 females and 6 males; 14 adults (>10 years old) and 4 adolescents (7-9 years old) [Badrian and Badrian, 1984]. Nut-cracking behaviour for any given individual was divided into 'sessions' and 'bouts'. Hand use and grip patterns for holding stone tools were recorded and analyzed for bouts. A 'session' was defined as a period in which one individual was engaged in nut-cracking. A session was considered continuous when the nut jumped away and was immediately picked up again; when the nut was changed; the stone broke apart and cracking continued with the same but smaller stone; or another individual interrupted shortly for sexual behaviour (a common occurrence in bonobos). In all of these instances, the individual did not leave the anvil site. A session was terminated when the individual stopped and walked away from the anvil, starting a new behaviour. A session was generally composed of multiple bouts. Hand use and grip patterns for holding stone tools were recorded and analyzed for bouts. A 'bout' was defined as a continued period of nut-cracking behaviour, in which the hand used did not change (regardless of the number of hits) [Humle and Matsuzawa, 2009]. A bout was considered terminated if there was a change in the hand(s) used (left vs. right), both hands vs. one hand/one foot, grip type, body posture, or when the nut was successfully or unsuccessfully cracked, or when nut-cracking was interrupted by another behaviour. Video data were analysed using The Observer XT12 (© Noldus Information Technology) to code hand-preference, hand grips and number of hits, frame by frame.

Hand preference

Similar to other studies, we considered the hand used for hammering to be the dominant hand for which aspects of hand use were recorded [Boesch, 1991; Humle, 2003]. Hand-preference or laterality was recorded for bouts to ensure independence of data points [e.g., McGrew and Marchant, 1997; Humle and Matsuzawa, 2009; Chapelain et al., 2011]. Only individuals for whom a minimum of 10 bouts or more were recorded were included in the analysis [Humle and Matsuzawa, 2009]. We consequently investigated laterality in 15 individuals with a total number of 609 bouts. Laterality was investigated as the relative frequency of right (R) vs. left (L) hand use within and across individuals (H0: $pR = pL$ vs. H1: $pR \neq pL$). We used a binominal test for proportions to test the null hypothesis of a 50/50 distribution (H0: $pR = pL$). We further tested the probability of success for the two proportions (R vs. L) in a Bernoulli trial (significance set at $p= 0.05$). We calculated a handedness index (HI) score ranging from -1 to +1 for each individual based on the total number of bouts: $HI=(R–L)/(R+L)$ [Humle and Matsuzawa, 2009; Chapelain et al., 2011]. Negative values indicate a left hand bias and positive values indicate a right-hand bias. We further calculated the relative frequency of bouts using both hands (bimanual) and one-hand/one-foot in addition to the one handed hammering strategy. In addition, we explored whether right-hand or left-hand use has an effect on the efficiency of nut-cracking (number of hits per nut, nut-per-minute variable) [Boesch, 1991] via a stepwise regression test. For the model presented here, we excluded age and sex as these factors had no effect.

Grip patterns when using hammerstones

Classification of hand grip types

We investigated hand grips used to hold the hammerstone during nut-cracking in all 18 individuals. Different grips were first categorized broadly into palm (power) and precision grips [Napier, 1980; Marzke and Wullstein, 1996] and then into more detailed classification schemes with more specific focus on precision pinching such as the human three-jaw chuck 'baseball grip' and cradle grip [Marzke, 2003], and grip repertoire that have been identified in both wild and captive bonobos, chimpanzees, macaques and/or capuchin monkeys [Costello and Fragaszy, 1988; Christel, 1993, 1998; Boesch and Boesch, 1993; Jones-Engel and Bard, 1996; Marzke and Wullstein, 1996; Spinozzi et al., 2004; Pouydebat et al., 2009; Gumert and Malaivijitnond, 2009; Macfarlane, 2009; Marzke et al., 2015]. Our initial categorization centred on precision pinch, precision/passive palm, and power grips that have been previously identified in both wild and captive bonobos and chimpanzees. We further described how the thumb and fingers were used to grip hammerstones and how different grips related to the size, weight, shape and thickness of the hammerstone (see Results, Table 1).

Measurements and categorization of hammerstones

A total of 28 potential hammerstones were placed next to the anvils of the enclosure. The maximum width (6cm - 25cm), maximum length (7cm – 30cm) and weight (0.10-4.48kg) were measured and the general shape (e.g. oval, triangular) was recorded. Stone weight was categorized as light (0.10-0.38kg), moderate (0.45-1.24kg) and heavy (1.38-4.48kg). An additional eight stones that the bonobo individuals had collected themselves from the forest were also used as hammerstones. Size and weight could only be inferred for these hammerstones. Stone size was categorized relative to the individual's hand size: small, when '-smaller than the size of the palm-' (i.e. small width; short length); medium, when roughly the size of the palm (i.e. moderate width; moderate length) and large, when '-larger than the palm and fingers-' (i.e. large width; long length). Stone shape (e.g., oval, rectangular) and thickness (narrow, medium, thick) were estimated and categorised by visual inspection. Patterns were compared across individuals using the same and different stones.

Analysis of hand grips and hammerstones

In our first analysis, we investigated the individual preference for specific hand grips used for 625 bouts and the diversity of grips across 18 bonobos. We recorded the use of each hand grip within a bout (as a bout is defined as the use of one grip only) for each individual and calculated the relative frequencies [Marzke et al., 2015]. A stepwise regression analysis was used to test how the stone characteristics influenced the choice of a grip type for each individual. Since the grip types used to hold a stone were categorical, we needed to estimate the parameter of these regression models using a multinomial logistic regression. In this model, the probability of observing a particular hand grip was transformed using the logit function. Both the quantities of deviance and the Akaike information criteria (AIC) were used as indicators of how well the proposed regression model fits the data. A good model displayed a small deviance and AIC value.

Nut-cracking efficiency

Following previous studies, we calculated three measures of efficiency during episodes of nut-cracking for each stone per individual: (1) Hits per nut: average number of hits required per successfully cracked nut [Boesch and Boesch, 1981]; (2) Nuts per minute: number of nuts (includes empty nuts and nuts yielding an edible kernel) cracked per minute [Boesch and Boesch, 1981]; (3) Success rate: number of nuts yielding an edible kernel cracked per minute [Humle, 2003]. We only considered sessions with a minimum of one minute duration of nut-cracking [Humle, 2003; Boesch and Boesch, 1981]. Thus, we analyzed a sample of 41 sessions and 30 different stones across 16 individuals. In our first analysis we investigated the potential influence of several factors on the efficiency of nut-cracking in bonobos: (1) the dependency of stone size (width, length), weight, shape and thickness on the average number of hits and (2) the influence of each stone characteristic on the number of nuts cracked per minute. To test our different models, we used the backward elimination in a stepwise regression test to show the dependence of one variable on another. We do not report here on the influence of age and sex as these factors had no effect in our model.

We further used our results for hits per nut and success rate to run a comparable analysis with a Mann-Whitney U-test (significance level at $p<0.05$), with the same data gathered from seven chimpanzees at Bossou, Guinea [Humle, 2003]. Wild Bossou chimpanzees are a valuable comparison, because they use stone hammers (as opposed to wood, for example) and also crack solely oil palm nuts (as opposed to Panda and Coula nuts, for example) [e.g., Biro et al. 2006; Humle and Matsuzawa, 2009]. The efficiency data were obtained through ad lib. behavioural sampling in the forest of Bossou.

Results

Laterality

When analysing the relative frequency of the dominant hand used for hammering with one hand, all 15 individuals used either the left or right hand exclusively (i.e., completely lateralized in 82% of total 609 bouts across all individuals; $p=0.000$). Additionally, the handedness index, was always significantly different from 0 (either +1, right-handed or -1, left-handed), confirming a bias in hand use (Table 1). Taking the proportion of right versus left hand use, ten individuals (66%; nine females, one male) used exclusively the right hand for hammering and five individuals (34%; three females, two males) used exclusively the left hand. The overall right-hand bias across all individuals was highly significant ($p <0.0001$). We additionally investigated how often the bonobos used another hand use strategy compared to exclusive right or left-handed hammering. Only five individuals - two right-handed females and three left-handed individuals (two females, one male) - occasionally preferred both hands (15% of total 609 bouts across all individuals) and three right-handed females rarely used the right hand/right foot (2.7% of total 609 bouts across all individuals) hammering with larger stones. The combination of left hand/left foot was not observed.

Table 1 Summary of bout data and Handedness Index (HI) for each bonobo individual.

Individual	Sex	Age	Total time of nut-cracking (min)	Bouts of using both hands	Bouts of right hand / right foot	Bouts of exclusive hand use	HI	Category
Opala	F	20	34:35	0	0	66	1.00	RH
Semendwa	F	19	13:40	0	0	21	1.00	RH
Salonga	F	18	09:23	0	0	13	1.00	RH
Elikya	F	10	23:17	0	0	44	1.00	RH
Katako	F	11	20:18	0	0	55	1.00	RH
Pole	M	9	04:56	0	0	10	1.00	RH
Ilebo	M	14	18:33	0	0	24	-1.00	LH
Malaika	F	8	54:45	35	1	50	1.00	RH
Masisi	F	10	17:54	0	5	34	1.00	RH
Muanda	F	12	38:48	22	0	40	-1.00	LH
Lisala	F	14	14:30	0	10	16	1.00	RH
Mbandaka	M	14	26:56	3	0	46	-1.00	LH
Isiro	F	18	19:55	10	0	23	1.00	RH
Kalina	F	17	16:58	23	0	40	-1.00	LH
Likasi	F	14	06:22	0	0	18	-1.00	LH
Bisengo	M	10	07:27	0	0	6	n/a	n/a
Yolo	M	12	04:40	0	0	6	n/a	n/a
Lomako	M	8	02:15	0	0	4	n/a	n/a

Sex: F, female; M, male; LH = left-handed individuals, RH = right-handed individuals. n/a: Individuals with less than 10 bouts were not included in the hand-preference analysis.

Hand grips used during nut-cracking

Fifteen different hand grips were observed across 18 bonobos (Table 2 and Fig.1). We identified three precision (PC) grips (Pc1-Pc3), in which the object is held away from the palm by the thumb and fingers (Fig. 1a-c), as well as six power (Pw) grips (Pw1-Pw6) with active involvement of the entire palmar surface and fingers (Fig. 1j-o). We also observed six grips that could not be categorised as either precision or power grips that we thus consider to be novel and important for functional interpretations of hand anatomy (Fig. 1d-i). These grips are most similar to the precision finger/passive palm grips identified previously in chimpanzees when stabilizing a food object in the hand as the teeth pulled against [Marzke et al., 2015], in long-tailed macaques when holding a stone to crack open oysters [Gumert and Malaivijitnond, 2009], and in humans when holding a core in the non-dominant hand during flake removal with the dominant hand [Marzke, 2006; 2013]. However, in bonobos the same grip is dynamic rather than passive, such that the palm is contributing to the force of the strike as the hammerstone hits the object. Since the digits have most contact with the stone and only one part of the palm is in contact with the object, we call this category “precision finger/active palm grips” (PcApm4 – PcApm9).

This study revealed 10 new hand grips that had not been previously reported in the grip repertoire of either wild or captive bonobos, chimpanzees, capuchin monkeys and macaques [Costello and Fragaszy, 1988; Christel, 1993, 1998; Boesch and Boesch, 1993; Jones-Engel and Bard, 1996; Marzke and Wullstein, 1996; Spinozzi et al., 2004; Pouydebat et al., 2009; Gumert and Malaivijitnond, 2009; Macfarlane, 2009; Marzke et al., 2015]. The remaining five grips (Pc1, Pc3, Pw1, Pw5 and Pw6) have either been reported or show interesting parallels to grips used in wild and captive chimpanzees (Pc1, Pw1, Pw5 and Pw6) [Boesch and Boesch, 1993; Jones-Engel and Bard, 1996; Marzke and Wullstein, 1996; Pouydebat et al., 2009; Marzke et al., 2015], macaques (Pc3, Pw6) [Gumert and Malaivijitnond, 2009] and studies of human manipulative behaviour (Pc1, Pc3, Pw6) [Marzke and Shakely, 1986; Marzke and Wullstein, 1996; Marzke, 2013; Bullock et al., 2013]. The similarities will be discussed in more detail below.

Furthermore, the thumb was particularly important in holding and stabilizing the hammerstone as has been recognized in wild nut-cracking chimpanzees and stone tool-using macaques [Boesch and Boesch, 1993; Gumert and Malaivijitnond, 2009]. The thumb was involved in each grip type, either adducted to the index finger, or opposing it, and was always in contact with the surface of the hammerstone throughout a nut-cracking bout. In 10 grips (Pc1-Pc3; PcApm5; PcApm8; PcApm9; Pw1; Pw2; Pw3; Pw5) the stone was pinched between thumb and fingers, suggesting potential forceful loading of the thumb (Fig.1).

Table 2 Bonobo hand grips used during nut-cracking.

Grasping category	Digit contact	Acronym	Description
Precision grip	1-2-3-4	Pc1	Stone held between the full thumb (including the region of the base of the thumb) and lateral aspect of distal and middle phalanges of flexed index finger, buttressed by the distal and middle phalanges of the flexed third and fourth finger. Thumb flexed at IP joint.
	1-2-3-4	Pc2	Stone held between thumb pad and dorsal aspect of distal phalanges of flexed digits 2-3-4, away from the palm. Thumb is opposed to Index finger.
	1-2-3-4-5	Pc3	Stone held between thumb at level of IP joint of ventral aspect of proximal phalanx and pads of flexed digits 2-3-4-5, without the palm. Thumb widely abducted and in opposition to the fingers.
Precision finger/ active palm grip	1-2	PcApm4	Stone held between lateral aspect of distal thumb and ventral aspect of index finger, supported by the distal palm. Thumb not flexed and adducted towards Index.
	1-5	PcApm5	Stone held between distal and proximal phalanges of the thumb and lateral aspect of distal phalanx of digit 5, supported by the hypothenar eminence of the extended palm. Thumb flexed at IP joint and abducted.
	1-2-3	PcApm6	Stone held between thumb pad and ventral proximal phalanges of digits 2-3, with support by the distal palm. Thumb is not flexed and adducted towards Index.
	1-2-3-4	PcApm7	Stone held between full thumb and flexed digits 2-3-4, supported by the distal palm. Thumb is not flexed and adducted towards Index.
	1-2-3-4	PcApm8	Stone held between thumb and dorsal aspect of distal & middle phalanges of the flexed digits 2-3 to the lateral aspect of digit 4, supported by the thenar eminence of the palm. Thumb can be flexed or extended.
	1-2-3-4-5	PcApm9	Stone held between lateral aspect of the thumb and dorsal aspect of distal phalanges of flexed digits 2-3-4-5, supported by the hypothenar eminence of the palm. Thumb flexed at MP and IP joints, held adducted towards Index.

Power grip	1-2	Pw1	Stone held between lateral aspect of proximal phalanx of thumb and flexed index finger, supported by the palm and the web at the V-shaped region between thumb and Index.
	1-2-3	Pw2	Stone held between full thumb and dorsal aspect of distal phalanges of flexed digits 2-3. Thumb flexed at IP joint.
	1-2-3-4	Pw3	Stone held between full thumb and dorsal distal phalanges of flexed digits 2-3-4, with support by the palm. Thumb slightly flexed.
	1-2-3-4-5	Pw4	Stone held between full thumb and dorsal aspect of distal phalanges of flexed digits 2-3-4-5, supported by the palm. Thumb adducted towards Index.
	1-2-3-4-5	Pw5	Stone held between thumb and flexed digits 2-3-4-5 at their ventral aspect of proximal phalanges and dorsal aspect of distal and middle phalanges. Stone lies in palm and in web at the V-shaped region between full thumb and index finger.
	1-2-3-4-5	Pw6	Stone held in the palm between the thumb and four fingers flexed at the MP or IP joints. Thumb either held opposed, abducted, inside or outside the grip. Hand wrist can adduct with this grip.

Fig. 1. Different hand grips used by the dominant hand during bonobo nut-cracking. Bonobo precision grips hold small and medium-sized hammerstones: (a) Pc1 grip; (b) Pc2 grip; (c) Pc3 grip. Novel precision finger/active palm grips typically used for small and medium-sized hammerstones: (d) PcApm4; (e) PcApm5; (f) PcApm6; (g) PcApm7; (h) PcApm8; (i) PcApm9. Power grips were most commonly used to hold all hammerstones: (j) Pw1; (k) Pw2; (l) Pw3; (m) Pw4; (n) Pw5; (o) Pw6 (photographs by J. Neufuss).

Relative frequencies of hand grip preference

We observed strong individual differences in hand grip preference and how often particular grips were used (Fig. 2). Precision grips were rarely used and only by two individuals. Precision finger/active palm grips occurred more often and across more individuals (n=7). In contrast, the power grips were much less variable, with the ‘Pw6’ (including all five digits, such that the stone is held between flexed fingers and the palm, with counter pressure from the thumb; Fig. 1o*)* being by far the most commonly used grip across all bouts and all individuals, regardless of stone weight and size (a multinomial logistic regression results found Residual Deviance: 20.05; AIC: 60.50). Table 3 represents the number of bouts a certain precision and power grip was used in relation to the hammerstone weight and size. These results also highlight the individual preferences for a particular hammerstone; moderate-weight and medium-sized stones were used in most bouts while small and light stones were rarely used.

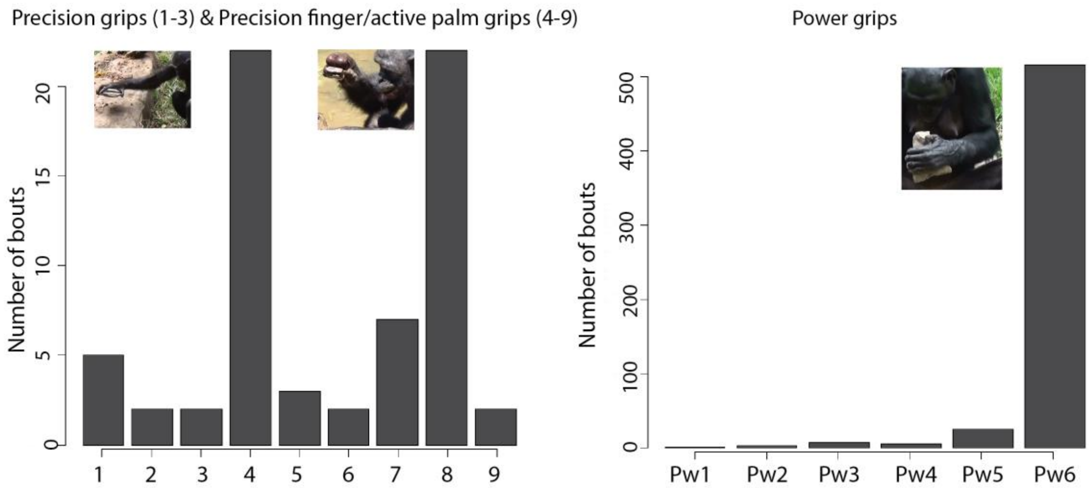

Fig. 2. Bar graph of relative frequency of hand grips used during nut-cracking. Precision grips (Pc1-Pc3) and precision finger/active palm grips (PcApm4-PcApm9) were used much more rarely and by fewer individuals than power grips (Pw1-Pw6). Note scales differ between graphs. See also Figure 1.

Table 3 Frequency of hand grips in relation to hammerstone weight and size.

grip type	heavy stone	moderate stone	light stone	large stone	medium-sized stone	small stone
Pc1	-	-	5	-	-	5
Pc2	-	-	2	-	-	2
Pc3	-	2	-	2	-	-
Pc4	-	-	18	-	-	18
Pc5	-	-	3	-	-	3
Pc6	-	-	2	-	-	2
Pc7	-	4	-	-	-	4
Pc8	-	-	20	-	-	20
Pc9	-	-	2	-	-	2
Pw1	1	-	-	-	1	-
Pw2	-	-	4	-	-	4
Pw3	-	-	7	-	7	-
Pw4	-	5	-	-	5	-
Pw5	-	14	11	-0	23	2
Pw6	220	219	28	228	210	29

Nut-cracking efficiency

Most individuals preferred moderate-weight and medium-sized stones while small and light stones were rarely used *(*Table 3 and Fig.3*).* Two step-wise regression tests, showed that hammerstone size, weight, thickness and shape all had a strong and significant effect on both measures of efficiency: (1) the average number of hits required to crack a nut ($p<0.0001$; R^2 values ranging from 0.87-0.96) and (2) the average number of nuts cracked per minute ($p<0.0001$; R^2 values ranging from 0.87-0.88). Large and heavy stones were significantly more effective than small and light stones, while medium and moderate weighted stones were not significantly different from larger stones. Thicker stones required significantly fewer hits to crack a nut than thinner stones, but were similarly effective when it came to the number of cracked nuts per minute. Regarding stone shape, square-shaped stones were most efficient (Table 4 and Fig. 3).

Table 4 Effect of stone characteristics on nut-cracking efficiency.

	Mean # of hits per nut			Mean # of nuts per minute		
	F-stat.	p-value	R^2	F-stat.	p-value	R^2
Stone size	12.87	p=1.265*10^(-7)	0.96	91.46	p ≈ 0	0.87
Stone weight	130.5	p≈ 0	0.88	105.2	p ≈ 0	0.88
Stone thickness	88.34	p≈ 0	0.87	95.4	p ≈ 0	0.87
Stone shape	53.35	p≈ 0	0.87	59.23	p ≈ 0	0.88

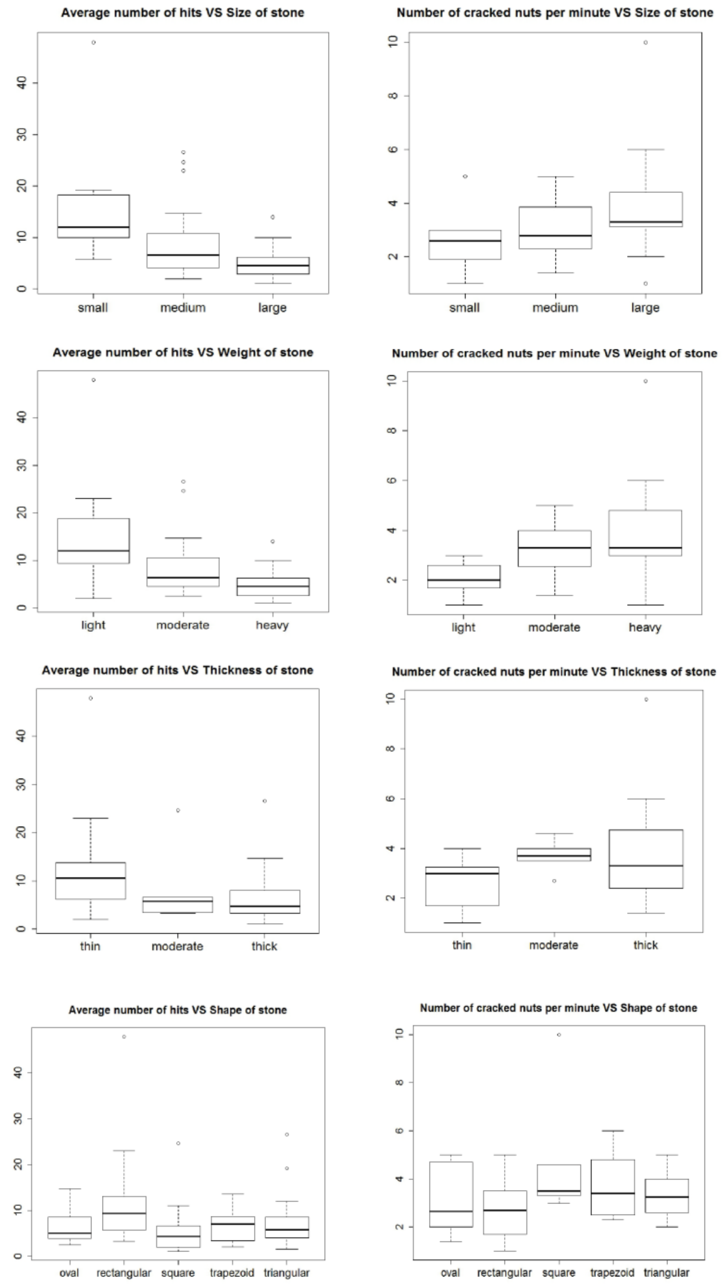

Fig. 3. Nut-cracking efficiency relative to aspects of hammerstone characteristics.

A simple linear regression test showed that the use of the right vs. left hand did not have a significant effect on (1) the average number of hits required to crack a nut (F-statistic: 133.3 on 2 and 49 DF, $p<0.0001$, R2 = 0.8447) and (2) the average number of nuts cracked per minute (F-statistic: 125.6 on 2 and 40 DF, $p<0.0001$, R2= 0.8624). Left-handed individuals needed 4.75 (SD: 5.46; range: 20.94) hits to crack 3.5 nuts/minute and right-handed individuals required 6.56 (SD: 8.85; range: 47) hits to crack 3 nuts/minute. Across our sample, we found more variability across the right-handed individuals (Fig. 4).

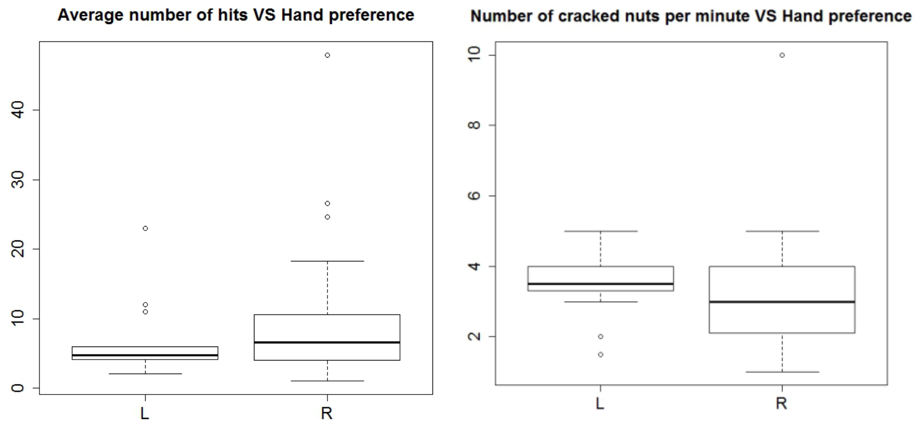

Fig. 4. Effect of right (R) vs. left (L) hand on the efficiency of nut-cracking.

Nut-cracking efficiency in bonobos and Bossou chimpanzees

We compared the (1) average number of hits per nut and (2) success rate (good nuts cracked per minute). A Mann-Whitney U test revealed that bonobos needed significantly ($p=0.003$) more hits per nut (median 7.3) than Bossou chimpanzees (median 3.8), but cracked significantly ($p=0.005$) more nuts per minute (median 2.8) compared with Bossou chimpanzees (median 1.9). Bonobos were also notably more variable across individuals in both efficiency measures (Fig. 5).

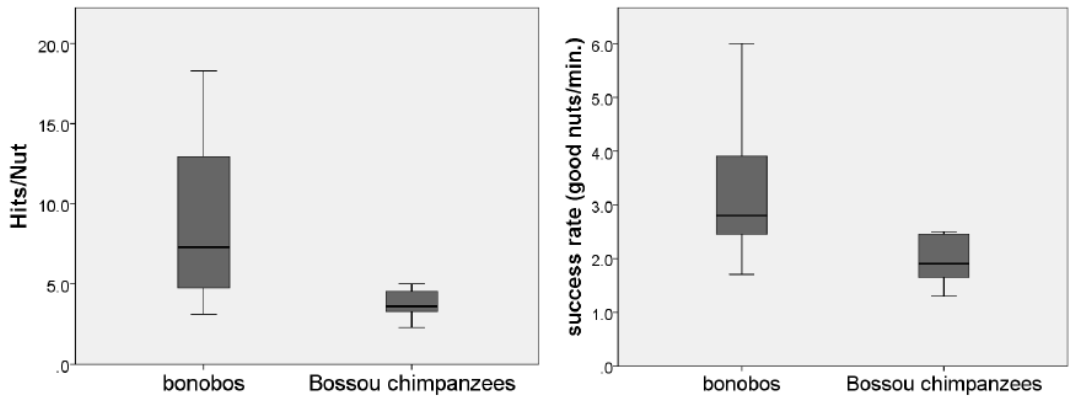

Fig. 5. Box-and-whisker plots showing variation in nut-cracking efficiency between wild-born, rehabilitated bonobos and habituated, wild Bossou chimpanzees. Bonobos required significant more hits to crack a nut (left) but cracked significantly more good nuts per minute (right).

Discussion

We present here the first detailed study of hand laterality and hand grips used in bonobos at cracking palm nuts with stone tools. We also present the first analysis of nut-cracking efficiency in relation to qualities of the hammerstone, and how bonobo nut-cracking compares to that of Bossou chimpanzees.

Laterality

Most previous studies assessing hand preferences in bonobos have analysed simple tasks (e.g. spontaneous actions like reaching or feeding) in relatively small samples (2-10 individuals) [De Vleeschouwer et al., 1995; Hopkins and de Waal, 1995; Ingmanson, 1996]. Although studies of more complex bimanual tasks found stronger individual hand preferences, no individuals were exclusively right- or left-handed [e.g., Chapelain et al., 2011; Hopkins et al., 2011; Bardo et al., 2015]. In contrast to this previous work, the individual bonobos in this study were exclusively right- or left-handed and there was an overall significant right-hand bias at the group-level during nut-cracking. The determination of group-level hand preference is generally based on two factors: the strength of the individual hand preference (i.e., handedness index) and the number of individuals investigated [e.g., Papademetriou et al., 2005]. Because bonobos (and other non-human primates) rarely exclusively use one hand for particular tasks (i.e., they have a relatively low handedness index), larger sample sizes are considered necessary to reliably detect a group-level bias (defined as >65% of the individuals in the group) [Hopkins and Cantalupo, 2005; Hopkins et al., 2012; Hopkins 2013a, 2013b]. In this study, the exclusive use of either the left- or right-hand (i.e., a high handedness index) by the 15 bonobo individuals suggests that use of the right-hand by 66% of the individuals may reliably estimate a group-level right-hand bias for this particular complex manipulative behaviour. Although a future study of more individuals is needed to confirm this bias, these results are consistent with previous reports of nut-cracking in chimpanzees [Matsuzawa, 1996; Humle and Matsuzawa, 2009]. Moreover, wild chimpanzees of Gombe show exclusive use of one hand or the other when pounding hard-shelled fruits (*Strychnos spp.*) on anvils [McGrew et al., 1999]. Wild western gorillas have been recently reported to demonstrate exclusive hand-preference and an overall right-hand bias during natural bimanual termite feeding [Salmi et al., 2016].

Hand use in relation to task complexity has been studied across four tool-using tasks in Bossou chimpanzees [Humle, 2003]. Nut-cracking, the most cognitively complex of the four behaviours studied and the only one requiring complementary coordination of both hands, revealed the strongest degree on laterality in all adult individuals (n=7). Humle (2003) suggested that Bossou chimpanzees have a right-hand bias at the population-level, which was supported by Biro et al. (2006), reporting a high proportion of right-handed individuals (62%) for nut-cracking in the same community. The Taï chimpanzees of Côte d'Ivoire show a hand-preference during nut-cracking at the individual-level, but the overall distribution was not biased to the left or right [Boesch, 1991]. The study reported that 18 individuals were significantly, but not completely lateralized, while another 18 individuals were exclusively lateralized, with 10 chimpanzees being right-handed [Boesch, 1991]. However, Taï chimpanzees typically use wooden hammers and more often use both hands and also the feet when the hammer is large.

In comparison to one-handed hammering, our study provides the first data on bonobos using a hand use strategy for different sized stone hammers. Most of the bonobos used one hand to hold small and medium-sized hammerstones. Five bonobo individuals occasionally preferred both hands (15%) and three rarely their right-hand/right foot (2.7%) when hammering with larger stones. For example, two females used both hands throughout a session when hammering with the same large and heavy stone (25cm wide, 30cm long, 3kg). Two other females were observed to switch between one-hand and both hands for the same large and heavy stones (a: 13cm wide, 14 long, 3kg; b: 15cm wide, 23cm long, 4.4kg), while the bimanual action was clearly more preferred for a higher number of bouts. A male bonobo also occasionally tended to use his right-hand to support the dominant left-hand when hammering with a large and heavy stone (17cm wide, 18cm long, 4.48kg). Three females used in addition to one-hand and both hands their right-hand/right-foot to handle large, heavy and large, moderate stones. One female switched several times between one-hand, both hands and her right-hand/right food when pounding nuts with four different large and heavy stones. Our results provide first evidence that bonobos do adapt an effective hand-use strategy in order to handle the different size and weight properties of their hammerstones.

Hand grips

This study revealed 10 new grips not previously reported in the literature and five grips that have either been previously reported or show interesting similarities to grips used by wild and captive chimpanzees and macaques, as well as in humans.

As Marzke and colleagues (1996) highlighted previously, the basic division of precision versus power grips as defined originally by Napier (1980) is not sufficient to describe and understand the complexity of manual manipulation in humans and other primates. Indeed, we observed three precision grips (Pc1-Pc3) between the fingers and thumb (i.e., without involvement of the palm), six power grips (Pw1-Pw6), with active contribution by the palm, and created a new category of grips called “precision finger/active palm” to accurately describe the manual manipulation of bonobo nut-cracking (Table 2 and Fig. 1). We also observed high variability across individuals in the use of precision grips and precision/active palm grips, showing the versatility of the bonobo hand in accommodating hammerstones of varying size and shape (Table 3 and Figure 2). Overall, this display of manipulative flexibility was unexpected given that previous work on hand grips or object manipulation during tool-use in captive bonobos has not reported this degree of variability [Jordan 1982; Christel, 1993; Christel et al., 1998].

Precision grips

Precision grips were only used by two bonobos, but to the best of our knowledge, none of the precision grips have been described in studies of captive bonobos [Christel, 1993; Christel et al., 1998] and capuchin monkeys [Costello and Fragaszy, 1988; Spinozzi et al., 2004] and wild nut-cracking chimpanzees [Boesch and Boesch, 1993]. The bonobos most often used precision grips when holding small hammerstones, which might explain why they have not been reported in wild chimpanzees that typically use much larger hammerstones [Boesch and Boesch, 1983]. However, the grips used by the chimpanzees in nut-cracking have not yet been systematically described in the same detail as presented here for the bonobos and thus future studies may reveal greater overlap in grip types between the two sister taxa. The Pc2 grip (in which the stone is held between the thumb and dorsal aspect of the distal phalanges of the flexed digits 2-3-4, and the thumb is opposed to the index finger, Fig. 1b) has to the best of our knowledge not been reported in the literature before. The grip was used by one male bonobo after the hammerstone broke apart and he continued hammering with the smaller stone. The other two precision grips were used for five bouts (Pc1) and two bouts (Pc3) by one individual, and offer insight into the manipulative capabilities of the bonobo hand. The Pc1 grip (in which the stone is held between the full thumb and lateral aspect of the distal and middle phalanges of the index finger, buttressed by the distal and middle phalanges of the third and fourth finger; Fig. 1a) is similar to the 'two-jaw chuck' pad-to-side grip reported in captive and wild chimpanzees [Marzke and Wullstein, 1996; Jones-Engel and Bard, 1996; Marzke et al. 2015]. While chimpanzees use only the thumb pad and side of the index finger when grasping different food objects, the bonobo recruits also the buttressed middle and fourth finger to stabilize the hammerstone. In humans, the buttressed pad-to-side grip is used when holding a flake and to pinch the tool tightly between the distal thumb pad and finger(s) [Marzke and Shackley, 1986; Marzke, 2006, 2013]. The bonobo also used the region of the base of the thumb to stabilise the stone firmly enough against the index finger and buttressed middle and fourth fingers to resist displacement of the tool by the reaction force of the nut. The Pc3- precision grip shows interesting parallels to the human 'four and five-jaw chuck' precision grip, with opposed pads of the thumb, index, and fingers 3-4,5 used for holding hammerstones (Fig. 1c) [Marzke and Shackley, 1986]. In bonobos the hand-sized stone is held between the thumb at level of the interphalangeal joint of the palmar aspect of the proximal phalanx and the pads of the four fingers, without contact to the palm. This grip appears to have a certain degree of finger-to-thumb pinching as the flexed fingers secure the stone and the widely abducted thumb serves as a prop. However, the grip is not as strong as in the human 'four and five-jaw chuck' grip to press objects firmly against the fingers, since the stone is held right above the nut and firm pressure by the thumb and fingers is not likely to be required. A similar form of finger-to-thumb pinching has been observed in wild long-tailed macaques for pound hammering and is described as a finger-to-thumb/passive palm grip [Gumert and Malaivijitnond, 2009]. Although the use of precision grips were rare, in all instances, the bonobos were able to hold the stone firmly enough between the thumb and fingers (without the palm) to crack the nut successfully with enough force that a relatively low number of hits (mean: 7.2) were needed. This action during nut-cracking suggests forceful loading of the thumb in a manner that is more similar to the human and wild long-tailed macaques pinch grips than would be typically incurred during power grips (see below). Although, the relatively rare use of these grips suggests that they may not be as comfortable or effective given bonobo hand morphology.

Precision finger/ active palm grips

During nut-cracking, bonobos grasped small and medium-sized hammerstones tightly between the thumb and fingers, with an additional force applied by the palm only at the moment of strike. Such grips have not been reported during nut-cracking in Taï chimpanzees [Boesch and Boesch, 1993] or feeding in Mahale chimpanzees [Marzke et al., 2015]. When the bonobos used small hammerstones, something also not observed in nut-cracking chimpanzees [Boesch and Boesch, 1983, 1993], there is relatively little room to strike the nut without smashing the fingers. The bonobos grasped the stone precisely in such a way as to expose the hammering surface and allow the palm to contribute force, but so the fingers would not be crushed (Fig. 1d). Thus, these grips are best described as 'precision finger/active palm grip' (PcApm4-PcApm9), as they describe the change that occurs as the hand goes from a 'precision finger/passive palm grip' of the stone [Marzke and Wullstein, 1996] to a more active involvement of the palm (Fig. 1d-i). This grip is different from the cup grip reported in captive chimpanzees [Marzke and Wullstein, 1996] or the pinch grip with passive palm support seen in wild long-tailed macaques during stone hammering [Gumert and Malaivijitnond, 2009]. Precision finger/active palm grips were used by eight bonobos, with 'PcApm4' (stone held between the lateral aspect of the distal thumb and palmar aspects of the distal and middle phalanges of the index finger; Fig. 1d) and 'PcApm8' (stone held between the thumb and dorsal aspect of distal & middle phalanges of the flexed digits 2-3 to the lateral aspect of digit 4, supported by the thenar eminence of the palm; Fig. 1h) being the most common (Fig. 2).

Power grips

The bonobos most often used power grips to hold the hammerstone during nut-cracking (Fig. 1j-o). Although six different power grips were used across all individuals, only three (Pw1, Pw5, Pw6) can be compared to studies on wild and captive chimpanzees and macaques. The Pw6-power grip was used among all individuals, in which the stone was held between all of the fingers and the palm with counter pressure from the thumb (Table 2) (Pw6; Fig.1o). This grip was used across different hammerstones, regardless of size, shape, thickness or weight, and appears to be the most effective grip for nut-cracking. A similar grip was also shown to be the most effective in humans during nut-cracking [Bril and Dietrich, 2015]. For larger stones, the thumb was normally held in opposition (Fig. 1j) to or adducted to the fingers, while for smaller stones the thumb was held outside or inside the grip (Pw6; Fig.1o). A similar power grip has been observed in wild long-tailed macaques during one-handed pound hammering [Gumert and Malaivijitnond, 2009] and in captive chimpanzees when grasping larger food objects [Jones-Engel and Bards, 1996; Pouydebat, 2009]. The bonobo power grip 'Pw6' appears also similar to the power grip typically used by the nut-cracking Taï chimpanzees [Boesch and Boesch, 1993]. However, only juvenile Taï chimpanzees grasped small stones with the thumb held inside the grip, whereas adult bonobos frequently used this grip (Fig. 1o). This type of power grip involves adduction of the wrist rather than flexion, so that the stone is exposed at the ulnar side of the palm and strikes the nut (Fig. 1o). This action would have the advantage of avoiding smashing of the fingers that would occur with hammering by flexion of the wrist, while at the same time allowing a firm grip by the thumb and fingers. We observed less frequent use of two power grips (Pw1, Pw5; Figure 2) involving the "V-shaped" region between the thumb and Index finger, first reported in Mahale chimpanzees during feeding [Marzke et al., 2015]. The chimpanzee "V-pocket" grip is used to securely hold large fruits in the web between the full thumb and index finger, buttressed by the flexed third, fourth and fifth digits [Marzke et al., 2015]. In bonobos, medium-sized hammerstones were rarely secured against the web of the palm either by the lateral aspect of the thumb and flexed index finger (Pw1; Fig. 1j) or more frequently by the thumb and the flexed four fingers at their ventral aspect of proximal phalanges and dorsal aspect of distal and middle phalanges (Pw5; Fig. 1n). Three new power grips (Pw2-Pw4) were also identified, typically used with small and medium-sized hammerstones and with relatively low frequency by four bonobos in our sample (Fig. 2). In most of these grips, the hammerstone was held between the palm, thumb and dorsal surface of the distal phalanges (i.e. fingers flexed) (Fig. 1k-m).

Bonobo hand grips (PcApm9, Pw5, Pw6; Fig. 1i, n, o) occasionally involved rotation of medium-sized hammerstones within the palm of one hand against the anvil surface, by movements at the carpometacarpal, metacarpophalangeal or interphalangeal joints of the thumb and finger(s). Re-positioning of the stone helped to expose a different side of the hammering surface or to change the grip (e.g., Pw6 to Pw5). Additionally, medium-sized and large stones were grasped by the opposite hand, turned over by the hand via movement at the wrist, elbow and shoulder joints, and then placed back in the other hand to be regrasped in the desired orientation. Unlike in humans, we did not observe translation (object moved between the palm and fingertips) or precision handling (object moved by the digits alone) [e.g., Marzke and Shackley, 1986; Marzke and Wullstein, 1996], but found interesting parallels to a captive study of chimpanzee “in-hand movements” [Crast et al., 2009]. Similar to the bonobo’s hand movements, chimpanzees perform in-hand movements for changing their grip on the object, sometimes use a surface when rotating an object and turn objects over in bimanual actions [Crast et al., 2009].

Nut-cracking efficiency

In this study of bonobo nut-cracking, we found that bonobos most often preferred the most efficient hammerstones. The weight, size, thickness and shape of a particular hammerstone had a significant effect on the number of hits required to crack a nut and on the number of nuts cracked per minute. The bonobos were significantly more efficient with larger and heavier stones, than with small and lighter (0.1-0.38kg) stones. However, most individuals chose to use moderate-weight (0.45-1.24kg) and medium-sized stones to crack open nuts, which appeared easier to handle than larger, heavier (1.38-4.48kg) stones and did not significantly differ in efficiency. Comparable studies on captive chimpanzees showed that, like bonobos, they preferred to use heavier hammers (1.2kg, 1.4kg; 56) that required fewer hits and less time to crack open nuts [Schrauf et al., 2012]. Wild Bossou chimpanzees differentiate stones by width, length and weight, choosing to use lighter stones as hammers and heavier stones as anvils during nut-cracking [Biro et al., 2006]. Nut-cracking capuchin monkeys also actively select particular hammerstones based on the material and weight that is most appropriate to crack open palm nuts [Schrauf et al., 2008; Visalberghi et al., 2009].

Given that bonobos are not known to nut-crack in the wild, we found, not surprisingly, significant differences in nut-cracking efficiency between bonobos and Bossou chimpanzees. The bonobos needed on average almost twice as many hits to crack open a palm nut compared with Bossou chimpanzees. However, contrary to our predictions, bonobos were able to crack on average nearly one more nut per minute than their congeneric wild chimpanzee. These differences may result from two factors. First, there was a difference in the general strategy of collecting nuts (as collection time was included in the measure; see Methods); although both the bonobos and Bossou chimpanzees cracked nuts next to the palm nut source (i.e., 1-2 meters), the chimpanzees tended to spend more time collecting multiple nuts at one time to transport back to the anvil whereas the bonobos spent less time collecting because nuts were more readily available around their nut-cracking area. Second, the bonobos likely required a greater number of hits because, unlike Bossou chimpanzees (preferred hammers have an average weight of 1.0 kg; Bril et al., 2006), they also used lighter (0.10-0.38kg) stones and were cracking fresher nuts that are much more challenging to crack than dry nuts. Regardless of these differences, these rehabilitated bonobos, which have only recently (i.e., last ~20 years) developed nut-cracking behaviour are surprisingly similar in efficiency to that of chimpanzees with a long history (i.e., 4.300 years; Mercader et al., 2002) of nut-cracking and other types of complex tool use.

Conclusion

This first detailed study of nut-cracking in bonobos revealed an unexpected manipulative versatility during stone tool-use, including 10 novel hand grips. This most complex tool-use behaviour showed 100% lateralization and a significant right-hand bias in most of the individuals studied, speaking to a group-level bias. Bonobos also have the ability, like nut-cracking capuchin monkeys [e.g., Schrauf et al., 2008] and chimpanzees [Boesch and Boesch, 1983; Biro et al., 2006] to select the most effective hammerstones. Moreover, bonobos can be efficient nut-crackers with a skill level not that different from wild chimpanzees. It is clear from this study, that more future studies on complex tool-use behaviour in bonobos under natural conditions are required, in order to explore the full range of their manipulative and tool-use capabilities.

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Figure Captions

Figure 1. Different hand grips used by the dominant hand during bonobo nut-cracking. Bonobo precision grips hold small and medium-sized hammerstones: (a) Pc1 grip; (b) Pc2 grip; (c) Pc3 grip. Novel precision finger/active palm grips typically used for small and medium-sized hammerstones: (d) PcApm4; (e) PcApm5; (f) PcApm6; (g) PcApm7; (h) PcApm8; (i) PcApm9. Power grips were most commonly used to hold all hammerstones: (j) Pw1; (k) Pw2; (l) Pw3; (m) Pw4; (n) Pw5; (o) Pw6 (photographs by J. Neufuss).

Figure 2. Bar graph of relative frequency of hand grips used during nut-cracking. Precision grips (Pc1-Pc3) and precision finger/active palm grips (PcApm4-PcApm9) were used much more rarely and by fewer individuals than power grips (Pw1-Pw6). Note scales differ between graphs. See also Figure 1.

Figure 3. Nut-cracking efficiency relative to aspects of hammerstone characteristics.

Figure 4. Effect of right (R) vs. left (L) hand on the efficiency of nut-cracking.

Figure 5. Box-and-whisker plots showing variation in nut-cracking efficiency between wild-born, rehabilitated bonobos and habituated, wild Bossou chimpanzees. Bonobos required significant more hits to crack a nut (left) but cracked significantly more good nuts per minute (right).