

1 **Title**

2 Extractive Foraging on Hard-Shelled Walnuts and Variation of Feeding Techniques in
3 Wild Japanese Macaques (*Macaca fuscata*)

4

5 **Short running title**

6 Feeding techniques of hard-shelled nuts in Japanese macaques

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Abstract

Extractive foraging is considered a key selective pressure for the evolution of primate cognitive abilities—the extractive foraging hypothesis. While tool-use and substrate-use are representatives of the foraging strategy, some primates engage extractive foraging without external objects. Manual processing skills of prickly foods have been described in some species, whereas there are few studies on other type of food defenses. Here, I described extractive foraging of hard-shelled walnuts by the wild Japanese macaques (*Macaca fuscata*), focusing on whether they accomplish the tasks only by their physical strength or require manual and/or oral processing skills to crack open the walnut shells. The study subjects comprised all members of troop B₁ and three non-troop males in Kinkazan Island, Japan. Walnut feeding was observed during the main walnut seasons (September to December), when the troop visited walnut patches for 79 days in two years. I categorized walnut feeding behavior into *complete cracking* and *partial cracking*. The number of times the five behavioral elements in the cracking stage occurred were counted from complete cracking. All six adult males and 11 of the 17 adult/adolescent females showed complete cracking, while the remaining females were never observed exhibiting this activity, despite their physical maturity. I observed four clearly distinguishable cracking methods during walnut feeding in the 17 subjects. The compositions of five

behavioral elements were different from each method. These results suggest that walnut feeding by Japanese macaques is not only by a brute force but requires the acquisition of at least one of four cracking methods for the achievement of complete cracking. In particular, females need to compensate their physical inferiority with increasing the walnut manipulations. To my knowledge, this is the first detailed description on feeding techniques in primates to overcome hard-shelled obstacles without the use of tools and even of substrates.

Keywords

extractive foraging, Japanese macaques, feeding technique, hard-shelled nuts, behavioral innovation

Research Highlights

Wild Japanese macaques in Kinkazan Island require not only physical strength but also feeding techniques for achieving the hard-shelled walnuts feeding tasks. The monkeys showed four clearly distinguishable cracking methods during the tasks.

Introduction

Many primate species consume foods that are not ready to eat but require some processing before ingestion. Such foods include hard-shelled nuts, piths or leaves with spines, underground plant storage organs, gastropods, invertebrates hiding in layers of wood, etc. Feeding on such not-ready-to-eat foods embedded or encased in other matrices is known as “extractive foraging” (Gibson, 1986). It is often assumed that extractive foraging requires complex processing skills in order to overcome the obstacles before getting to the food, and is thus, sometimes considered to be a key selective pressure in the evolution of primate cognitive abilities—the extractive foraging hypothesis (Gibson, 1986; King, 1986; Melin, Young, Mosdossy, & Fedigan, 2014; Parker, 1996; 2015; Parker & Gibson, 1977; Reader, Hager, & Laland, 2011; Yamakoshi, 2004).

Extractive foraging is represented by food processing accompanied by the use of external objects, such as tool-use and substrate-use. For instance, the use of hammerstones to crack open nuts and of sticks to extract insects from mounds by wild chimpanzees (*Pan troglodytes*) are representative of tool-aided extractive foraging (reviewed in McGrew, 1992). Species other than chimpanzees are also known to use

tools for feeding in the wild, such as orangutans (*Pongo* spp.: Fox, Sitompul, & van Schaik, 1999; van Schaik, Fox, & Sitompul, 1996; van Schaik & Knott, 2001), capuchins (*Sapajus* spp.: Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004; Ottoni & Mannu, 2001), and long-tailed macaques (*Macaca fascicularis*: Gumert, Hoong, & Malaivijitnond, 2011; Malaivijitnond et al., 2007). As to substrate-use, some capuchin monkey species are well known as skillful substrate users. White-faced capuchin monkeys (*Cebus capucinus*) extract seeds from hard *Luehea candida* fruits by *pounding* or *scrubbing* the fruits against a rough substrate (O'Malley & Fedigan, 2005a, b; Perry, 2009). Likewise, behavioral variation in palm-nut smashing against a tree trunk has been described in large-headed capuchin (*S. macrocephalus*) (Struhsaker & Leland, 1977). So far, extractive foraging with tool-use and substrate-use has been well documented in several primate species, and they are main concerns while discussing the hypothesis (Barton, 2012; Parker, 1996; 2015; Parker & Gibson, 1977; Tomasello & Call, 1997; van Schaik, Deaner, & Merrill, 1999; Yamakoshi, 2004).

Not all extractive foragers, however, are categorized into tool users or substrate users. Gibson (1986) and Parker (2015) suggested that extractive foragers are classified into other two groups in addition to tool user group. The first group shows specialized anatomical manipulators, such as several pitheciin primates (e.g. *Pithecia pithecia* and

Chiropotes spp.) and sooty mangabeys (*Cercocebus atys*), which have thick-enameled molars to consume mechanically protected foods year-round (Martin, Olejniczak, & Maas, 2003; Norconk & Veres, 2011; Daegling et al., 2011; McGraw, Vick, & Daegling, 2011; 2014); marmosets (*Cebuella* spp.) having a modified dental apparatus that permits the extraction of sap from bark (Sussman & Kinsey, 1984). The second group includes primates who use dexterous manual object manipulation including substrate-use. A classic example of the second group is mountain gorillas (*Gorilla beringei beringei*), which feed on herbaceous foods with physical defenses (stings, hook, fibrous outer casing) using dexterous manual skills (Byrne & Byrne, 1993). Similar feeding techniques have also been reported in chimpanzees (Corp & Byrne, 2002; Stokes & Byrne, 2001). Although these food processing skills do not include tools and substrates, they have been discussed in terms of cognitive complexity and hierarchical organization (see Russon, 1998 for criteria) that are regarded as essential to problem-solving and planning abilities (Byrne, 1997; Russon, 1998). Thus, feeding techniques without external objects have also recently been considered a crucial factor that promoted enlargement of brain size in primate lineage (Heldstab et al., 2016; Parker, 2015). Furthermore, because tool-use and substrate-use are limited to a small number of primate genera (Yamakoshi, 2004), inclusion of this type of feeding technique may

facilitate the debate about the extractive foraging hypothesis (Byrne, 2001).

Old World monkeys usually do not use tools, and their feeding behaviors have often been thought to be simple processing with rudimentary actions (e.g., “pick up”, “pull off”, and “put in the mouth”). However, when focusing on feeding behaviors without tools and investigating them minutely, the monkeys engage in several type of extractive foraging using various food processing. Baboons (*Papio* spp.), for instance, are known to dig the soil to extract underground rhizomes (Altmann, 1998; Altmann & Altmann, 1970). Xiang, Liang, Nie, & Li (2013) revealed that gray snub-nosed monkeys (*Rhinopithecus brelichi*), that are typically considered non-extractive foragers so far (Dunbar, 1995), utilized extracted food items year-round using six extractive actions from detailed observations. Japanese macaques (*Macaca fuscata*) pull grass roots from the ground, carry them to the waterside and wash them: a behavior known as “grass roots washing” (Nakamichi, Kato, Kojima, & Itoigawa, 1998). More recently, three finer descriptions of extractive foraging techniques by macaque species have been presented, such as prickly pear cactus feeding by long-tailed macaques (Tan, Luncz, Haslam, Malaivijitnond, & Gumert, 2016), toxic caterpillar feeding by pig-tailed macaques (*Macaca leonine*: Trébouet, Reichard, Pinkaew, & Malaivijitnond, 2018), and coconut and invertebrate feeding by Nicobar long-tailed macaque (*M. fascicularis umbrosu*: Pal,

Kumara, Mishra, Velankar, & Singh, 2018). These detailed descriptions of food processing will be useful for comparisons of manual and cognitive complexity on extractive foraging contexts among different primate lineages. However, such studies on Old World monkeys are limited to a small number of species. Further, most previous studies have focused only on manual food processing for the consumption of prickly foods, including in great apes (e.g. Byrne & Byrne, 1993; Corp & Byrne, 2002; Stokes & Byrne, 2001; Tan et al., 2016; Trébouet et al., 2018). As to hard-object feeding, on the other hand, although many researchers investigated morphological adaptations to oral processing of hard foods in an array of primate species (e.g. Daegling et al., 2011; Martin et al., 2003; McGraw et al., 2011; 2014; Norconk & Veres, 2011; van Casteren, Wright, Kupeczik, & Robbins, 2019), there is no published study that describes hard foods processing in detail and refers to the presence of certain feeding techniques against the type of food defense.

In this study, I report extractive foraging of hard-shelled walnuts by wild Japanese macaques. Tsuji, Wada, & Watanabe (2011) reported that 11 populations of this macaque species (Shimokita, Shirakami, Kinkazan, Shiga, Kurobe, Hakusan, Chichibu, Okutama, Nakatomi, Minowa, and Gagyusan) are known to feed on Japanese walnuts (*Juglans mandshurica*), a commonly seen species in Japan. The walnuts have

large high-nutrition cotyledons which are colloquially referred to as “walnut meat” and are edible for humans too. However, the cotyledons are covered by an extremely hard shell, the endocarp, that a human usually requires a tool, such as hammers or heavy stones, for cracking (Fig. 1). Despite the extremely hard shell, the Japanese macaques in Kinkazan Island employ only their hands and teeth for cracking open the shells and extracting the cotyledons (thus a type of extractive foraging without tools and even substrates). Then, it is interesting to examine whether they can accomplish this task only by their physical strength or they require manual and/or oral processing skills to crack open the walnut shells. First, in this study, I reveal which age-sex class individuals engage the walnut feeding task and succeed in cracking open the shell. Second, I examine whether all feeding individuals process a walnut solely with brute force or they require certain feeding techniques to crack the shell completely. Furthermore, if some techniques are detected, I investigate whether there are differences in *processing duration* and in composition of behavioral elements during the feeding process among the techniques.

Methods

Study site and subjects

This study was conducted on Kinkazan Island (38°2' N, 141°4' E; see Nakagawa, Nakamichi, & Sugiura, 2010 for details of the study site), Miyagi Prefecture, Japan, where a long-term study of wild Japanese macaques started in 1982. Among six troops of wild Japanese macaques inhabiting the island, I focused on troop B₁. As this troop has been a subject of a long-term study (e.g., Kazahari & Agetsuma, 2008), all troop members are well habituated and there is detailed information about ages and kin relations. Researchers can observe the behaviors of macaques easily, because the visual range has been estimated at a radius of approximately 40 m (Koda, Shimooka, & Sugiura, 2008). During the study period, the troop comprised 34–39 individuals, including 2–3 adult males (7 years old and older), 14–15 adult females (7 years old and older), 2–3 adolescent females (5–6 years old), 12–14 juveniles (1–4 years old), 2–6 infants. In addition, three identified non-troop males (7 years old and older), who were often observed near the group during the study periods, were also included as the study subjects.

At the onset of the long-term study at Kinkazan in the 1980s, none of the monkeys were observed feeding on walnuts (Izawa, 2009; Nakagawa, 1997) but troop B₁ was first observed walnut-feeding in 1991. Only adult males fed on walnuts in the

beginning, later followed by some females (Izawa, 2009). Currently, walnuts are one of the main autumn foods for both sexes in Kinkazan. Despite its increased importance, however, there have been no descriptions about how macaques crack open the hard shells.

Japanese walnut

The Japanese walnut is a deciduous tall tree with a height of 10–20 m. This tree annually produces fruits of 250–350 mm diameter, that ripen and fall gradually from September to October (Yamazaki, 1989). After that, the husks (exocarp and mesocarp) of walnuts start to rot on the ground and gradually disappear. A seed weighs between 4.00 and 13.99 g on a fresh weight basis (Seiwa, 2000). Tamura & Hayashi (2008) reported the proportion of total fresh weight of cotyledon weight to total fresh weight is 22.3% on average (range: 17.1–30.0%). Walnut cotyledon is well known as a highly nutritious food, containing 21.7–25.7 g protein, 59.9–64.1 g lipid, and 6.7–8.0 g carbohydrate per 100g on a wet weight basis (Chiba, 2016).

Japanese walnut is widely distributed from the central to the southern part of Kinkazan Island (Izawa, 2009). A total of seven walnut patches were confirmed within the range of troop B₁ during the study period. All patches were sufficiently large to

encompass many members of the troop at a time.

Data collection

Walnut feeding was observed during main walnut season from October to December 2015 and September to November 2016. I followed the troop for 64 days (545.0 h) in 2015 and 42 days (321.6 h) in 2016. In this study, I categorized walnut feeding behavior into *complete cracking* and *partial cracking*. In the former, an individual picks an intact walnut, cracks the shell completely, and exposes the whole cotyledon inside. The latter differs from the former in that a monkey cracks the shell partly and exposes only a part of the cotyledon. At the beginning of this study, from October 12 to November 7 in 2015, every effort was made to collect information of individuals that did or did not show walnut feeding behavior. I rotated through the monkeys feeding on walnuts in a patch, recording whether the monkeys showed complete cracking, only partial cracking, or none. This recording continued throughout the study period while conducting other data sampling (see below). Observations on the number of complete cracking and partial cracking attempts were later tallied on a daily basis for each individual. Although monkeys often scrounged debris of the cotyledon in a patch, I focused on only walnut feeding accompanied by cracking behavior in this

study.

From November 8 to December 27, 2015, I conducted focal animal sampling (Altmann, 1974). Subject individuals were six adult females (*Tm*, *Tt*, *Mk*, *Nt*, *Ak*, *My*) and one adolescent female (*Ac*). I followed one of them for an entire day (average 7.3 hours per day), and when the focal animal entered a walnut patch, I recorded behavioral elements in the processing of walnuts continuously using a video camera (SONY HDR-CX630V).

In 2016, detailed walnut processing was observed for all troop members over the age of five years and three identified non-troop males. I rotated through the monkeys feeding on a walnut and recorded the feeding behavior continuously from the time a monkey began processing a walnut using a video camera or fieldnotes.

Data analysis

I identified 21 behavioral elements across six stages of walnut feeding behaviors (Table 1; Fig. 2). Some of these elements and stages were categorized with reference to previous studies (Tan et al., 2016; Trébouet et al., 2018). In the present study, I focused on the “cracking stage” for detailed behavioral analysis because a variation of cracking methods was observed in this stage (descriptions of different cracking methods will

appear in Results). These behavioral data were extracted from only complete cracking in the following manner: at first, I measured the *processing duration*, which is defined as a duration from the beginning of the cracking stage to the moment when the monkey moved away or touched another walnut after walnut consumption. Second, I counted the number of times the five elements in cracking stage occurred during the processing duration. When the monkeys switched their behavior from one element to another element, I regarded the previous element as complete. For this analysis, I used only video-recorded complete cracking in which these five elements were completely countable throughout the entire process.

Statistical analysis

I conducted 10,000 runs randomization test to examine whether each individual has a preferred cracking method. I calculated test statistics for each individual as follows: subtracting the number of the second most observed cracking method from the number of the most observed method. Then, the total number of observations for the four cracking methods were repeatedly rearranged with the random assignment procedure 10,000 times. The test statistics for each result of data randomizations were calculated to construct the randomization distribution of the test statistic. Finally, I

examined whether the observed test statistic deviated significantly from chance based on the randomization distribution.

I ran a generalized linear mixed model (GLMM) to examine whether processing duration of one walnut differed between sexes and among four cracking methods within same sex. The response variable was processing duration. As the predictor variables, I included the sex of feeding individuals for comparing between sexes, and cracking methods for comparing among the four methods within same sex. The GLMM was run with a Gamma distribution and a log link function. I also included identity of each feeding individual as the random effect.

For comparing the compositions of five behavioral elements in cracking stage among four cracking methods, I performed three sets of analyses with GLMM. First, I focused on the proportion of two biting elements (i.e., bite with “molars” and with “incisors”). For each complete cracking in the sample, I calculated the “proportion of bite with molars” (i.e., the number of “bite with molars”, divided by the sum total of “bite with molars” and “bite with incisors”). Second analysis focused on the proportion of two elements which monkeys conducted after biting (i.e., “rotate” and “look”). I calculated the “proportion of rotate” using the same set of samples (i.e., the number of “rotate”, divided by the sum total of “rotate” and “look”). For a third analysis, the

frequency of “shift” per one biting action was calculated (i.e., the number of “shift”, divided by the sum total of “bite with molars” and “bite with incisors”). As the response variable, I included the two proportions and the frequency calculated above. The predictor variables were cracking methods in all analyses. The GLMM was run with a Binomial distribution for the analyses of the proportions, and with a Poisson distribution and a log link function for the analysis of the frequency. The sum total of “bite with molars” and “bite with incisors” was included as an offset variable for the analysis of the frequency. I also included identity of each feeding individual as the random effect.

To assess the statistical significance of each predictor variable, I conducted likelihood ratio tests and Tukey’s multiple comparison tests by comparing the full model with a reduced model. All statistical analyses were performed with R version 3.3.2 (R Core Team, 2016), and I used the functions of *glmer* and *lme4* package (Bates, Maechler, Bolker, & Walker, 2015). Throughout the analysis, the statistical significance level was set at $\alpha = 0.05$. The data that support the findings of this study are available from the corresponding author upon reasonable request.

Ethical note

This study complies with the American Society of Primatologists principles for

the ethical treatment of nonhuman primates and conformed to the Guidelines for Field Research established by the Ethics Committee of the Primate Research Institute, Kyoto University.

Results

Feeding behaviors

Troop B₁ visited walnut patches for 54 days in 2015 and 25 days in 2016. During these days, all six adult males and 11 of 17 adult/adolescent females showed complete cracking at least once (Table 2). Minimum and maximum ages of these monkeys were five (*Mb*) and 18-years (*Tr*), respectively. Four adult females and two adolescent females, aged from five to 19 years, never showed complete cracking during the study period. Among them, four (*Ak*, *Nt*, *My*, and *Ac*) showed partial cracking, but two (*Na* and *Kn*) never showed even partial cracking (Table 2). *Tr*, an 18-year-old female, showed complete cracking in 2015, but only partial cracking in 2016.

Although I sometimes observed juveniles or infants picking up walnuts and putting them in their mouths while I observed their mothers, none of them achieved complete or even partial cracking throughout the study period.

305

306 **Six stages and behavioral elements of walnut feeding**

307 At each stage, multiple elements were either omitted, repeated, or combined
308 depending on whether they were essential for processing. Obviously, for example,
309 “remove husk” occurred only when monkeys picked up a walnut with the husk. In this
310 case, this behavioral element will never be a constraint on subsequent walnuts
311 processing because the husks are really soft and easy to remove for all individuals. The
312 rubbing stage did not always occur before cracking stage, but monkeys frequently
313 rubbed walnuts against fallen trees or rocks (seemingly for removing dirt of walnuts),
314 being accompanied by the transporting stage. At the cracking stage, all five elements
315 could be combined and conducted repeatedly until the shell was cracked completely.

316

317 **Variation of cracking methods**

318 I identified four methods to crack open walnuts from observations of complete
319 cracking sequences supplemented by feeding traces.

320

321 **Crunch:** An individual, bites a whole walnut with molars, and the resulting force breaks
322 the shell. The shell is unevenly broken, and fine fragments of the shell remain on the

ground after feeding (Fig. 3a; Supplement 1). Only three adult males (*AS*, *FM*, *KR*) showed this cracking method. *AS* and *FM* preferred this method significantly (Table 3; $P < 0.001$).

Bilateral-crack: An individual, bites only one hemisphere (divided by the suture line) of a walnut and cracks two opposed points on the hemisphere. The monkey then cracks the shell linearly and outwards from the points along the suture line with the molars. Then, the monkey evenly and simultaneously cracks the two opposing damaged areas. When the two sites of damage are cracked broadly and deeply enough, the monkey splits the walnut into halves by mouth or hands (Fig. 3b; Supplement 2). After splitting, it eats the cotyledon of one half, while keeping the other half in its hand or foot or keeping it on the ground. Similarly, it finally eats the remaining cotyledon of the other half. When a monkey gives up feeding before splitting the walnut, two cracks remain on the shell (Fig. 3b). All females that showed complete cracking used this method, except for *Mk*, but males never did so. Seven females preferred this method significantly (Table 3; $P < 0.001$).

Unilateral-crack: As with bilateral-cracking, a monkey would bite only one

hemisphere. However, it cracks only one point of the shell in this method. It then cracks the shell linearly on only one side along the suture line with the molars. When the crack on the shell is broad and deep enough, the monkey splits the walnut into halves by mouth or hands (Fig. 3c; Supplement 3). The subsequent feeding sequence is identical to bilateral-cracking. When a monkey gives up feeding before splitting the walnut, only one cracking line occurs on the discarded nut (Fig. 3c). This method was seen in all adult males and in two adult females, *Ku* and *Tn*. Two adult males, *TY* and *KR*, significantly preferred this method (Table 3; $P < 0.001$).

Hole-punch: An individual monkey bites and breaks a hole in a walnut shell with the molars. It then gradually expands the hole using both molars and incisors (Fig. 3d; Supplement 4). No splitting of the shell occurs in this method. When a monkey stops the feeding process before completion, the remaining trace is amorphous (Fig. 3d). Only one adult female, *Mk*, showed this method and showed significant preference for it (Table 3; $P < 0.001$).

Processing duration

Processing duration of one walnut was significantly shorter in males than in

females (male: $N = 79$, female: $N = 317$, $\chi^2 = 11.94$, $df = 1$, $P = 0.0005$; Fig. 4). Comparison among cracking methods within same sexes showed that the duration of crunch was significantly shorter than that of unilateral-crack in males (crunch: $N = 42$, unilateral-crack: $N = 37$, $\chi^2 = 7.11$, $df = 1$, $P < 0.01$; Fig. 4). On the other hand, in females, the durations did not differ significantly among three cracking methods (unilateral-crack: $N = 12$, bilateral-crack: $N = 284$, hole-punch: $N = 21$, $\chi^2 = 5.54$, $df = 2$, $P = 0.06$; Fig. 4).

Cracking stage

I compared composition of five behavioral elements in cracking stage among four cracking methods (crunch: $N = 9$, unilateral-crack: $N = 19$, bilateral-crack: $N = 41$, hole-punch: $N = 10$).

When I looked at the proportion of two biting elements, *hole-punch* showed significantly lower proportion of “bite with molars” than other three methods. This means that the proportion of “bite with incisors” was higher ($\chi^2 = 51.44$, $df = 3$, $P < 0.001$, Tukey’s multiple comparison test: crunch vs. hole-punch: $z = 3.23$, $P < 0.05$; unilateral-crack vs. hole-punch: $z = 3.80$, $P < 0.001$; bilateral-crack vs. hole-punch: $z = 4.59$, $P < 0.001$, Fig. 5).

Then, when I looked at the proportion of two elements which monkeys conducted after biting, the proportion of “rotate” in *bilateral-crack* was significantly higher than in *crunch* and *unilateral-crack* ($\chi^2 = 31.69$, $df = 3$, $P < 0.001$, Tukey’s multiple comparison test: bilateral-crack vs. crunch: $z = 4.06$, $P < 0.001$; bilateral-crack vs. unilateral-crack: $z = 4.93$, $P < 0.001$, Fig. 6).

The frequency of “shift” per one biting action was significantly higher in *bilateral-crack* than other three methods ($\chi^2 = 28.06$, $df = 3$, $P < 0.001$, Tukey’s multiple comparison test: bilateral-crack vs. crunch: $z = 4.136$, $P < 0.001$; bilateral-crack vs. unilateral-crack: $z = 2.573$, $P < 0.05$; bilateral-crack vs. hole-punch: $z = 3.341$, $P < 0.01$, Fig. 7). *Crunch* showed the lowest frequency, significantly lower than *unilateral-crack* (crunch vs. unilateral-crack: $z = 2.989$, $P < 0.05$, Fig. 7).

Discussion

The present study provides the first detailed description of extractive foraging for hard-shelled walnuts in wild Japanese macaques of Kinkazan Island. This extractive foraging task was performed by only manual and oral processing without tools and even substrates. Although all the six adult males and 11 of the 17 adult/adolescent females in

troop B₁ showed complete cracking, some of the remaining adult/adolescent females showed only partial cracking, while others never showed either of the two extractive feeding behaviors. I identified 21 behavioral elements across six stages of walnut feeding. Some elements and stages were omitted, combined, or repeated during a walnut processing. From observation of complete cracking, four clearly distinguishable cracking methods were detected, and most individuals preferentially used one of them. These methods also differed in terms of the composition of the five behavioral elements within the cracking stage.

Neither complete nor partial cracking were observed in juveniles and infants. This is likely to be explained by the lack of physical strength. In Japanese macaques, body growth lasts until approximately 10 years (Hamada & Yamamoto, 2010), and eruption of permanent teeth is completed at around six years (Iwamoto, Watanabe, & Hamada, 1987). Additionally, in rhesus macaques (*M. mulatta*), the occlusal force of the incisor of juveniles is half of that of adults (Dechow & Carlson, 1990), and infant Japanese macaques are known to prefer food items that smaller, softer, or easy-to-process, compared to that preferred by their mothers (Taniguchi, 2015). Therefore, small mouth and feeble occlusal force of immatures may be the major constraint for not feeding on large and hard walnuts. Such requirement of sufficient physical strength and

dental development in extractive foraging is also reported in tufted capuchin monkeys to feed on *Maximailiana maripa* fruit (Gunst, Leca, Boinski, & Frgaszy, 2010), larvae in a bamboo stalk (Gunst, Boinski, & Frgaszy, 2010), and in western lowland gorillas (*G. gorilla gorilla*) to feed on the hard seeds of *Coula edulis* (van Casteren et al., 2019). Five-year-old female (*Mb*) was the youngest monkey that showed complete cracking. Thus, Kinkazan Japanese macaques may acquire enough physical strength to crack a walnut shell at around this age. However, growth rate of Japanese macaques shows considerable individual differences during adolescence (Hamada & Yamamoto, 2010). This may explain why another five-year-old female (*Kn*) did not show even partial cracking. The absence of complete and/or partial cracking in older monkeys can also be caused by influence of physical strength. In Japanese macaques, decrease in body weight and musculoskeletal aging start around 15 years of age (Hamada & Yamamoto, 2010). Thus, a lack of complete and even partial cracking in two 19–20-year old females (*Na* in both years and *Tr* in 2016) may be explained by declining dental strength by aging. These results imply that Japanese macaques require certain physical strength for cracking the hard shell of the walnuts.

However, it should be noted that physical strength may not be the only prerequisite for complete cracking behavior. In fact, four adult females aged 7–9 years

(*Nt*, *Ak*, *Ac*, and *My*) never showed complete cracking despite their physical maturity. As they exhibited partial cracking, they seemed to have acquired adequate physical strength to crack the walnut shell but only partially, suggesting that the achievement for complete cracking requires the acquisition of certain feeding techniques in addition to physical strength.

In this study, I identified four cracking methods from 17 complete cracking individuals and found that composition of five behavioral elements within the cracking stage varied with the methods. *Crunch* is regarded as a strength-dependent method for only fully matured males because of paucity of walnut manipulation actions (i.e., “rotate” and “shift”) and short processing duration. Although *bilateral-crack* and *unilateral-crack* involved the identical process of splitting walnuts, composition of the elements was different from each other. In *bilateral-crack*, high proportion of “rotate” and high frequency of “shift” may be effective to adjust biting point for cracking two opposed places on the shell efficiently. On the other hand, in *unilateral-crack*, low proportion of “rotate” (it means high proportion of “look”) and low frequency of “shift” may be effective in checking biting point precisely and to crack only one side of the shell without gaps between each biting action. *Hole-punch* was observed in only *Mk*, and noticeable manipulation feature was a low proportion of “bite with molars” (it means high proportion

of “bite with incisors”). Since the occlusal force of incisors was less than half of that of molars in rhesus macaques (Dechow & Carlson, 1990), use of incisors may not be appropriate to crack the hard shell. However, there were no significant differences in processing duration among the three methods within females. This result implied that hole-punch, which seems maladapted to crack walnuts, is able to achieve feeding efficiency equivalent to other methods in terms of processing duration. However, as the monkeys sometimes left some debris of cotyledon with cracked shell fragments, especially in *crunch* and *hole-punch*, the actual intakes of cotyledon were unclear. Measurement of intake of cotyledon will be necessary for detecting feeding efficiency in future studies. The presence of the four methods suggests that walnut feeding by these macaques is not only by a brute force but requires manual and oral processing skills for the achievement of complete cracking.

I found some sex-specific differences in walnut feeding behavior in wild Japanese macaques. Sexual differences in feeding efficiency are reported in some primate species and are likely to be observed when species with large sexual dimorphism feed on foods which require physical strength (Gunst et al., 2010; Nakagawa, 1999; Post, Hausfater, & McCuskey, 1980; van Casteren et al., 2019). Additionally, in such cases, the food processing pattern also seems to be different between sexes. For instance, in stone

tool-use of wild long-tailed macaques where body size of males is 1.5 times as large as that of females, males use large stones with small number of strikes, while females use small stones with large number of strikes to open shelled food items (Gumert et al., 2011). In the current study, males processed a walnut significantly more rapidly than females. Since Japanese macaque males become heavier than females in their fourth year (Inoue, 1988), the observed sexual difference in processing duration on walnuts can mainly be attributed to sexual difference in body size. Moreover, there were sex-specific differences in cracking methods as well, and it may also be influenced by body size. It is easy to understand that the crunch method, the simplest of all methods, was employed only by males that are equipped with more physical strength. Females, on the other hand, may need to compensate their physical inferiority with increasing the walnut manipulations, such as “rotate” and “shift”, in their methods. It will suggest that acquiring at least one of three cracking methods except for crunch is necessary for females to achieve complete cracking.

In walnut feeding, Japanese macaques conducted frequent omitting, combining, and repeating of some behavioral elements and stages. As I discussed above, the composition of five behavioral elements within cracking stage differed from each cracking method. For example, the monkeys that employed *bilateral-crack* combined

“bite with molars” and “rotate” and omitted “bite with incisors”. In *unilateral-crack*, on the other hand, the monkeys combined “bite with molars” and “look” and omitted “rotate” frequently. Moreover, the frequent use of “bite with incisors” instead of “bite with molars” was observed only in *hole-punch*. The identical flexibility in composition of behavioral elements have been observed in food processing by other macaque species. They emphasized that these food processing by the macaques showed some behavioral features of hierarchical organization that has mainly been reported in great apes (Tan et al., 2016; Trébouet et al., 2018). The finding suggests that the walnut processing by wild Japanese macaques may also be considered as a cognitively challenging behavior in terms of hierarchical organization.

Primate species will require either specialized morphological adaptation or technical skill adaptation for engaging extractive foraging. Some primate species, for instance, show dental adaptation for the consumption of mechanically protected foods (Martin et al., 2003; Norconk & Veres, 2011; Daegling et al., 2011; McGraw et al., 2011; 2014). Wild western lowland gorillas’ robust masticatory apparatus enables them to access the nutrient endosperm of *C. edulis* (van Casteren et al., 2019). Aye-ayes (*Daubentonia madagascariensis*) have an unusually thin middle finger for tap-scanning behavior to excavate insects from deadwoods (Erickson, 1994). On the other hand, some

primates such as chimpanzees, capuchin monkeys and long-tailed macaques, gain access to nutritious hard foods without the morphological adaptations through the innovation of technical skills, i.e. the use of hammer stones (McGrew, 1992; Frigaszy et al., 2004; Ottoni & Mannu, 2001; Gumert et al., 2011; Malaivijitnond et al., 2007). Behavioral innovation, that occurs most often in foraging context, can enhance the fitness of primates by allowing individuals to access new food sources or acquire more efficient feeding techniques (Byrne & Byrne, 1993; Day, Coe, Kendal, & Laland, 2003; Reader & Laland, 2001). Kato et al. (2014) revealed that Japanese macaques had the highest enamel thickness among six *Macaca* species, but the authors suggested that the thick enamel is not an adaptation to hard-object feeding due to a low proportion of hard foods in their diets. In fact, the case that a female chipped her tooth while feeding a walnut (Tamura, personal observation; Supplement 5) implies that the dental morphology of Japanese macaques is not strong enough to crack the hard shells. Although there is the potential risk of the damage of teeth and high energetic cost for cracking actions, the nutritious cotyledon will encourage the macaques to consume the walnuts without morphological adaptations. Also, given no observations of walnut feeding by the macaques in Kinkazan for over 10 years despite the presence of walnuts (Izawa, 2009; Nakagawa, 1997), it can be said that Japanese macaques somehow innovated novel flexible feeding techniques to

access the new nutritious food source.

The ability of innovation has long been considered as an important force of brain evolution, and many previous studies has shown a significant correlation between the frequency of behavioral innovation and brain size in primates (Lefebvre, Reader, & Sol, 2004; 2013; Navarrete, Reader, Street, Whalen, & Laland, 2016; Reader et al., 2011; Reader & Laland, 2001; 2002). Japanese macaques showed several innovative behaviors so far, such as “sweet-potato washing” and “wheat placer mining” behaviors (Hirata, Watanabe, & Kawai, 2008; Kawai, 1965), and *Macaca* genera was included high intelligence lineage in primates in term of the innovativeness (Reader et al., 2011). Therefore, the innovative behavior in walnut feeding lends further support the fact and will provide a new insight of intelligence of the species.

In extractive foraging, many primate species deal with similar types of food defenses with or without external objects. Whereas, wild chimpanzees use tools for extracting termites from the mound (McGrew, 1992), wild western lowland gorillas adopt manually pounding technique for gathering termites onto a palm from a termites’ mound fragment (Cipolletta et al., 2007; Salmi, Rahman, & Doran-Sheehy, 2016). As to food with prickly defenses, wild Sumatran orangutans (*Pongo pygmaeus*) use a short straight branch as a tool to detach the seeds of *Neesia* (*Neesia cf. malayana*) fruits

which have stinging hairs (van Schaik & Knott, 2001), in contrast wild mountain gorillas, chimpanzees, and some Old World monkey species cope with prickly plant foods by only dexterous manual processing as mentioned above. On the other hand, in the case of hard-shelled foods, only tool-use of stone hammer by chimpanzees, capuchins, long-tailed macaque, and some substrate use by capuchins have been well reported to date. To my knowledge, this study is the first report that illustrates the presence of certain feeding techniques to overcome hard-shelled obstacle without tools and even substrates in primate lineage.

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806

Table 1. Twenty-one elements within six stages used in the processing of walnuts by Japanese macaques

Behavioral element	Description
Acquiring stage	
<i>Pick up</i>	A monkey picks up a walnut on the ground with thumb and fingers.
<i>Remove husk</i>	A monkey detaches husk (exocarp and mesocarp) over a seed with mouth or hands.
<i>Glance</i>	A monkey watches a walnut in its hand, possibly investigating the surface of the walnut.
<i>Sniff</i>	A monkey sniffs a walnut from its hand, possibly investigating the smell of the walnut.
<i>Mouth</i>	A monkey puts a walnut in its hand and into mouth in an instant, possibly investigating the texture and/or hardness of the walnut.
<i>Discard</i>	A monkey drops a walnut on the ground.
Transporting stage	
<i>Pinch-carry</i>	A monkey walks carrying a walnut in one fist.
<i>Bite-carry</i>	A monkey walks carrying a walnut in its mouth.
Rubbing stage	
<i>Rub</i>	A monkey repeatedly pushes and pulls a walnut with one hand against the ground, fallen tree, or rock.
Cracking stage	
<i>Bite with molars</i>	A monkey places a walnut between upper and lower right/left molars and bites on the shell.
<i>Bite with incisors</i>	A monkey places a walnut between upper and lower incisors and bites the shell.
<i>Look</i>	A monkey pulls a walnut out of its mouth and looks at it holding with one or both hands.
<i>Rotate</i>	A monkey pulls a walnut out of its mouth and rotates it with both hands.
<i>Shift</i>	A monkey shifts a walnut from right molars to left or <i>vice versa</i> before biting.
Splitting stage	
<i>Hand-split</i>	A monkey holds both hemispheres of walnut with both hands and pulls in opposite directions to split into halves.
<i>Mouth-split</i>	A monkey holds both hemispheres of walnut with one hand and mouth and pulls by hand to split into halves.
Cotyledon-eating stage	
<i>Keep with hand</i>	A monkey holds one half of walnut with one hand while eating another half with the opposite hand.
<i>Keep with foot</i>	A monkey holds one half of walnut with one foot while eating another half with one or both hands.
<i>Put on ground</i>	A monkey puts one half of walnut on the ground while eating another half with one or both hands.
<i>Extract with mouth</i>	A monkey extracts cotyledon from seeds directly by mouth and ingests it.
<i>Extract with finger</i>	A monkey picks cotyledon from shell by the index finger and ingests it

Table 2. Observation days of *complete cracking* and *partial cracking*

		<i>Complete cracking</i>		<i>Partial cracking</i>
Name	Age	in 2015	in 2016	in both years
Males				
<i>AS</i>	12	48	20	-
<i>FM</i>	11	34	-	-
<i>TY</i>	9	39	17	-
<i>RK</i>	7<	32	9	-
<i>KR</i>	7<	32	5	-
<i>TM</i>	7	7	1	-
<i>NO</i>	1	0	0	0
<i>TP</i>	1	0	0	0
<i>TO</i>	1	0	0	0
<i>MT</i>	0	0	0	0
Females				
<i>Na</i>	19	0	0	0
<i>Tr</i>	18	13	0	1
<i>Ku</i>	14	37	15	-
<i>Mk</i> [†]	12	27	6	-
<i>Kr</i>	11	40	12	-
<i>Tm</i> [†]	10	31	18	-
<i>Kh</i>	9	44	12	-
<i>Ak</i> [†]	9	0	0	2
<i>Nt</i> [†]	7	0	0	2
<i>Tn</i>	7	38	19	-
<i>Tt</i> [†]	7	46	19	-
<i>An</i>	7	16	3	-
<i>Ht</i>	7	41	15	-
<i>My</i> [†]	7	0	0	6
<i>Ac</i> [†]	6	0	0	3
<i>Kn</i>	5	0	0	0
<i>Mb</i>	5	26	12	-
<i>Kt</i>	4	0	0	0
<i>Ke</i>	3	0	0	0
<i>Mf</i>	2	0	0	0
<i>Kc</i>	1	0	0	0
<i>KK</i>	1	0	0	0
<i>Ns</i>	1	0	0	0
<i>Az</i>	1	0	0	0
<i>Tl</i>	1	0	0	0
<i>Hr</i>	0	0	0	0

[†] : Females for focal animal sampling in 2015.

Table 3. The number of each cracking method by individuals who showed at least one *complete cracking*

Individual	<i>Crunch</i>	<i>Unilateral-crack</i>	<i>Bilateral-crack</i>	<i>Hole-punch</i>
Males				
<i>AS</i>	22*	4	0	0
<i>FM</i>	12*	2	0	0
<i>TY</i>	0	13*	0	0
<i>RK</i>	0	1	0	0
<i>KR</i>	9	17*	0	0
<i>TM</i>	0	3	0	0
Females				
<i>Kr</i>	0	0	17*	0
<i>Kh</i>	0	0	20*	0
<i>Ku</i>	0	2	17*	0
<i>Tn</i>	0	10	4	0
<i>Tm</i>	0	0	62*	0
<i>Tt</i>	0	0	138*	0
<i>An</i>	0	0	4	0
<i>Ht</i>	0	0	14*	0
<i>Mk</i>	0	0	0	21*
<i>Mb</i>	0	0	22*	0

*: cracking type which was significantly biased ($P < 0.05$).

Figure legend

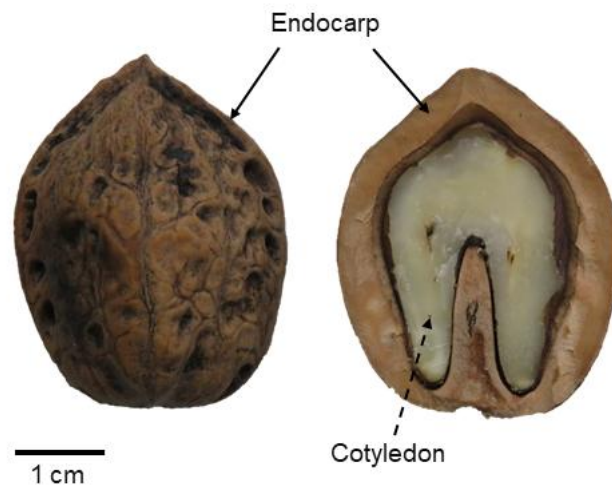
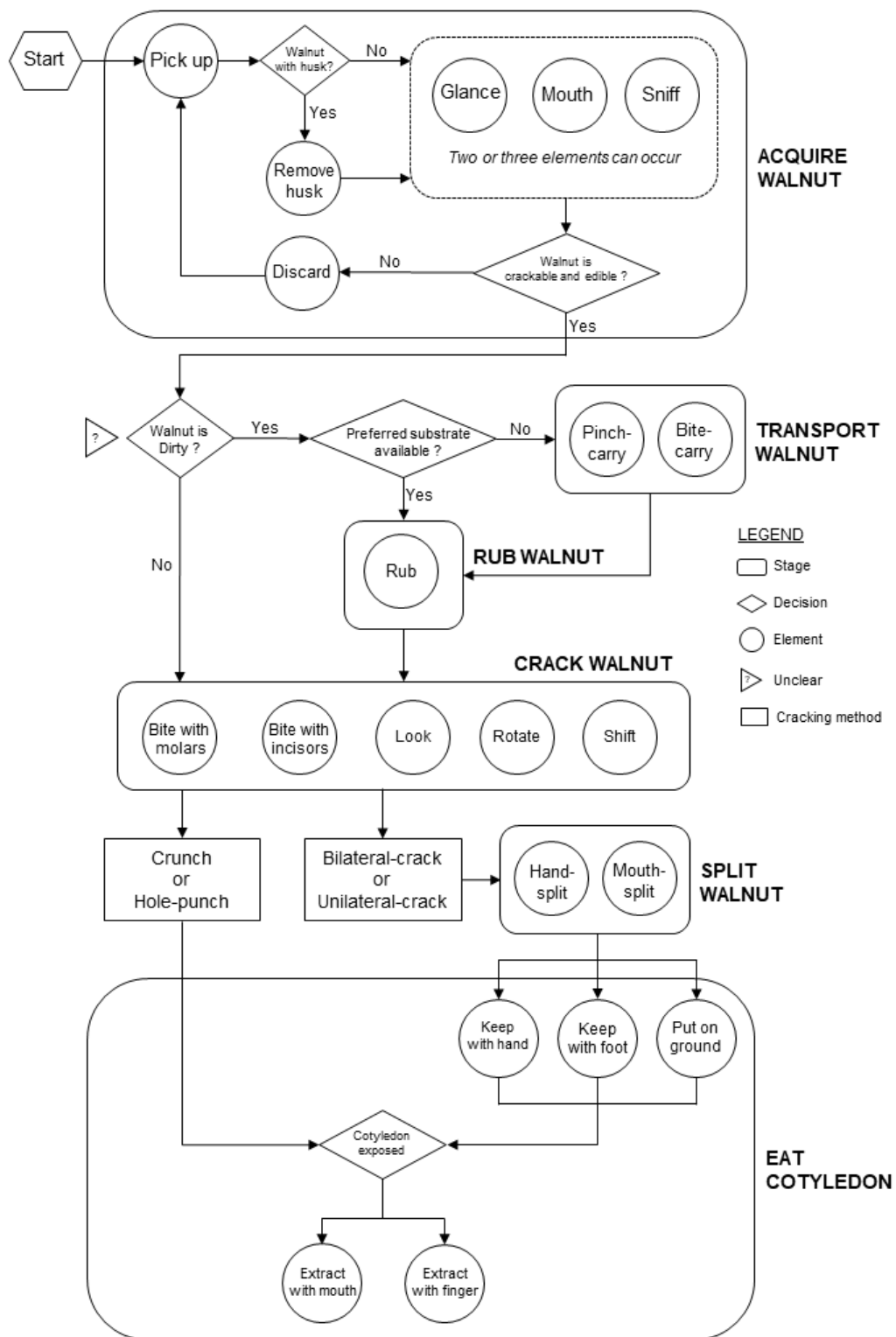


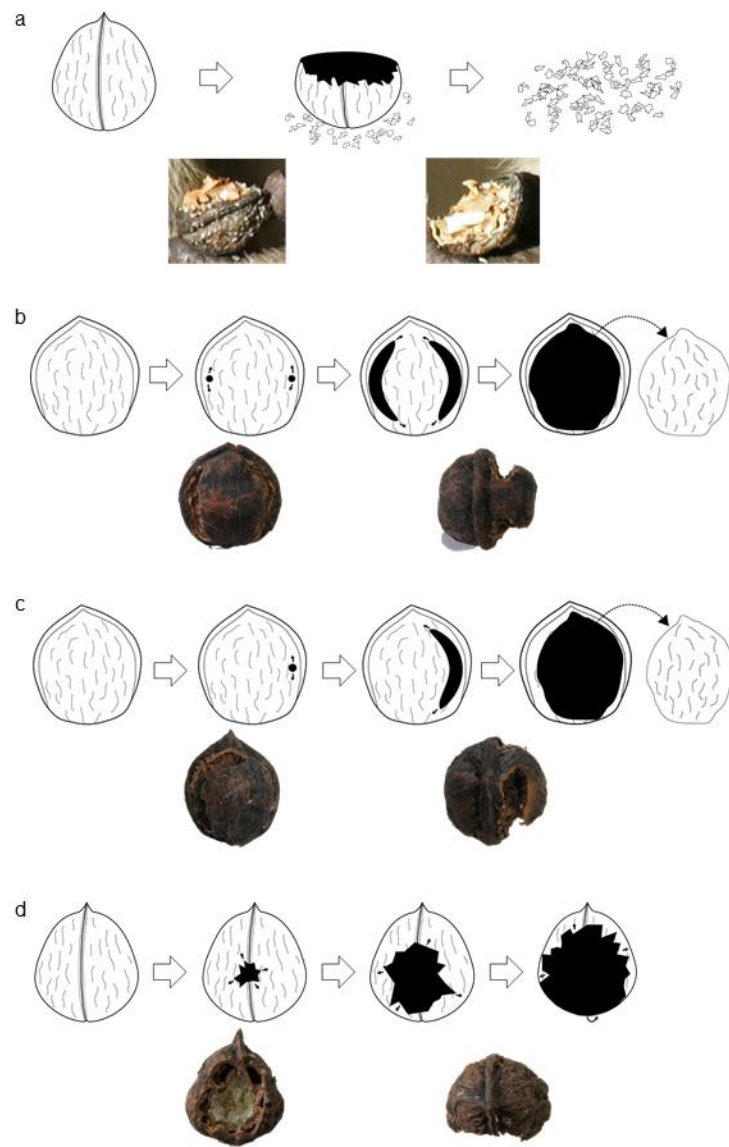
Figure 1

Photograph of a Japanese walnut which was consumed by Japanese macaques in Kinkazan Island. Arrows with a solid line indicate hard-shell, the endocarp, that the monkeys cracked. Arrow with a dotted line indicates the cotyledon that the monkeys extracted.



818 Figure 2

819 Six stages and 21 elements of walnut feeding by wild Japanese macaques.



820 Figure 3

821 Illustrations and photographs of walnuts being processed with four cracking methods. (a)

822 crunch, (b) bilateral-crack, (c) unilateral-crack, and (d) hole-punch. Photos accompanying

823 crunch are from video footages. Other photos are of feeding traces when monkeys gave

824 up feeding. Black areas in the illustrations indicate cracked parts of the shell. Small

825 arrows on the walnuts indicate directions of cracking.

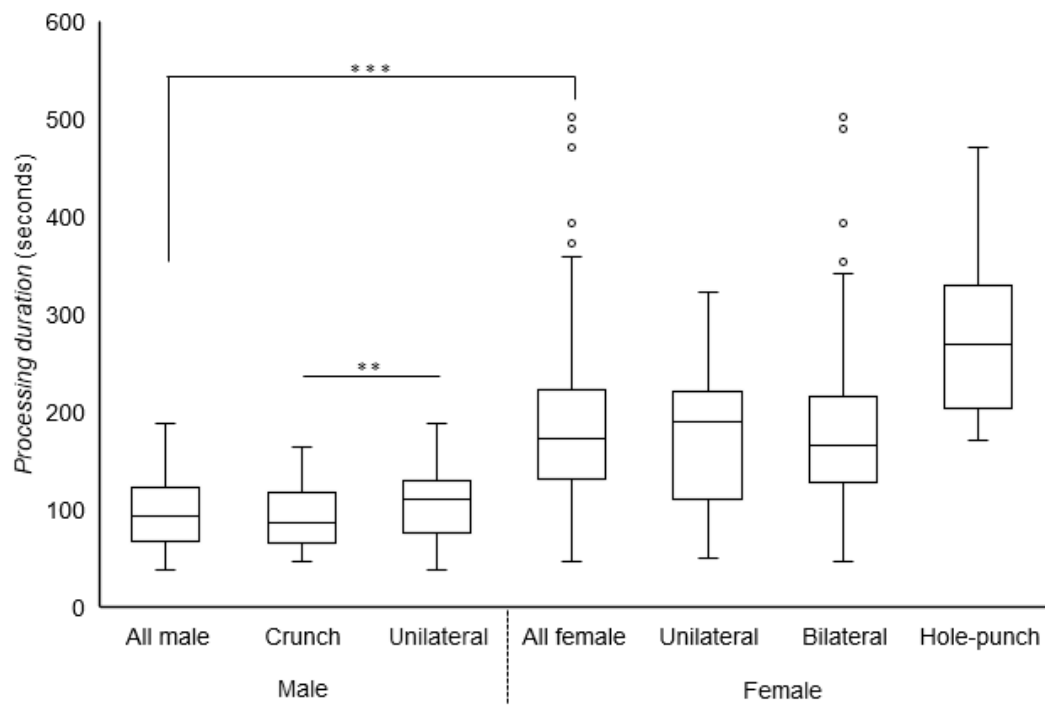


Figure 4

Processing duration of one walnut in each sex and cracking method. Line within the box, top of the box, bottom of the box, upper of the whisker, lower of the whisker and white circle indicate median, first quartile, third quartile, maximum, minimum, and outlier, respectively (The same applies hereinafter). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

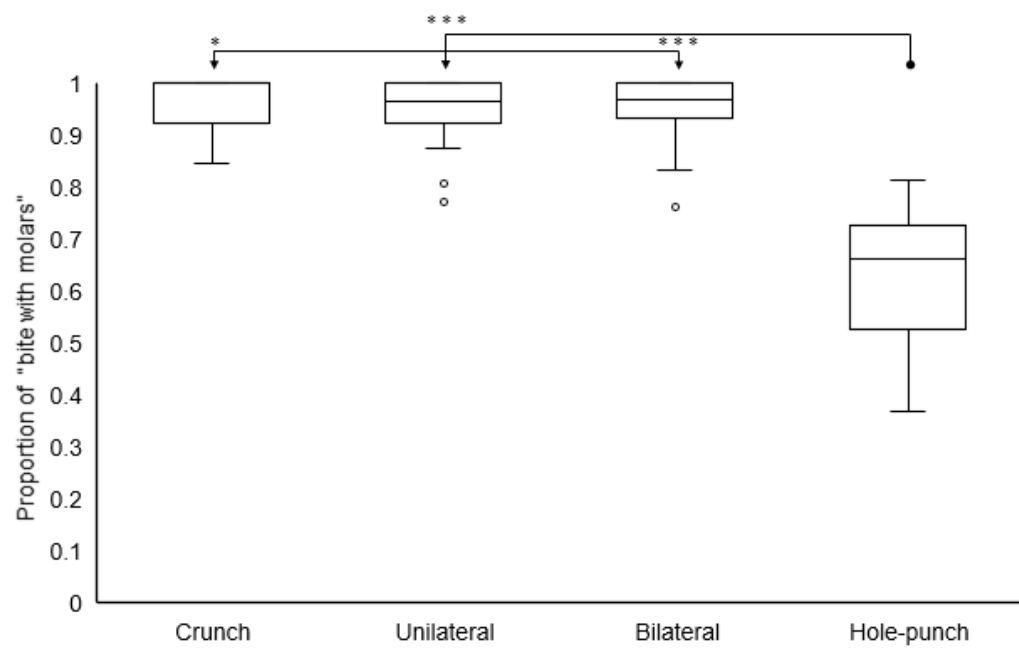
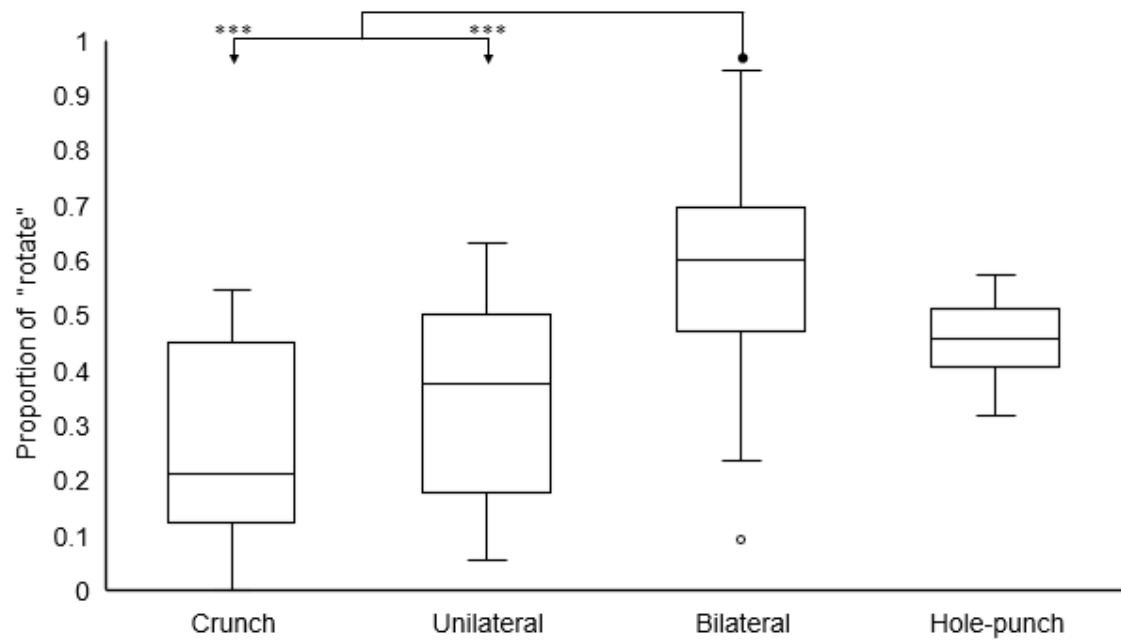


Figure 5

Proportion of "bite with molars" in each cracking method. Significant difference is found between a sample with a black circle and samples with arrows (The same applies hereinafter). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

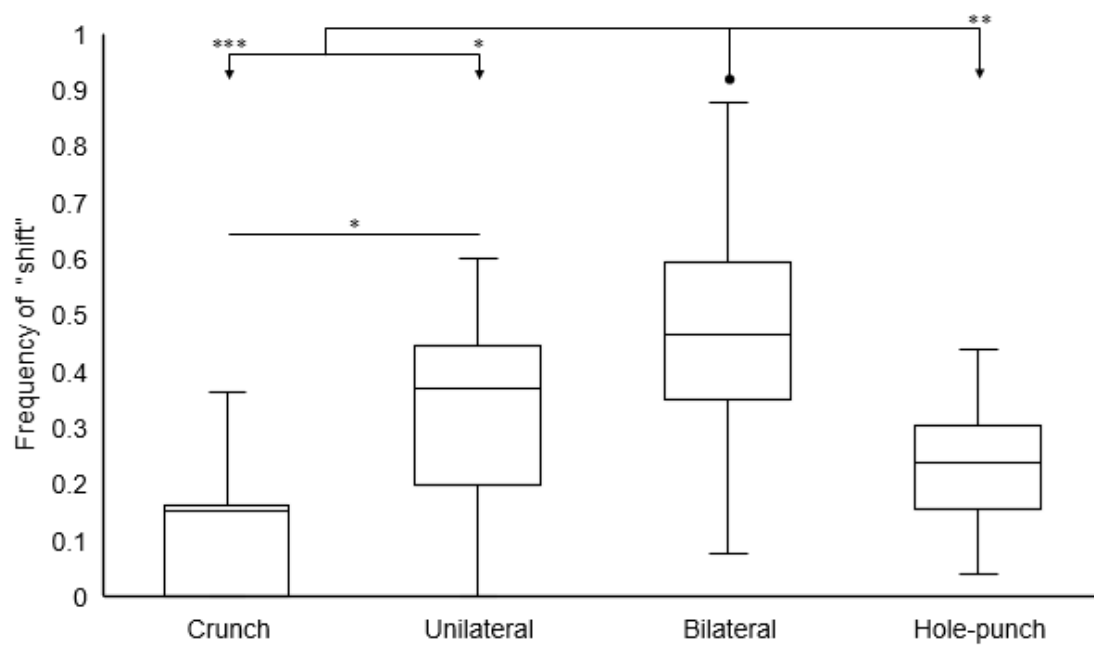


836 Figure 6

837 Proportion of “rotate” after monkeys put walnut out of mouth in each cracking method. *

838 $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

839



840 Figure 7

841 The occurrences of "shift" per one biting action in each cracking method. * P < 0.05, **

842 P < 0.01, ***P < 0.001.