Biological Journal of the Linnean Society, 2019, **127**, 543–562. With 7 figures.

Manual skills for food processing by mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda

JOHANNA NEUFUSS[1*], MARTHA M. ROBBINS[2], JANA BAEUMER[2], TATYANA HUMLE[3] and TRACY L. KIVELL[1,4]

[1]*Animal Postcranial Evolution (APE) Laboratory, Skeletal Biology Research Centre, School of Anthropology & Conservation, University of Kent, Canterbury, UK*
[2]*Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
[3]*Durrell Institute of Conservation and Ecology, School of Anthropology & Conservation, University of Kent, Canterbury, UK*
[4]*Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*

Received 19 March 2018; revised 7 May 2018; accepted for publication 14 May 2018

Although gorillas rarely use tools in the wild, their manipulative skills during plant processing may be similar to those of other tool-using great apes. Virunga mountain gorillas (*Gorilla beringei beringei*) are known for the complexity in their methods of thistle and nettle plant preparation in the wild. However, there are no comparable data on food processing in the population of mountain gorillas from the Bwindi Impenetrable National Park, Uganda. We investigated the manual actions and hand grips used when accessing edible parts of two hard-to-process plants defended by stinging hairs, epidermis or periderm (i.e. peel of *Urera hypselodendron* and pith of *Mimulopsis arborescens*), and one undefended plant (i.e. leaves of *Momordica foetida*) in 11 Bwindi wild mountain gorillas using video records *ad libitum*. Similar to thistle feeding by Virunga gorillas, Bwindi gorillas used the greatest number of manual actions for the most hard-to-process plant (*U. hypselodendron*), and the actions were ordered in several key stages and organized hierarchically. The demands of processing plant material elicited 19 different grips and variable thumb postures, of which three grips were new and 16 grips have either been previously reported or show clear similarities to grips used by other wild and captive African apes and by humans. Moreover, our study only partly supports a functional link between diet and hand morphology in mountain gorillas and suggests that the gorilla hand is best adapted to forceful grasping that is required for both manipulation and arboreal locomotion.

ADDITIONAL KEYWORDS: dexterity – feeding skill –gorillas – great ape –manipulative behaviour – precision grip – thumb.

INTRODUCTION

Although gorillas rarely use tools in the wild (Breuer, Ndoundou-Hockemba & Fishlock, 2005; Grueter *et al.*, 2013; Kinani & Zimmerman, 2015), they eat foods that require complex processing and thus arguably require enhanced manipulative skills similar to those of other great apes that more commonly use tools (e.g. chimpanzees). The work of Byrne and colleagues (e.g. Byrne & Byrne, 1991, 1993; Byrne, 1994; Byrne, Corp, Byrne, 2001a, b) in the Virunga Mountains, Rwanda, was the first to highlight the complex methods of plant preparation used by wild mountain gorillas (*Gorilla beringei beringei*). Some of the main herbaceous foods in the Virguna mountain gorilla diet (e.g. thistle leaves and stems, nettle leaves) involve the need to first remove the physical defences as well as indigestible parts of the plants such as stings, spines, minute hooks and hard casings (Byrne & Byrne, 1991). Thus, these foods require a hierarchy of multi-stage processes of manual preparation before they can be eaten. It has long been hypothesized that complex behaviour

*Corresponding author. E-mail: jn259@kentforlife.net

typically is hierarchically organized, which is made up of regular sequences of actions that include relational combinations, is used repeatedly and occurs under voluntary control (Lashley, 1951; Dawkins, 1976). If an animal's behaviour is hierarchically structured, as has been argued for great apes (Byrne, 1994; Byrne & Russon, 1998), then the number of levels in the hierarchy could be counted (Byrne et al., 2001a). The hierarchical organization of mountain gorilla food processing is complex because it involves several functionally distinct hand actions ordered from the start to the end, different types of hand grips, and digit role differentiation (Byrne & Byrne, 1993; Byrne *et al.*, 2001a, b; Byrne, 2004). Processing leaves of the thistle *Carduus* by Virunga mountain gorillas is considered the most complex task, involving the greatest hierarchical organization of all the plants eaten to overcome the thistle's physical defences (Byrne et al., 2001a). However, we do not know whether plant foods with other types of strong physical defences, such as woody stems, require a similar level of processing complexity to that of thistle-stemmed plants, and there are no comparable data on any type of food processing in the other population of wild mountain gorillas, those of the Bwindi Impenetrable National Park, Uganda. Furthermore, a thorough investigation of the hand grips used during food processing has not been done for any gorilla population. Thus, here we investigate the processing steps (i.e. manual actions) and hand grips used by Bwindi mountain gorillas when eating three plant foods: two with physical defences, *Urera hypselodendron* with stinging hairs on the edible peel of the hard or soft tissue stems (i.e. epidermis), and *Mimulopsis arborescens* with a bark (i.e. periderm) as a barrier that gorillas need to go through to access the pith, and one without a physical defence, i.e. the leaves of *Momordica foetida*.

The Bwindi mountain gorillas live at a lower altitude (2100–2600 m; Robbins & McNeilage, 2003), with a higher mean annual temperature and greater plant diversity (Butynski, 1984) compared to the mountain gorillas of the Karisoke Research Center in the Virunga Volcanoes. Thus, the diet of Bwindi mountain gorillas differs greatly that of Virunga mountain gorillas, with more and different species of both arboreal fruits and terrestrial herbaceous vegetation (Watts, 1984; McNeilage, 2001; Ganas *et al.*, 2004; Ganas, Ortmann & Robbins, 2009; Wright *et al.*, 2015). The Bwindi gorillas consume a range of fibrous foods, including vines and stems defended by herbaceous or woody casings, as well as leaves that lack physical defences (Ganas *et al.*, 2004, 2009). They also consume several plant parts (i.e. leaves, pith, peel or bark) of various abundant plant species but eat thistle (*Carduus nyassanus*) only about once a month on average (Ganas *et al.*, 2004; Robbins, Nkurunungi & McNeilage, 2006). This is in contrast to Virunga gorillas that frequently consume leaves (22.1%; Watts, 1984) and stems (9.4%; Watts, 1984) of the highly abundant thistle *C. nyassanus* in the high altitude of the areas surrounding the Karisoke Research Center (e.g. Watts, 1984; McNeilage, 2001). This ecological variation between Bwindi and the Virunga mountains leads to different adaptive foraging strategies between the two mountain gorilla populations, which may reveal differences in the complexity of their food-processing behaviour.

Alongside tool-use, herbaceous food processing presents a good model of the demands of object manipulation on the non-human primate hand, and on the gorilla hand in particular. The range of manipulative actions used to procure and process available foods has been shown to elicit different grip patterns and hand movements in Virunga mountain gorillas, as well as in Mahale chimpanzees (e.g. Byrne *et al.*, 2001b; Marzke *et al.*, 2015). However, only six hand grips were described for gorilla thistle preparation based on broad grip categories and the number of digits involved (e.g. scissor precision grip, hook and power grips; Byrne *et al.*, 2001b), which do not provide the detail needed for a comparative functional analysis of gorilla manipulation to that of other apes (including humans). To better understand what the hands of gorillas can do when they manipulate an object, systematic study of the repertoire of grips and hand movements as well as the role of each hand and their possible complementary roles is needed (e.g. Byrne *et al.*, 2001b; Marzke *et al.*, 2015; Heldstab *et al.*, 2016). Thus, the present study provides a detailed description of the areas of contact within the gorilla hand and quantifies the relative frequency of grips used during the manipulation of three different plant foods. Processing plant materials to access edible parts may provide substantial challenges, as the hand has to adjust to varying sizes, shapes and toughness, including physical defences (i.e. stinging hairs, epidermis, periderm), and accommodate loadings exerted on the hand during retrieval and processing.

Furthermore, Marzke (2006) suggested that potential stresses associated with forceful retrieval and processing of tough vegetation and fauna may have been a factor in the evolution of features in hominin hands that were preadapted to the requirements of forceful precision grips in tool making.

Additionally, data on how apes use their thumb during food processing are rare and, to our knowledge, exist only for Mahale chimpanzees (Marzke *et al.*, 2015). This research will fill the gap by examining how gorillas use their thumb when manipulating plant foods.

The aim of this study is to provide the first insights into the behavioural complexity and manual skills of Bwindi mountain gorillas during the processing of three different plants: two woody-stemmed plants (*U. hypselodendron*, *Mimulopsis arborescens*) for which the food is more challenging to access in comparison to leaves (*Momordica foetida*), which are relatively simple to process because they lack physical defences. First, we predict that plants with physical defences (i.e. stems with stinging hairs, epidermis or periderm) require a higher number of manual actions and thus are more complex to process than undefended plants (i.e. leaves). Second, we predict that defended plants would elicit a greater number of hand grips as they require more manual actions than undefended plants.

MATERIAL AND METHODS

Study site and data collection

Mountain gorillas were observed in the Bwindi Impenetrable National Park (331 km²). Data were collected on 11 individuals of one fully habituated group of gorillas (Kyagurilo) between February and March 2015 (Table 1). The subjects included seven adult females and four males, which included one subadult (6–8 years), one blackback (8–12 years) and two silverbacks (≥ 12 years) (Czekala & Robbins, 2001; Robbins, 2001). The mountain gorillas were observed for an average of 4 h/day, and a minimum of 7 m had to be maintained between the gorillas and the observer to reduce the risk of disease transmission. High-definition video was filmed *ad libitum* at a frequency of 50 Hz (HDR-CX240E, Sony). All processing sequences were recorded at relatively close range (7 m to ~20 m) and from multiple angles (i.e. frontal, lateral, back-view) during plant processing. Focal samples, periods in which specified information is collected from only one individual at a time (Altmann, 1974), were used to collect data from all individuals.

Plant foods

The three plant foods studied here were plant species that are a common part of the Bwindi mountain gorilla's diet (e.g. Ganas *et al.*, 2004, 2009). The plant parts consumed are fibrous foods, including (1) the peel (epidermis of a herb's stem) of the soft wooded liana *U. hypselodendron*, (2) the pith of the woody tissue stem of *Mimulopsis arborescens* and (3) the leaves of the climbing vine *Momordica foetida*.

Data analysis

We compared the processing techniques of Bwindi gorillas to what is known of processing the strongly defended *Carduus* thistle in Virunga mountain gorillas. We referred to the ordered sequence of discrete behavioural elements (Byrne & Byrne, 1993) as 'manual actions' performed by one individual.

Manual actions of plant processing

Gorillas often accumulate edible items by the handful and eat then all at once, and thus the basic unit for the quantitative analyses was the 'handful', following Byrne & Byrne (1991). Usually, gorillas process and eat several handfuls of a food type one after the other, before switching to a new food, or stopping feeding. Food processing behaviour for any given individual was divided into 'sessions' and 'bouts'. A session was defined as a period in which one individual was engaged in food processing. A session was terminated when the individual stopped feeding and walked away, and/or started a new behaviour. A session was generally composed of multiple bouts. A bout was defined as a period of feeding on a single food type for 10 s or more, without interruption, and can include many separate handfuls of the same food object. A bout was considered terminated if there was a change of plant type (e.g. change from stem to leaf eating) or when food preparation was interrupted by another behaviour. A bout was composed of multiple isolated acts of 'manual actions' of plant processing that are required to resolve particular problems of a task and could involve repetitions of the same action until each stage of processing was completed. These manual actions are described in terms of the grip, posture and/or movement, and they can be either 'manipulative' (i.e. moving or processing the object) or 'supportive' (i.e. stabilising the object). Following Byrne *et al.* (2001a), actions were scored in two ways: (1) 'functionally similar' when the result achieved was the same, even when the manipulative movement was different ('picking off' as a variant of 'stripping up' leaves) and (2) 'functionally distinct' when the resulting changes were different (e.g. 'stripping up' leaves versus 'brush-off' debris). Among these actions, there are 'obligate-actions' that are required to resolve a task and consistently used across all studied individuals, and 'optional-actions' that are more variably used across individuals. To analyse the frequency of distinct manual actions per plant, functionally similar actions were pooled into a single functionally distinct action category if they effected the same result (yank stem was pooled into pulling; rotate-push was pooled into break-off; spaghetti-feed was pooled into sausage-feed, see Table 2), following Byrne *et al.* (2001a). The frequency of each action was first tallied across the number of bouts for each individual to examine the individual frequency. Then a total mean frequency was calculated across all individuals for each action. Only those manual actions used with more than 25% frequency across all individuals were considered frequent enough to be retained for statistical analysis.

Table 1. Summary of data for each gorilla individual

Plant species	Individual ID	Sex/age	Total number of sessions	Total number of bouts	Total number of of hand actions	Number of functionally distinct hand actions
Urera hypselodendron (consuming peel)	JN	Female/adult	3	7	36	7
	ST	Female/adult	8	23	72	8
	KR	Female/adult	3	3	15	5
	TN	Female/adult	1	3	9	4
	TW	Female/adult	2	2	11	6
	MG	Female/adult	1	4	25	6
	BY	Female/adult	3	7	46	7
	RC	Male/silverback	13	24	157	7
	MK	Male/silverback	2	2	33	8
	HP	Male/subadult	2	2	9	5
	KA	Male/blackback	8	20	116	7
Total			**45**	**101**	**529**	
Mimulopsis arborescens (consuming pith)	JN	Female/adult	2	6	37	5
	ST	Female/adult	7	10	61	6
	KR	Female/adult	6	18	119	7
	TN	Female/adult	2	4	27	5
	TW	Female/adult	3	5	42	5
	MG	Female/adult	3	9	42	5
	BY	Female/adult	4	13	41	5
	RC	Male/silverback	5	12	115	8
	MK	Male/silverback	4	9	55	6
	HP	Male/subadult	6	10	51	5
	KA	Male/blackback	2	7	23	5
Total			**44**	**103**	**613**	
Momordica foetida (consuming leaf)	JN	Female/adult	3	13	55	4
	ST	Female/adult	2	7	25	5
	KR	Female/adult	4	13	56	5
	TN	Female/adult	2	5	23	4
	TW	Female/adult	6	12	71	5
	BY	Female/adult	9	26	117	5
	RC	Male/adult	6	37	172	5
	HP	Male/subadult	3	18	103	5
	KA	Male/blackback	3	10	60	5
Total			**38**	**141**	**682**	

Each session of processing comprised several manual actions that mountain gorillas use in the same ordered and coordinated manner (e.g. Byrne & Byrne, 1993). The order of different manual actions can be organized into stages, which follow a structural logic because each stage is dependent on the last one. We describe these processing stages as 'key stages' following Byrne & Byrne (1993). Several different key stages must be sequenced during processing, some of which may be iterated to build up larger amounts of food and thus are 'hierarchically organized' to function as subroutines (for details of hierarchical organization see Byrne & Byrne, 1993; Byrne & Russon, 1998; Byrne *et al.*, 2001a).

Hand grips during plant processing

For each individual, grips and movements were identified within a manual action of processing. For all three plants, a bout often involved repetitions of the same manual action with the same grip, and changes in grips occurred

Table 2. Manual actions used across all three plant foods

Manual action	Description
bite-off*[a]	Use teeth to cut off portion of naturally attached or hand-supported object; hands resist pull of teeth.
break-off*[b]	Both hands pull stem away from teeth to break it apart; teeth resist pull of hands; same effect as rotate-push.
brush-off*[a], [c]	Using flexed index and thumb crossed over (held in 'C' shape) to gently brush along stem, midrib or bundle in order to dislodge debris.
accumulate**[c]	Accumulate food items in hand and move for feeding towards mouth. Typically used for handful of leaves.
knuckle-push*[b]	Fist held as is in knuckle-walking to apply force to break naturally attached object, supported by opposite hand.
peel-back*[a]	One or both hands are used to pull stem away from teeth while teeth detach outer casing. Occasionally opposite hand is used as support.
pick-up*[a], [b]	Pinch-grip used to lift stem from ground.
pick-off, pick-out*[c]	Pinch grip on small item that is pulled off an object held in other hand or picked out from among a mass of items.
pulling*[a], [b]	Holding a naturally attached object with one hand and pull into range, thus applying force to detach item; same effect as yank.
rotate-push*[b]	Turn or twist long stem held in firm hand grip (e.g. power grip) and pushed against to break and detach from its natural attachment, supported by opposite hand; same effect as break-off.
sausage-feed*[a]	Repeated loosening grip and re-grasping lower down an approximately sausage-shaped food bundle, in order to insert it into the mouth as a whole (without the bundle coming apart).
scrape-off**[b]	Incisor teeth are used to scrape off soft pith while object is supported with hand(s); hand(s) move up and down.
snip-case**[b]	Use incisor teeth to clip off outer casing in order to discard the casing and expose edible pith.
spaghetti-feed*[a]	With peel held in mouth without use of the hands, lips used to feed in rest of its length – similar to eating spaghetti; same effect as sausage-feed.
strip-up*[c]	Flexed index and thumb held in 'C' shape around leafy stem or midrib of leaf, sliding the hand upwards against force of detachment or the other hand's supporting grip, ending up with holding a bundle of leaves in the hand.
swap-hand*[a], [b], [c]	Transfer object or handful from one hand to other.
tooth-strip**[a]	Hand(s) pull stem through partially closed incisors; hand(s) pull stem either sideways or frontal away from teeth. Typically used for stripping off peel.
twist-off*[c]	Holding a naturally attached object in one hand and twisting, thus applying force to detach object. Occasionally used when picking off leaves.
yank*[a], [b]	Hand(s) used to apply force on object, which is pulled against natural attachment (often to detach the object), or to part of object supported by other hand.

Functionally distinct actions are highlighted in bold. Actions are labelled as optional* and as obligate** (terminology equivalent and follows that of Byrne & Byrne, 1993; Byrne *et al.*, 2001a, b). Actions are labelled for stem-(peel)-[a], stem-(pith)-[b] and leaf-processing[c].

only rarely across repeated hand actions (i.e. 13 grip changes across 1954 hand actions). Thus, only the first grip was recorded during the first occurrence of a hand action to maintain data point independence required for statistical analyses. Hand grips were classified as (1) precision grips, (2) power (palm) grips, (3) hook grips and (4) compound grips following previous studies that have identified these grips in both the wild and captivity (e.g. Napier, 1956; Marzke & Wullstein, 1996; Macfarlane & Graziano, 2009; Pouydebat *et al.*, 2011; Marzke *et al.*, 2015, Bardo *et al.*, 2017). Grip frequency was calculated in two ways: (1) by tallying the number of grip responses with the number of elements per individual to examine the individual frequency for each plant type, and (2) by calculating the total mean percentage from the individual frequencies per hand grip for each plant type. We further examined the frequency of grips relative to elements, to investigate the relationship between a particular grip and the hand action used across the three plant foods.

Statistical analysis

The data on manual actions of plant processing did not meet the normality and homogeneity assumptions for parametric tests. Thus, Mann–Whitney *U*-tests were performed to compare individuals (i.e. sex classes) in their number of functionally distinct actions used to process each plant. This analysis provides further insight into the potential variability of particular manual actions across different plants. The overall sample size was relatively small and thus results of this statistical analysis should be interpreted with caution. The comparison of grip use relative to plant food among individuals was assessed using Friedman rank sum tests (Q). If results were significant, pairwise comparisons were performed using the Wilcoxon signed rank test (Z) with continuity correction. Each individual contributed only one data point to ensure independence of data points.

RESULTS

We recorded 86 video sequences of stem-peel (*U. hypselodendron*) processing and 45 sequences of stem-pith (*Mimulopsis arborescens*) processing in 11 individuals, and 45 sequences of leaf-processing (*Mormodica foetida*) in nine individuals.

Manual actions of plant processing

Analysis of 345 bouts across 11 individuals revealed 19 manual actions for processing all three plant materials, including 16 functionally distinct actions and three functionally similar actions (Table 2). The functionally distinct actions typically included obligate (i.e. used by 100% of individuals) and optional manipulative actions (Table 2). These actions occurred typically in an ordered and coordinated sequence of key-stages within a bout.

Stem-(peel)-processing

(*U. hypselodendron*): This involved one obligate action and six optional actions, which occurred in four key stages (Table 3). A Mann–Whitney U-test revealed that female and male gorillas did not significantly differ in their number of functionally distinct actions ($U = 10$, $N = 11$, $P = 0.436$). The average number of distinct actions used by females was comparable to that used by males (range for females: 4–8 distinct actions; range for males: 5–8) (Table 1).

Stem-(pith)-processing

(*Mimulopsis arborescens*): This involved two obligate actions and two optional actions, which occurred in three key stages (Table 3). Females and males were not significantly different in their number of functionally distinct actions ($U = 10.5$, $N = 11$, $P = 0.442$). Females performed on average a slightly lower number of different actions (range for females: 5–7) as compared to males (range for males: 5–8) (Table 1).

Leaf-processing

(*Mormodica foetida*): This revealed one obligate action and three optional actions, which together occurred in four key stages (Table 3). There was no significant difference in the number of functionally distinct actions ($U = 10$, $N = 9$; $P = 0.260$) between females (range for females: 4–5) and males (range for males: 5) (Table 1).

Table 3. Functionally distinct actions of plant-processing that were most frequently used (i.e. > 25% across all individuals) among the gorilla group ($N = 11$)

Plant part processed	Sequence of actions	Mean absolute frequency (%)	Order of key stages
stem-(peel)-processing	pick up or pull stem	47	1. Initial procurement of the plant
	brush-off leaves	29	2. Remove unwanted parts with support of stem
	bite off length	34	
	peel-back outer casing	64	
	tooth-strip peel**	100	3. Gather stripes of peel into hand
	insert into mouth	77	4. Insert edible peel into mouth
stem-(pith)-processing	pick up stem	49	1. Initial procurement of the plant
	break off length	63	2. Remove unwanted parts with support of stem
	snip-case: bite off hard case**	100	
	scrape-off edible pith**	100	3. Consume edible pith
leaf-processing	pull into range	72	1. Initial procurement of leaves
	pick leaves	65	2. Leaf detachment with support
	accumulate handful of leaves	92	3. Acculuation of items into hand
	put handful into mouth**	100	4. Insert leaf bundle into mouth

**Obligate act(s).

Across the tested individuals for stem-(pith)-processing ($N = 11$) and leaf-processing ($N = 9$), the total mean frequency for each action (i.e. > 25% frequency across all individuals) showed that both plant materials most frequently involved four functionally distinct actions, while stem-(peel)-processing ($N = 11$) required six functionally distinct actions (Table 3).

Hand grips during plant processing

Analysis of the hand grips during plant processing found a total of 19 different hand grips across the 19 actions of plant-processing (Table 4). Bwindi mountain gorillas used eight precision grips, six hook grips, three power grips and two compound grips. This study revealed three hand grips (distal palm grip; interdigital 2/3 brace – pad-to-side; power – pad-to-side; Table 4) that have not been previously reported in the literature and thus are considered to be novel.

Stem-(peel)-processing

(*U. hypselodendron*): This elicited 15 hand grips and showed a significant preference within the group ($Q = 29.04$, $N = 11$, d.f. = 3, $P < 0.001$), using significantly more precision ($Z = 2.94$, $P = 0.003$) and hook ($Z = 2.94$, $P = 0.003$) grasping (Fig. 1) than power grasping (Fig. 2). Figure 3 shows the typical sequence of processing and associated hand grips used by all gorillas studied.

Stem-(pith)-processing

(*Mimulopsis arborescens*): This involved 12 hand grips with a significant preference within the group ($Q = 26.32$, $N = 11$, d.f. = 3, $P < 0.001$). Precision grasping was used significantly more often than hook ($Z = 2.63$, $P = 0.009$) and compound grasping ($Z = 2.94$, $P = 0.003$) (Figs 1, 4). Similarly, power grasping occurred significantly more often than hook ($Z = 2.04$, $P = 0.004$) and compound grasping ($Z = 2.94$, $P = 0.003$). Figure 5 shows the typical processing sequence and associated hand grips used by all gorilla individuals.

Leaf-processing

(*Mormodica foetida*): This elicited 14 hand grips and showed a significant preference within the group ($Q = 23.53$, $N = 9$, d.f. = 3, $P < 0.001$), with precision grasping being often used significantly more often than hook ($Z = 2.55$, $P = 0.011$), power ($Z = 2.67$, $P = 0.008$) and compound ($Z = 2.67$, $P = 0.008$) grasping (Figs 1, 6). Figure 7 provides the typical sequence of processing and associated hand grips used by all subjects.

DISCUSSION

Since the first studies by Byrne & Byrne (1991, 1993) on processing thistle stem and leaves (*C. nyassanus*) in Virunga mountain gorillas, there have been no comparable analyses of stem- or leaf-processing in the other population of wild mountain gorillas.

Manual actions of gorilla plant processing

Bwindi gorillas used a repertoire of 19 manual actions to process the three plants, including 16 functionally distinct actions and three functionally similar actions (see Table 2). Plant processing by Bwindi gorillas involved obligate manual actions (used by 100% of individuals) while others were optional and dependent on whether they were required by the task (Table 3). The use of 'optional' behavioural components is a feature of hierarchical organization that is also present in the food preparation of Virunga mountain gorillas as well as in the imitations of rehabilitated orangutans (Byrne & Russon, 1998). Stem-(peel)-processing required more functionally distinct actions ($N = 6$) across the four key stages than stem-(pith) and leaf-processing ($N = 4$ each) and involved one obligate action but up to five optional actions. The greater number of manual actions and the greater flexibility of their use in different stages indicate that accessing peel is more complex than stem-(pith) or leaf-processing.

A similar large repertoire of manual actions ($N = 20$) was recorded only for Virunga mountain gorillas processing *Carduus* thistle leaf and stem defended by stings or hooks (Byrne & Byrne, 1993; Byrne *et al.*, 2001a). In contrast, the behavioural repertoire of extracting honey from underground bee nests by wild chimpanzees with 14 manual actions is comparatively smaller (Estienne, Stephens & Boesch, 2017). However, our study found that the 19 manual actions performed by Bwindi gorillas were also used by Virunga gorillas (Byrne *et al.*, 2001a), indicating that both mountain gorilla populations share the same manual action repertoire regardless of which plant material is being processed. Moreover, the current study provides support that the thistle plant does not require more complex processing in terms of the repertoire size of actions than the other three plants studied here.

We identified four key stages of stem-(peel) and leaf-processing while three key stages were used when accessing pith. To consume peel, all gorillas followed a sequence of key stages: (1) procure plant, (2) remove inedible parts with support of the stem, (3) gather strips of peel into hand and (4) insert edible peel into the mouth. Although stem-(pith)-processing showed only three key stages, all gorillas used similar

Table 4. Hand grips used in Bwindi mountain gorilla plant processing.

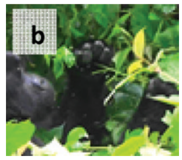
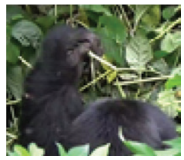
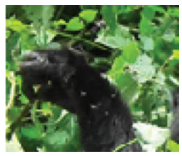
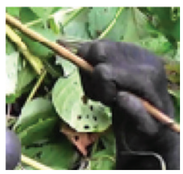
Gripping category	Digit contact	Name (acronym)*	Description	Mean absolute frequency (%) for each plant food	Illustrations
Precision grip	1,1–2	V-pocket grip[1] (VPG)	Object held either in web between full thumb and side of flexed index finger or held only by the full thumb in web.	(peel): 5% (pith): – (leaf): –	
	1–2	Thumb wrap[1,3] (TW)	Thumb and index finger cross over object forming a 'C' shape, thumb pad contacts side of middle phalanx of index finger, other fingers are flexed and either (a) not in contact with the object or (b) the third finger is involved and crosses with the index finegr over the object.	(peel): 8% (a), – (b) (pith): 0.9% (a, b) (leaf): 28% (a), 6% (b)	a)  b) 
	1–2	Two-jaw chuck pad-to-side[1,2] (2JCPS)	Object held between thumb pad and side of index finger.	(peel): 19% (pith): 18% (leaf): 17%	
	1–2	Two-jaw chuck pad-to-pad[1] (2JCPP)	Object held between pad of the thumb and pad of index finger.	(peel): – (pith): 0.2% (leaf): –	
	2–3	Scissor hold[2] (SH)	Object held between lateral side of second and third finger, excluding the thumb.	(peel): – (pith): – (leaf): 0.5%	
	2–3	Interdigital 2/3 brace[4] (I2-3B)	Object is braced in the webbing of the thumb and weaving under the index finger, exiting the hand between the proximal or middle phalanges of the second and third digits.	(peel): 16% (pith): 27% (leaf): 13%	
	1–2–3–4	Interdigital 3/4 brace[4] (I3-4B)	Object held either (a) by strongly flexed digits 3-2 to side of digit 4 and side of distal or proximal phalanx of the thumb, or (b) by less flexed digits 3-2 to side of digit 4 and lying in web of the thumb. Wrist can be strongly flexed in this grip.	(peel): 14% (a), 5% (b) (pith): 8% (a), 2% (b) (leaf): 9% (a), 0.5% (b)	a)  b) 

Table 4. Continued

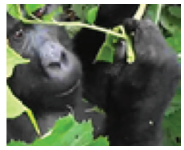
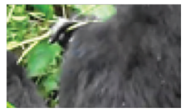
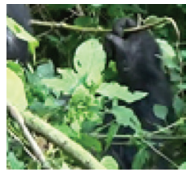
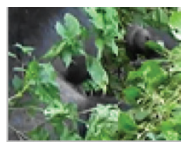
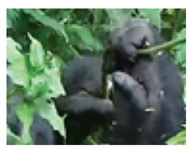
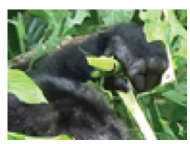
Gripping category	Digit contact	Name (acronym)*	Description	Mean absolute frequency (%) for each plant food	Illustrations
	1–2–3	Lateral tripod grasp[5] (LTG)	Object stabilized against radial side of third finger with index finger pulp on top of the object, and the thumb adducted and braced over or under anywhere along lateral side of index finger.	(peel): 3% (pith): – (leaf): 0.2%	
Hook grip	(1)-–2,4–5	Finger hook[1,2] (FH)	Object stabilized either by flexed index finger only or by digits 4 and 5. Thumb can be involved for stabilization.	(peel): 1% (pith): – (leaf): 2%	
	1–2–3	Interdigital 2-3 finger hook[6] (I2-3FH)	Object held by flexed index finger, exiting the hand between the middle phalanx of index finger and proximal phalanx of third finger. Thumb slightly flexed at interphalangeal (IP) joint contacting the dorsal side of distal phalanx of index finger and locking index finger.	(peel): 4% (pith): – (leaf): 0.5%	
	2–3–4	Interdigital 3-4 finger hook[6] (I3-4FH)	Object held by flexed digits 2–3, exiting the hand between the side of middle phalanx of third and side or dorsal side of middle phalanx of fourth finger. Thumb is not involved.	(peel): 2% (pith): – (leaf): 0.2%	
	1–2–(3), 2–3, 2–3–4–(5)	Transverse hook[1,2] (TH)	Object held by fingers flexed at IP joint with the thumb either opposed or adducted in contact with side of index finger or without thumb. Distal part of palm is not involved.	(peel): 20% (pith): 5% (leaf): 9%	
	(1)–2–3–4–(5)	Extended transverse hook[1,2] (ETH)	Object held between all four fingers flexed at all joints with the thumb either opposed, adducted and in contact with the side of index finger or not involved. Distal area of the palm can be partly involved.	(peel): 36% (pith): 5% (leaf): 9%	

Table 4. Continued

Gripping category	Digit contact	Name (acronym)*	Description	Mean absolute frequency (%) for each plant food	Illustrations
	1–2–3–4–5	Diagonal hook[7] (DH)	Object held diagonally across the fingers. Thumb is involved in this variant.	(peel): – (pith): – (leaf): 0.3%	
Power grip	1–2–3–4–5	Power grip[2] (PG)	An object is held between all five fingers and main part of the palm. The full power grip, in which the thumb is opposed and provides counter pressure, occurred in leaf processing. A type was used in pith processing, where the thumb is held adducted to the index finger and braces over the object at level of metacarpophalangeal (MCP) joint. Lower palm partially without contact, depending on object's diameter.	(peel): – (pith): 3% (leaf): 3%	
	1–2–3–4–5	**Distal palm grip** (DPM)	Type of power grip, where an object is held between all five fingers and only the distal area of the palm. Thumb either opposed and braced under the object at level of MCP joint or abducted to index finger and held in line to the object. Counter pressure is applied by the thumb.	(peel): 1% (pith): 34% (leaf): –	
	1–2–3–4–5	Diagonal power grip[2] (DPW)	Object held diagonally across the fingers and the palm. Typically used to pull vegetation into range.	(peel): 3% (pith): 2% (leaf): –	
Compound grip	1–2–3	**Interdigital 2/3 brace – pad-to-side** (I2-3B-PS)	Two objects are held in one hand using an interdigital 2/3 brace and pad-to-side grip.	(peel): 1% (pith): 0.2% (leaf): –	
	1–2–3–4–5	**Power – pad-to-side** (DPW-PS)	Two objects are held with power and pad-to-side grip.	(peel): – (pith): 0.3% (leaf): –	

*Hand grips that have been named and/or described previously by Marzke *et al.* (2015)[1], Marzke & Wullstein (1996)[2], Byrne *et al.* (2001b)[3], Lesnik *et al.* (2015)[4], Schneck (1987), cited in Schneck & Henderson (1990)[5], Bardo *et al.* (2016)[6], Marzke, Wullstein & Viegas (1992)[7]. Newly observed hand grips are highlighted in bold. A dash '–' denotes absence of grip data.

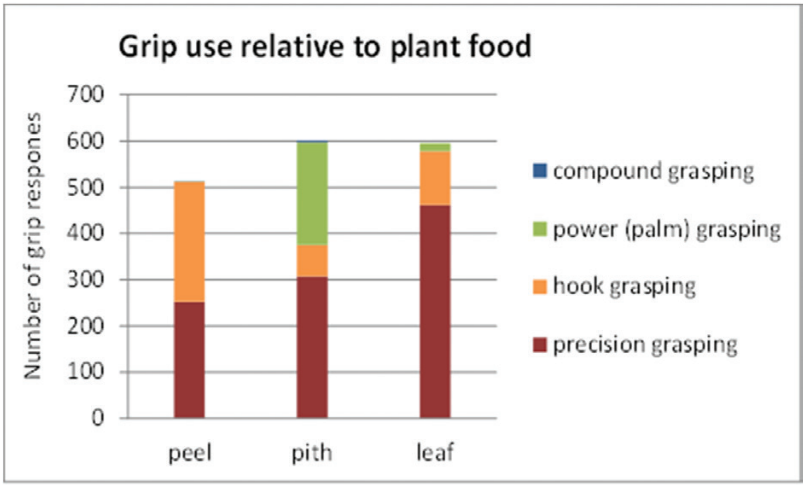


Figure 1. Number of grip responses relative to plant food.

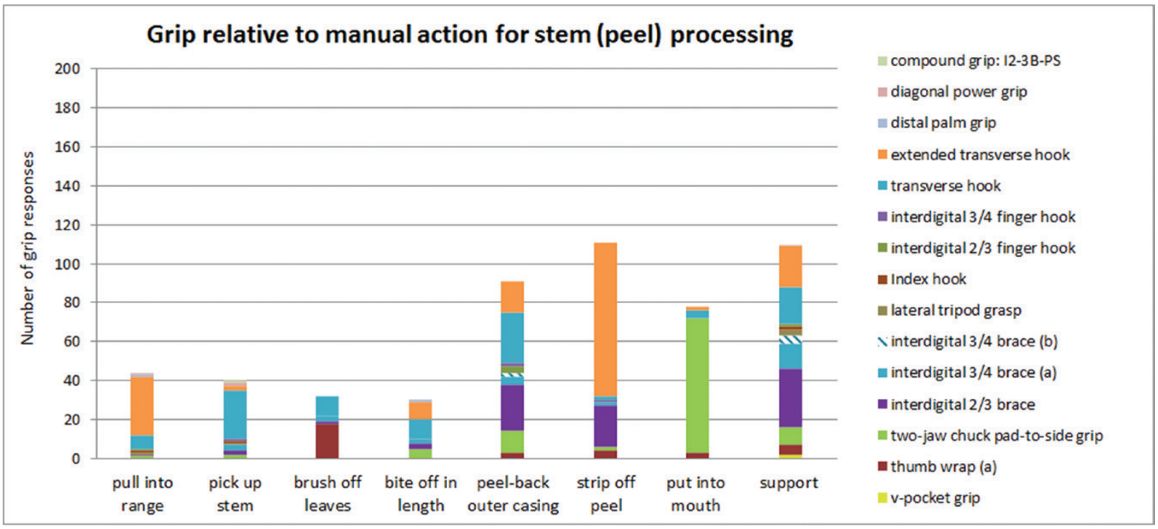


Figure 2. Relative frequencies of grips across the most frequent manual actions for stem-(peel)-processing.

key stages as for accessing peel: (1) procure plant, (2) remove inedible parts such as bark with support of stem and (3) consume edible pith. In contrast, during leaf-processing all gorillas followed a different sequence of key stages: (1) procure plant, (2) detach leaves with support, (3) accumulate leaves into hand and (4) insert leaf bundle into the mouth. The preparation of both stems and leaves by Bwindi gorillas showed that the key stages of processing were routinely ordered and coordinated, which is the second feature of hierarchical organization found in this study (criteria outlined by Russon, 1998). Such an ordered and coordinated flow is also present in stem- and leaf-processing behaviours by Virunga gorillas (Byrne & Byrne, 1993). A similar structural organization in the manipulative behaviours to process plant foods with physical defences has also been documented in wild chimpanzees (*Pan troglodytes schweinfurthii*) and long-tailed macaques (*Macaca fascicularis*) (Byrne & Stokes, 2001; Corp & Byrne, 2002; Tan *et al.*, 2016).

Byrne *et al.* (2001a, b) described the processing of thistle stem as consisting of four key stages: (1) initial procurement of the stem, (2) support of the stem, (3) detachment of stem item and (4) insertion of the stem into the mouth. The processing of thistle leaves was broken down into six key stages: (1) procurement of the plant or leaf, (2) support of the plant, (3) leaf detachment, (4) accumulation of several items into a hand, (5) removing debris from the leaf bundle and (6) inserting the leaf bundle into the mouth. Thus, processing of thistle stem by Virunga mountain gorillas is similar in terms of the number of key stages to

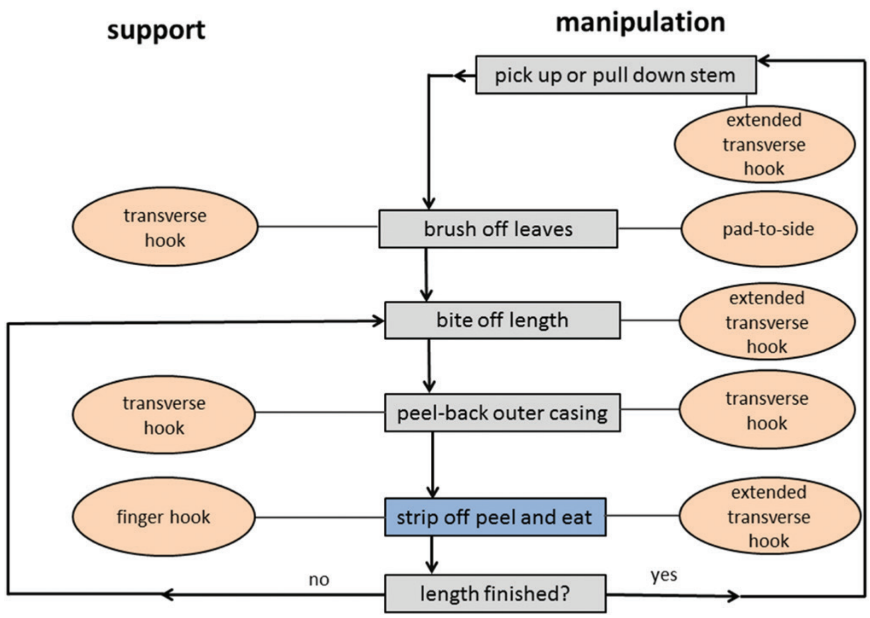


Figure 3. Typical sequence of stem-(peel)-processing and associated hand grips used by all gorilla individuals. The chart is divided into hand functions (manipulation vs. support). Optional actions are highlighted in grey and the obligate action is highlighted in blue. The most frequent grip is indicated with thin lines and highlighted in orange.

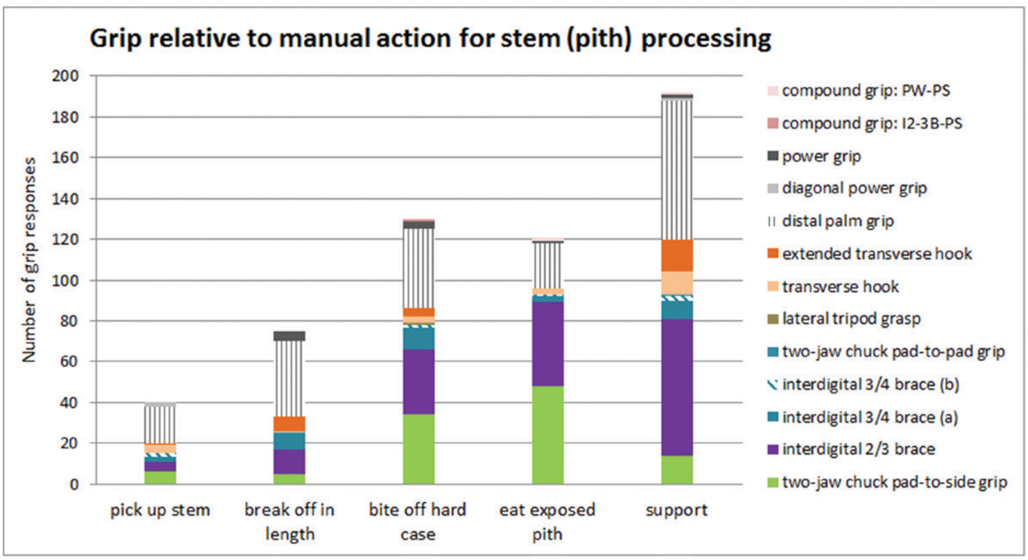


Figure 4. Relative frequencies of grips across the most frequent manual actions for stem-(pith)-processing.

processing other plant stems by Bwindi gorillas, while processing thistle leaf involves a greater number of key stages. Based on the data thus far, thistle leaf appears to require a longer sequence of processing in Virunga mountain gorillas but future investigation of and comparison with thistle preparation in Bwindi gorillas, which consume thistle but more rarely, is needed.

Bwindi gorillas demonstrated a third feature of hierarchical organization seen in great ape food-processing behaviours, which is repeating an action(s) within the key stages of processing (Russon, 1998). For example, the Bwindi gorillas repeated actions involved in gathering leaves until a handful was obtained, or when stripping the peel off from the stem until the peel was fully removed. Similar observations were documented during leaf-processing for Virunga gorillas and wild chimpanzees (Byrne & Byrne, 1993; Byrne & Stokes, 2001). Thus, wild gorillas, like other great apes,

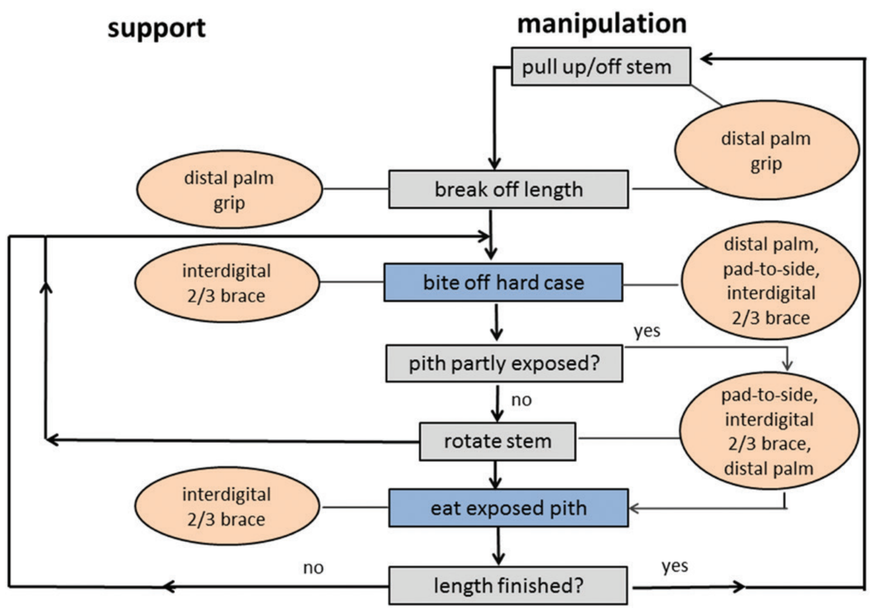


Figure 5. Typical sequence of stem-(pith)-processing and associated hand grips used by all gorilla individuals. The chart is divided into hand functions (manipulation vs. support). Optional actions are highlighted in grey and obligate actions are highlighted in blue. The most frequent grip is indicated with thin lines and highlighted in orange.

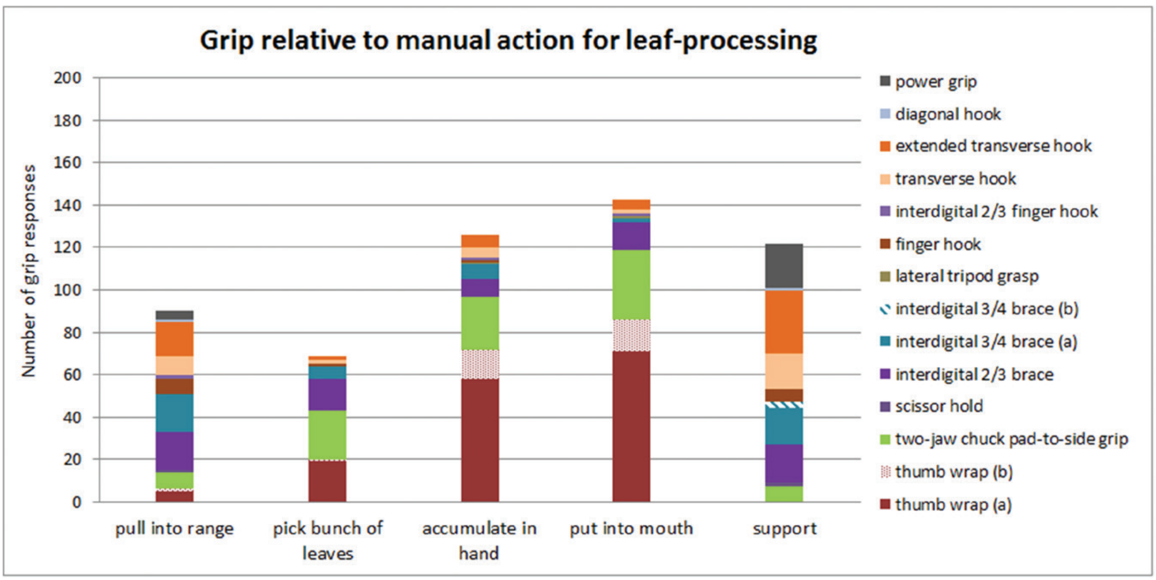


Figure 6. Relative frequencies of grips across the most frequent manual actions for leaf-processing.

use behavioural routines that they repeat until the task is achieved or to maximize efficiency (Russon, 1998).

Processing thistle is also occasionally performed by Bwindi mountain gorillas (e.g. Ganas *et al.*, 2004; Robbins *et al.*, 2006). Although the repertoire of manual actions used to process thistle in Bwindi gorillas has not yet been systematically studied, the gorillas appear to use similar manual actions and apply the same six key stages of processing to those of the Virunga gorillas (M. M. Robbins, pers. observ. stated in Sawyer & Robbins, 2009). Moreover, one female gorilla in Bwindi showed a novel manual action for thistle processing when tidying up the bundle before inserting it into the mouth. Her 'palm roll' action (forming a tight ball of thistle leaves by rubbing the palms of both hands against one another)

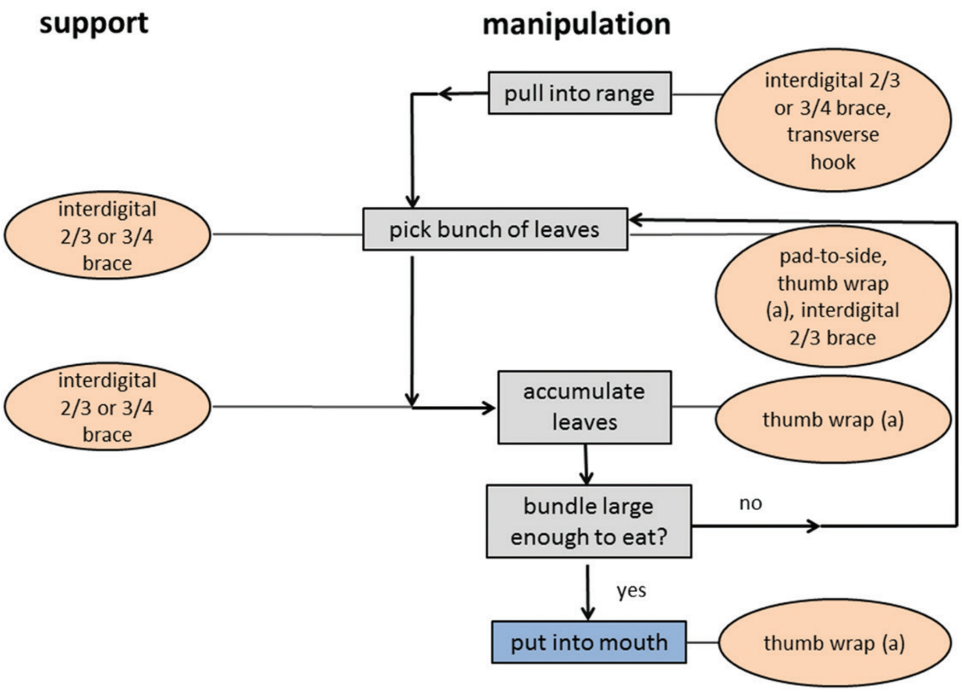


Figure 7. Typical sequence of leaf-processing and associated hand grips used by all gorilla individuals. The chart is divided into hand functions (manipulation vs. support). Optional actions are highlighted in grey and the obligate action is highlighted in blue. The most frequent grip is indicated with thin lines and highlighted in orange.

was distinctly different from all actions described for Virunga gorillas (Sawyer & Robbins, 2009). A similar 'rolling' action and several other manual actions have been described for nettle feeding in western lowland gorillas (*Gorilla gorilla gorilla*) in captivity (Tennie *et al.*, 2008; Byrne, Hobaiter & Klailova, 2011), supporting the idea that gorillas are capable of using their hands in a flexible and diverse functional manner when processing various plant foods.

Hand grips during gorilla plant processing

We predicted that mountain gorillas would show a greater number of hand grips when processing physically defended plants. This hypothesis was not supported; although the gorillas used the highest number of different hand grips ($N = 15$) to access peel, they used 14 grips during leaf processing and 12 grips for accessing pith. This suggests that all three plant foods involve a range of specific manual actions of manipulation and support that elicit a diverse use of grips.

The analysis of how mountain gorillas grip the plant during processing revealed 19 different hand grips across the four main grip categories (i.e. precision grips, power grips, hook grips and compound grips; see Table 4), 16 of which have either been previously reported or show clear similarities to grips used by wild and captive gorillas, chimpanzees, bonobos and humans (Napier, 1956; Marzke, 1997; Byrne *et al.*, 2001a; Lesnik, Sanz & Morgan, 2015; Marzke *et al.*, 2015; Bardo *et al.*, 2017). These include grips that are typically used for arboreal locomotion such as hook grips and power grips (e.g. Alexander, 1994; Marzke & Wullstein, 1996; Neufuss *et al.*, 2017). The remaining three grips have not been previously reported in the literature. Although most of the grips described here have been reported for animals in captivity, it is important to document that similar grips are also used in a more complex and variable natural environment. The greater range of manual actions and plant foods available in a natural context generate new insights into both the function of particular manipulative strategies and the possible morphological links between the gorilla's hand and these strategies.

Precision handling and in-hand movements, which are typical of humans (Marzke, 1997) and have been documented in western lowland gorillas, chimpanzees and bonobos (Crast *et al.*, 2009; Bardo *et al.*, 2017), were never observed in the plant-processing activities of any mountain gorillas in this study and thus are not discussed.

New hand grips observed

This study revealed three grips that have not been previously described: two new types of compound grips and one new type of power grip, the distal palm grip (Table 4). Compound grips, where more than one object is held in one hand and two distinct grips are used at the same time, have been described by Napier (1956) for humans, by Macfarlane and Graziano (2009) for captive macaques and by Jones & Fragaszy (2015) for captive capuchin monkeys. The compound grips used by Bwindi gorillas to process plant stems best resemble Napier's (1956) illustration of the human hand holding a smaller object with a precision grip as the dominant grip and the three inner digits are free to be used in a supplementary role for holding a larger cylindrical object. Mountain gorillas are capable of using their digits asynchronously and grasp more than one food object in a single hand at a time (Table 4). This type of grasping requires independent control of parts of the same hand used for separate purposes at the same time, indicating higher motor skills compared with synchronous digits (e.g. Christel & Fragaszy, 2000; Byrne, Corp, Byrne, 2001b, Heldstab *et al.*, 2016). Compound grips were only observed during support while other grips were used for both manipulative and supportive actions (Fig. 4). However, the rare frequency of these grips might be due to the small sample size in this study, and thus the effectiveness of compound grips for processing plants compared to non-compound grips requires further research. In the distal palm grip, an object is held between all five digits and only the distal area of the palm with the thumb either opposed and braced under the object at the level of the metacarpophalangeal joint, or abducted to the index finger and held in line with the object (Table 4). The thumb provides counter pressure and appears to enhance stability in both postures. This grip seemed to be most effective for processing the hard tissue stems to access pith of *Mimulopsis arborescens*, because it was frequently used across most individuals and used for all manual actions (Fig. 4). The gorilla's distal palm grip shows similarities to the human digitopalmar grip described by Marzke & Shackley (1986), although in mountain gorillas less of the palm was used.

Precision, hook and power grasping required for feeding in the wild

This study revealed that precision grips were used to process all three plants but that leaf-processing involved the most frequent use of precision grasping (Fig. 1), with the thumb wrap (type a) being the most frequently used precision grip (Fig. 6). Nevertheless, the two-jaw chuck pad-to-side precision grip occurred frequently across all the plant foods. The results for precision grips have some interesting parallels to previous observations on grips used for processing thistle leaf in Virunga gorillas (Byrne & Byrne, 1993), for feeding in the Mahale chimpanzees in Tanzania (Marzke *et al.*, 2015) and for termite nest perforation in the Goualougo chimpanzees in the Republic of Congo (Lesnik *et al.*, 2015). Similar to Virunga gorillas, Bwindi gorillas used precision grips, hook grips, power grips and compound grips across the three plants (seven described grips; Byrne & Byrne, 1993). However, because Byrne & Byrne (1993) and Byrne *et al.* (2001a, b) did not describe most of the grips in more detail beyond these four main categories and did not quantify the relative frequency of use, the results here will be compared to the grasping strategies in wild chimpanzees and other captive primates that examined this detail.

Similar to Bwindi gorillas, Mahale chimpanzees used precision grips for feeding such as the two-jaw chuck pad-to-side grip, two-jaw chuck pad-to-pad grip, scissor hold and the V-pocket grip (Marzke *et al.*, 2015). The grip between the thumb and the side of the index finger (two-jaw chuck pad-to-side grip, Marzke & Wullstein, 1996; Marzke *et al.*, 2015) was the most frequent grip by Mahale chimpanzees and was described as a strong grasp applied to pick up and release food objects. One advantage of this grip is that it may help to place a food item in position where other parts of the hand do not get in the way during manipulation, and where wrist rotation is easy. This explanation applies well to gorilla manipulative strategies when shorter plant stems are held against pulling actions during feeding (peel and pith; Figs 2, 4), leaves are picked off from stems and small food objects are inserted into the mouth (Fig. 6). This observation is also consistent with previous findings on herbaceous termite or ant fishing in wild chimpanzees and a food-extraction task in captive bonobos (e.g. Lesnik *et al.*, 2015; Marzke *et al.*, 2015; Bardo *et al.*, 2017).

This study showed that mountain gorillas used hook grasping significantly more often to process stems for consuming peel than to process stems for pith and leaves (Fig. 1), including two hook grips that are typical for ape arboreal locomotion and suspensory postures (extended transverse hook, transverse hook; Napier, 1960; Marzke, Wullstein & Viegas, 1992; Marzke & Wullstein, 1996). These arboreal hook grips were essential for pulling vines into range, biting or breaking off stems in length, contributing strength to the removal of edible plant parts (peel, pith) and for counter support. While most experimental studies of animals in captivity tend to focus on precision grips in connection with simple feeding (e.g. Christel, 1993; Jones-Engel & Bard, 1996; Pouydebat *et al.*, 2011), other studies have documented similar locomotor hook grips in Virunga gorillas, wild chimpanzees and captive western lowland gorillas and bonobos during complex object manipulation (Byrne *et al.*, 2001a; Marzke *et al.*, 2015; Lesnik *et al.*, 2015; Bardo *et al.*, 2017).

The mountain gorillas in this study used power grasping significantly more often for processing stems for accessing pith compared to the other two plants (Fig. 1). However, similar to other primate studies the gorilla's opposed thumb involved in the full power grip and distal palm grip did not show the squeeze form of power grip as seen in humans when manipulating cylindrical wooden tools (e.g. humans: Marzke, Wullstein & Viegas, 1992; Marzke, 2013; chimpanzees: Marzke & Wullstein, 1996; bonobos: Bardo *et al.*, 2016). It is also important to note that the variable postures of the thumb in the power and distal palm grips (i.e. thumb adduction and abduction; Table 4) were associated with larger plant stems when consuming pith. Counter pressure by the thumb was typically used in seemingly forceful manipulative actions that were coordinated between the mouth and both hands (i.e. mouth–bimanual hand, asymmetrical coordination; for more details see Neufuss, 2017) such as breaking the stem off in length, biting off the periderm and for support against resistance. Processing of physically defended food objects was only documented in wild chimpanzees (Marzke *et al.*, 2015). In captive studies, large and/or cylindrically shaped food objects are rarely used (e.g. Christel, 1993; Jones-Engel & Bard, 1996; Pouydebat *et al.*, 2011) and, when they are used, they have not elicited variable thumb postures when using power grips (Pouydebat, Gorce & Bels, 2009).

Implications of grip functions for gorilla hand morphology

The skeletal hand morphology of gorillas differs somewhat from that of other great apes, with a significantly longer thumb relative to the length of their fingers, such that their hand proportions (defined as thumb length relative to length of the fourth digit) are more similar to those of humans than those of all other great apes (Susman, 1979; Almécija, Smaers & Jungers, 2015). A relatively longer thumb is thought to enhance opposability to the fingers during grasping (e.g. Napier, 1993; Marzke, 1997) and is usually discussed within the context of human manipulation during the manufacture of stone tools (e.g. Marzke, 1997). Although gorillas have a longer thumb compared to other great apes, (e.g. Susman, 1979), our study suggests that the thumb is still too short to generate, together with the fingers, a firm enough pinch grip to resist more than moderate forces when dislodging the food objects in stem- and leaf-processing. This may explain why Bwindi gorillas never processed plant materials with the thumb held opposed to the tip of the index finger but most frequently used the two-jaw chuck pad-to-side grip in precision grasping. Furthermore, the gorilla's thumb is not long enough to lock with its full length or stabilize against the index finger on larger plant stems as seen in humans when power squeeze gripping (e.g. Napier, 1960; Marzke, Wullstein & Viegas, 1992).

However, this does not imply that the thumb plays no functional role during food manipulation. The thumb was involved in the majority of grips and in a variety of postures (Table 4). Opposition of the thumb seemed to enhance the effectiveness of extended transverse hook grips during procurement and processing of plant foods. The opposed thumb provides leverage and appeared to enhance the ability to exert force by the hand on the manipulated plants against resistance by the teeth when the peel is stripped off from stems or by the other hand when stems and vines are pulled into range. This cylindrical plant food is regularly lodged in the space between the base of the opposed thumb and the index finger metacarpophalangeal region. The gorilla's opposed thumb is long enough to bridge the space between the side of the index finger and the palm, where it acts as a fulcrum for breaking the food that lies across the space. A relatively robust first metacarpal in mountain gorillas can cope with the mechanical demands of strong grasping involving the thumb (Hamrick & Inouye, 1995). Hence, the gorilla's thumb shows an apparent functional adaptation to variations in requirements for grasp strength, stabilization and leverage of objects manipulated during plant processing. The incorporation of the opposed thumb and the use of a strong extended transverse hook grip is also frequently used by Virunga gorillas and wild chimpanzees when processing plant food of tough, cylindrical shapes as well as when chimpanzees process carcasses and fruits (Byrne, 1994; Marzke *et al.*, 2015).

Gorillas and other apes share long and powerful digital flexors that provide strong grip strength (Myatt *et al.*, 2012). Strong power grips and hook grips are important for moving safely within an arboreal environment (e.g. Hunt, 1991; Marzke, 1992; Neufuss *et al.*, 2017) and arboreal hook grips also enable fine and forceful manipulation of objects, necessary for stick tool-use (e.g. Lesnik *et al.*, 2015; Bardo *et al.*, 2017) and elaborate preparation of various food types (e.g. Byrne & Byrne, 1993; Byrne *et al.*, 2001b; Marzke *et al.*, 2015). Therefore, it can be assumed that the powerful digital flexors in apes are associated with the functional versatility of the digits as they reflect the broad range of mechanical demands acting on the hand during arboreal locomotion and manipulative behaviours. This might explain why Bwindi mountain gorillas and other apes use locomotor grips during manipulative behaviours.

Implications of the gorilla study for the evolution of the human hand

We propose that the biomechanical and manual adaptations in the African ape hand that facilitate arboreal locomotion, such as vertical climbing (Neufuss *et al.*, 2017, 2018), appear to be fundamentally compatible with adaptations that facilitate complex and precise manipulations. Our hypothesis is further supported by the fact that this study only partly supports a functional link between diet and hand morphology in mountain gorillas as was first suggested and discussed by Marzke (2006). The external forces of vertical climbing are considered to be much higher compared to those of feeding behaviours (Preuschoft & Chivers, 1993; Jouffroy, Godinot & Nakano, 1993) and thus probably place greater selective pressures on hand anatomy. It is this foundation of arboreally selected morphological features of the ape hand that might allow for effective manual actions during complex manipulative behaviours, such as processing technically difficult food and stone tool use. For example, strong recruitment of the digits and base of the thumb during power (palm) grasping and hook grasping in gorilla plant-processing requires the powerful digital flexors and thumb joint (i.e. trapeziometacarpal) features that were probably already adapted to high external forces incurred during the use of arboreal climbing grips (i.e. power and diagonal power grasping; Neufuss *et al.*, 2017).

The results of this study lend further support to the idea that humans and other primates may have developed high-precision manual skills in respect to the demands of their foraging niche, and that manipulation complexity and cognitive complexity would have coevolved with brain size and terrestriality (Meulman *et al.*, 2012; Heldstab *et al.*, 2016). Mountain gorillas, for example, demonstrate a high level of manual dexterity and complex bimanual coordination in processing tough, fibrous plants of their terrestrial foraging niche (see Neufuss, 2017) while only simple reaching and picking actions are seemingly predominately needed for obtaining arboreal fruits from tree crowns (J. Neufuss, pers. observ.). These data also add support to the suggestion that terrestrial foraging would have had a relevant role in the evolution of technological abilities and associated cognitive traits during human evolution. Technically difficult foods are thought to be key selection pressures for the evolution of intelligence (Russon, 1998), supporting abilities to solve extractive foraging problems, and organize multi-step processing techniques efficiently (Parker & Gibson, 1977). Hierarchical organization of behavioural programmes is currently known to be a shared capability between great apes, humans, capuchins and long-tailed macaques (Russon, 1998; Byrne & Stokes, 2001; Byrne, 2005, Sabbatini *et al.*, 2014; Tan *et al.*, 2016; Estienne *et al.*, 2017). Additionally, digit role differentiation during compound grasping and the pattern of bimanual role differentiation between both hands (i.e. one hand supports and stabilizes while the other hand facilitates forceful manipulation) appear to have interesting implications for the evolution of hominin perceptual-motor processes relevant to tool-making. These manipulative patterns appear to be an example of a perceptual-motor skill for food acquisition activities that Rein, Bril & Nonaka (2013) suggest may have underlain the stone knapping capabilities in early hominins.

CONCLUSION

This is the first quantitative analysis of hand use of Bwindi mountain gorillas during plant-food processing. Bwindi gorillas showed a repertoire of 19 manual actions to process defended plant-stems and undefended leaves, including 16 functionally distinct actions. Similar to plant feeding by Virunga gorillas, the actions of Bwindi gorillas were ordered in several key stages and their organization was hierarchically structured, reflecting trial and error learning as well as a strong cognitive capacity (Byrne *et al.*, 2001a). The demands of manipulating natural food objects elicited a great variety of hand grips and variable thumb postures, which have not yet been documented in wild foraging gorillas (e.g. Byrne *et al.*, 2001b; Parnell, 2001). This high diversity of hand grips elicited in the plant preparation of Bwindi mountain gorillas shows that more extensive comparative studies of wild apes in their natural environment are needed.

ACKNOWLEDGEMENTS

We are grateful to the Uganda Wildlife Authority and the Ugandan National Council for Science and Technology for permission to conduct research in the Bwindi Impenetrable National Park, Uganda. We thank the Institute for Tropical Forest Conservation (ITFC) in Bwindi for providing logistical support and to all the field assistants of ITFC who assisted in the project. This research was supported by a University of Kent 50th Anniversary PhD Scholarship (JN), the Max Planck Society (MMR, JB and TLK) and European Research Council Starting Grant #336301 (TLK, JN). We also thank the Editors as well as M. Marzke and R. W. Byrne for their helpful comments that greatly improved the manuscript. The authors have no competing interests. This paper is based on a contribution to the European Federation for Primatology symposium 'What an interdisciplinary approach can tell us about the evolution of grasping and manipulation' held on 21–25 August 2017 at the University of Strasbourg in France and organized by Emmanuelle Pouydebat and Ameline Bardo. The proceedings have been collated into a Special Issue of the *Biological Journal of the Linnean Society*, guest edited by Emmanuelle Pouydebat and Ameline Bardo.

REFERENCES

Alexander CJ. 1994. Utilisation of joint movement range in arboreal primates compared with human subjects: an evolutionary frame for primary osteoarthritis. *Annals of the Rheumatic Diseases* **53:** 720–725.

Almécija S, Smaers JB, Jungers WL. 2015. The evolution of human and ape hand proportions. *Nature Communications* **6:** 7717.

Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* **94:** 227–267.

Bardo A, Borel A, Meunier H, Guery JP, Pouydebat E. 2016. Behavioral and functional strategies during tool use tasks in bonobos. *American Journal of Physical Anthropology* **161:** 125–140.

Bardo A, Cornette R, Borel A, Pouydebat E. 2017. Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology* **164:** 821–836.

Breuer T, Ndoundou-Hockemba M, Fishlock V. 2005. First observation of tool use in wild gorillas. *PLoS Biology* **11:** 2041–2043.

Butynski TM. 1984. *Ecological Survey of the Impenetrable (Bwindi) Forest, Uganda, and Recommendations for its Conservation and Management*. Unpublished report to the Uganda Government.

Byrne RW. 1994. Complex skills in wild mountain gorillas: techniques for gathering plant foods. In: Anderson JR, Roeder JJ, Thierry B, Herrenschmidt N, eds. Behavioural neuroscience, physiology and reproduction. Strasbourg: Universite Louis Pasteur. *Current Primatology* **13:** 51–59.

Byrne RW. 2004. The manual skills and cognition that lie behind hominid tool use. In: Russon AE, Begun DR, eds. *The evolution of thought: evolutionary origins of great ape intelligence.* Cambridge: Cambridge University Press, 31–44.

Byrne RW. 2005. The maker not the tool: the cognitive significance of great ape manual skills. In: Roux V, Bril B. eds. *Stone knapping: the necessary conditions for a uniquely hominid behaviour*. McDonald Institute monograph series. Cambridge: Mcdonald Institute, 159–169.

Byrne RW, Byrne JME. 1991. Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla gorilla berengei*). *Cortex* **27:** 521–536.

Byrne RW, Byrne JME. 1993. Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardization. *American Journal of Primatologica* **31:** 241–261.

Byrne RW, Corp N, Byrne JME. 2001a. Estimating the complexity of animal behaviour: how mountain gorillas eat thistles. *Behaviour* **138:** 525–557.

Byrne RW, Corp N, Byrne JME. 2001b. Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. *Animal Cognition* **4:** 347–361.

Byrne RW, Hobaiter C, Klailova M. 2011. Local traditions in gorilla manual skill: evidence for observational learning of behavioral organization. *Animal Cognition* **14:** 683–693.

Byrne RW, Russon AE. 1998. Learning by imitation: a hierarchical approach. *Behavioral and Brain Sciences* **21:** 667–721.

Byrne RW, Stokes EJ. 2001. Effects of manual disability on feeding skills in gorillas and chimpanzees. *International Journal of Primatology* **23:** 539–554.

Christel MI. 1993. Grasping techniques and hand preferences in Hominoidea. In: Preuschoft H, Chivers D, eds. *Hands of primates*. Berlin: Springer, 91–108.

Christel MI, Fragaszy D. 2000. Manual function in *Cebus apella*. Digital mobility, preshaping, and endurance in repetitive grasping. *International Journal of Primatology* **21:** 697–719.

Crast J, Fragaszy D, Hayashi M, Matsuzawa T. 2009. Dynamic in-hand movements in adult and young juvenile chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology* **138:** 274–285.

Czekala NM, Robbins MM. 2001. Assessment of reproduction and stress through hormone analysis in gorillas. In: Robbins MM, Sicotte P, Stewart KJ, eds. *Mountain gorillas: three decades of research at Karisoke.* Cambridge: Cambridge University Press, 317–339.

Corp N, Byrne RW. 2002. Leaf processing by wild chimpanzees: Physically defended leaves reveal complex manual skills. *Ethology* **108:** 673–696.

Dawkins R. 1976. Hierarchical organization: a candidate principle for ethology. In: Bateson PPG, Hinde RA, eds. *Growing points in ethology*. Cambridge: Cambridge University Press, 7–54

Estienne V, Stephens C, Boesch C. 2017. *Extraction of honey* from underground bee nests by central African chimpanzees (Pan troglodytes troglodytes) in Loango National Park, Gabon: Techniques and individual differences. *American Journal of Primatology* **79:** e22672.

Ganas J, Ortmann S, Robbins MM. 2009. Food preferences of wild mountain gorillas. *American Journal of Primatology* **70:** 927–938.

Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, McNeilage A. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National park, Uganda. *International Journal of Primatology* **25:** 1043–1072.

Grueter CC, Robbins MM, Ndagijimana F, Stoinski TS. 2013. Possible tool use in a mountain gorilla. *Behavioural Processes* **100:** 160–162.

Hamrick MW, Inouye SE. 1995. Thumbs, tools, and early humans. *Science* **268:** 586–587.

Heldstab SA, Kosonen ZK, Koski SE, Burkart JM, van Schaik CP, Isler K. 2016. Manipulation complexity in primates coevolved with brain size and terrestriality. *Scientific Reports* **6:** 24528.

Hunt KD. 1991. Mechanical implications of chimpanzee positional behavior. *American Journal of Physical Anthropology* **86:** 521–536.

Jones C, Fragaszy D. 2015. Compound grip in capuchin monkeys (*Sapajus* spp. and *Sapajus libidinosus*). *Folia Primatologica* **86:** 301.

Jones-Engel LE, Bard KA. 1996. Precision grips in young chimpanzees. *American Journal of Primatology* **39:** 1–15.

Jouffroy FK, Godinot M, Nakano Y. 1993. Biometrical characteristics of primate hands. In: Preuschoft H, Chivers DJ, eds. *Hands of primates*. New York: Springer, 133–172.

Kinani JF, Zimmerman D. 2015. Tool use in food acquisition in a wild mountain gorilla (*Gorilla beringei beringei*). *American Journal of Primatology* **77:** 353–357.

Lashley KS. 1951. The problem of serial order in behavior. In: Jeffress LA, ed. *Cerebral mechanisms in behavior: the Hixon symposium.* Oxford: Wiley, 112–146.

Lesnik JJ, Sanz CM, Morgan DB. 2015. The interdigital brace and other grips for termite nest perforation by chimpanzees of the Goualougo Triangle, Republic of Congo. *American Journal of Physical Anthropology* **157:** 252–259.

Macfarlane N, Graziano MSA. 2009. Diversity of grip in *Macaca mulatta*. *Experimental Brain Research* **197:** 255–268.

Marzke MW. 1997. Precision grips, hand morphology, and tools. *American Journal Physical Anthropology* **102:** 91–100.

Marzke MW. 2006. Who made stone tools? In: Roux V, Brill B, eds. *Stone knapping: the necessary conditions for a uniquely hominin behaviour*. Cambridge: McDonald Institute Monograph Series, 243–255.

Marzke MW, Wullstein KL, Viegas SF. 1992. Evolution of the power ("squeeze") grip its morphological correlates in hominids. *American Journal of Physical Anthropology* **89:** 283–298.

Marzke MW. 2013. Tool making, hand morphology and fossil hominins. *Philosophical Transactions of the Royal Society B* **368:** 20120414.

Marzke MW, Marchant LF, McGrew WC, Reece SP. 2015. Grips and hand movements of chimpanzees during feeding in Mahale Mountains National Park, Tanzania. *American Journal of Physical Anthropology* **156:** 317–326.

Marzke MW, Shackley MS. 1986. Hominid hand use in the Pliocene and Pleistocene: evidence from experimental archaeology and comparative morphology. *Journal of Human Evolution* **15:** 439–460.

Marzke MW, Wullstein KL. 1996. Chimpanzee and human grips: a new classification with a focus on evolutionary morphology. *International Journal of Primatology* **17:** 117–139.

McNeilage A. 2001. Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. In: Robbins MM, Sicotte P, Stewart KJ, eds. *Mountain gorillas: three decades of research at Karisoke*. Cambridge: Cambridge University Press, 265–292.

Meulman EJM, Sanz CM, Visalberghi E, van Schaik CP. 2012. The role of terrestriality in promoting primate technology. *Evolutionary Anthropology* **21:** 58–68.

Myatt JP, Crompton RH, Payne-Davis RC, Vereecke EE, Isler K, Savage R, D'Aout K, Guenther MM, Thorpe SKS. 2012. Functional adaptions in the forelimb muscles of non-human great apes. *Journal of Anatomy* **220:** 13–28.

Napier JR. 1956. The prehensile movements of the human hand. *The Bone & Joint Journal* **38-B:** 902–913.

Napier JR. 1960. Studies of the hands of living primates. *Journal of Zoology* **134:** 647–657.

Napier JR. 1993. *Hands (revised edition).* Princeton: Princeton University Press.

Neufuss J. 2017. *Hand use and posture during manipulative behaviours and arboreal locomotion in African apes*. D. Phil. Thesis, University of Kent.

Neufuss J, Robbins MM, Baeumer J, Humle T, Kivell TL. 2017. Comparison of hand use and forelimb posture during vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology* **164:** 651–664.

Neufuss J, Robbins MM, Baeumer J, Humle T, Kivell TL. 2018. Gait characteristics of vertical climbing in mountain gorillas and chimpanzees. *Journal of Zoology*. doi:10.1111/jzo.12577

Parker ST, Gibson KR. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution* **6:** 623–641.

Parnell RJ. 2001. Hand preference for food processing in wild western lowland gorillas. *Journal of Comparative Psychology* **115:** 365–375.

Pouydebat E, Gorce P, Bels V. 2009. Biomechanical study of grasping according to the volume of the object: Human versus non-human primates. *Journal of Biomechanics* **42:** 266–272.

Pouydebat E, Reghem E, Borel A, Gorce P. 2011. Diversity of grip in adults and young humans and chimpanzees (*Pan troglodytes*). *Behavioral Brain Research* **218:** 21–28.

Preuschoft H, Chivers DJ. 1993. Introduction. In: Preuschoft H, Chivers DJ, eds. *Hands of primates.* Vienna: Springer-Verlag, 1–3.

Rein R, Bril B, Nonaka T. 2013. Coordination strategies used in stone knapping. *American Journal of Physical Anthropology* **150:** 539–550.

Robbins MM. 2001. Variation in the social system of mountain gorillas: the male perspective. In: Robbins MM, Sicotte P, Stewart KJ, eds. *Mountain gorillas: three decades of research at Karisoke.* Cambridge: Cambridge University Press, 29–58.

Robbins MM, McNeilage A. 2003. Home range and frugivory patterns of mountain gorillas in Bwindi impenetrable national park, Uganda. *International Journal of Primatology* **24:** 467–490.

Robbins MM, Nkurunungi JB, McNeilage A. 2006. Variability of the feeding ecology of eastern gorillas. In: Hohmann G, Robbins MM, Boesch C, eds. *Feeding ecology in apes and other primates: ecological, physiological and behavioural aspects*. Cambridge: Cambridge University Press, 25–47.

Russon AE. 1998. The nature and evolution of intelligence in Orangutans (*Pongo pygmaeus*). *Primates* **39:** 485–503.

Sawyer SC, Robbins MM. 2009. A novel food processing technique by a wild mountain gorilla (*Gorilla beringei beringei*). *Folia Primatologica* **80:** 83–88.

Sabbatini G, Manrique HM, Trapanese C, De Bortoli Vizioli A, Call J, Visalberghi E. 2014. Sequential use of rigid and pliable tools in tufted capuchin monkeys (*Sapajus* spp.). *Animal Behaviour* **87:** 213–220.

Schneck CM, Henderson A. 1990. Descriptive analysis of the developmental progression of grip position for pencil and crayon control in nondysfunctional children. *American Journal of Occupational Therapy* **44:** 893–900.

Susman RL. 1979. Comparative and functional morphology of hominoid fingers. *American Journal of Primatology* **50:** 215–236.

Tan AWY, Luncz L, Haslam M, Malaivijitnond S, Gumert MD. 2016. Complex processing of prickly pear cactus (*Opuntia* sp.) by free-ranging long-tailed macaques: preliminary analysis for hierarchical organisation. *Primates* **57:** 141–147.

Tennie C, Hedwig D, Call J, Tomasello M. 2008. An experimental study of nettle feeding in captive gorillas. *American Journal of Primatology* **70:** 584–593.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology* **7:** 323–356.

Wright E, Grueter CC, Seiler N, Abavandimwe D, Stoinski TS, Ortmann S, Robbins MM. 2015. Energetic responses to variation in food availability in the two mountain gorilla populations (*Gorilla beringei beringei*). *American Journal of Physical Anthropology* **158:** 487–500.