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Manual skills for food processing by mountain gorillas in Bwindi Impenetrable National Park, Uganda

Johanna Neufuss[1], Martha M. Robbins[2], Jana Baeumer[2], Tatyana Humle[3], 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

*__Corresponding author__

Johanna Neufuss. Animal Postcranial Evolution Laboratory, Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, CT2 7NR, UK. email: jn259@kentforlife.net

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Abstract

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 are known for the complexity in their methods of thistle and nettle plant preparation in the wild. However, there has been 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 (*Gorilla beringei beringei*) 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*), the actions were ordered in several key stages and organised 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 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.

Key words: feeding skill - dexterity - great ape - gorillas - manipulative behaviour - precision grip - thumb

Introduction

Although gorillas rarely use tools in the wild (Breuer, Ndoundou-Hockemba, Fishlock, 2005; Grueter, Robbins, Ndagijimana 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; 2001b) in the Virunga Mountains, Rwanda, was the first to highlight the complex methods of plant preparation used by wild mountain gorillas. 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 hypothesised that complex behaviour typically is hierarchically organised, 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, 1993; Byrne & Russon, 1998), then the number of levels in the hierarchy could be counted (Byrne, Corp, Byrne, 2001a). The hierarchical organisation 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, Corp, Byrne, 2001a; 2001b; Byrne, 2003). Processing leaves of the thistle *Carduus* by Virunga mountain gorillas is considered the most complex task, involving the greatest hierarchical organisation of all the plants eaten to overcome the thistle's physical defences (Byrne, Corp, Byrne, 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 in 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, Robbins, Nkurunungi et al., 2004; Ganas, Ortmann, Robbins; 2009; Wright, Grueter, Seiler 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, Robbins, Nkurunungi et al., 2004; Ganas, Ortmann, Robbins; 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, Robbins, Nkurunungi 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 *Carduus 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 both 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 studying 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, Corp, Byrne, 2001b; Marzke, Marchant, McGrew 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, Corp, Byrne, 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 are needed (e.g., Byrne, Corp, Byrne, 2001b; Marzke, Marchant, McGrew et al., 2015; Heldstab, Kosonen, Koski 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, Marchant, McGrew 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 (*Urera 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.

Materials and Methods

Study site and data collection

Mountain gorillas (*Gorilla beringei beringei*) were observed in the Bwindi Impenetrable National Park (331 km^2). Data were collected on 11 individuals of one fully habituated group of gorillas (Kyagurilo) between February and March, 2015 (see 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 hours/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, Japan). 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, Robbins, Nkurunungi et al., 2004; Ganas, Ortmann, Robbins; 2009). The plant parts consumed are fibrous foods, including (1) the peel (epidermis of an herb's stem) of the soft wooded liana *Urera 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 seconds 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 leave 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 and colleagues (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 functional-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 and colleagues (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.

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 organised into stages, which follow a structural logic since each stage is dependent on the last one. We describe these processing stages as '**key stages'** following Byrne and 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 (see for hierarchical organisation in Byrne & Byrne, 1993; Byrne *et al.,* 2001a; Byrne & Russon, 1998).

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 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, Reghem, Borel, 2011; Marzke, Marchant, McGrew et al., 2015, Bardo, Comette, Borel 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 only contributed one data point to ensure independence of data points.

Table 1: Summary of data for each gorilla individual.

Plant species	Individual ID	Sex/Age	Total no. of sessions	Total no. of bouts	Total no. of hand actions	No. 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**	

Results

We recorded 86 video sequences of stem-peel (*Urera 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 happened typically in an ordered and coordinated sequence of key-stages within a bout.

Stem-(peel)-processing (*Urera hypselodendron*) 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*) involved two obligate actions and two optional actions, which occurred in three key stages (Table 3). Females and males were not significant 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*) 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 males: 5) (Table 1).

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).

Table 2: Manual actions used across all three plant foods. 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, Corp, Byrne, 2001a,b). Actions are labelled for stem-(peel)- [(a)], stem-(pith)- [(b)] and leaf-processing[(c)] .

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.

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). Obligate act(s) are labelled as**.

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. accumulation of items into hand
	put handful into mouth**	100	4. insert leaf bundle into mouth

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 (see 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.

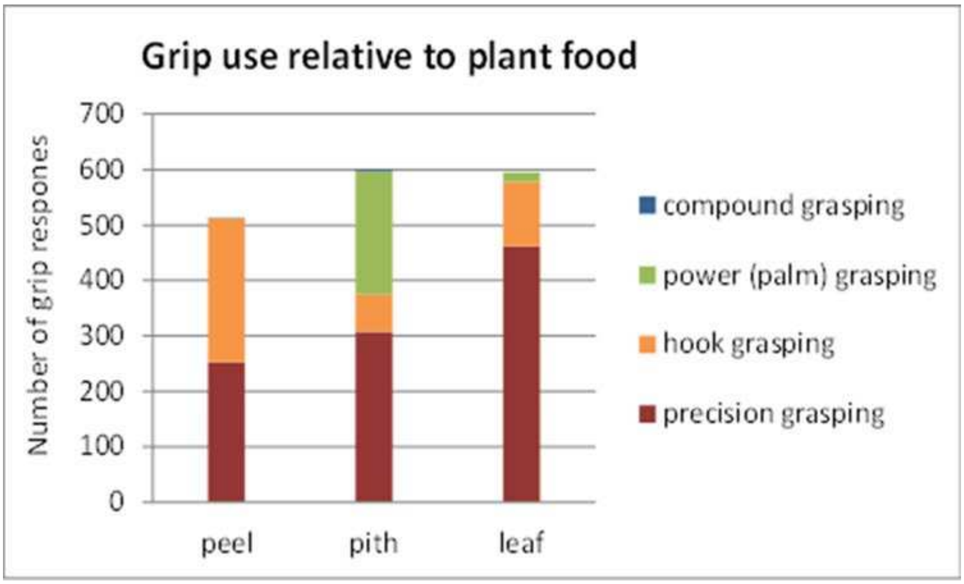


Fig.1. Number of grip responses relative to plant food.

Stem-(peel)-processing (*Urera hypselodendron*) elicited 15 hand grips and showed a significant preference within the group (Q=29.04, N=11, df=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). See Figure 3 for the typical sequence of processing and associated hand grips used by all gorillas studied.

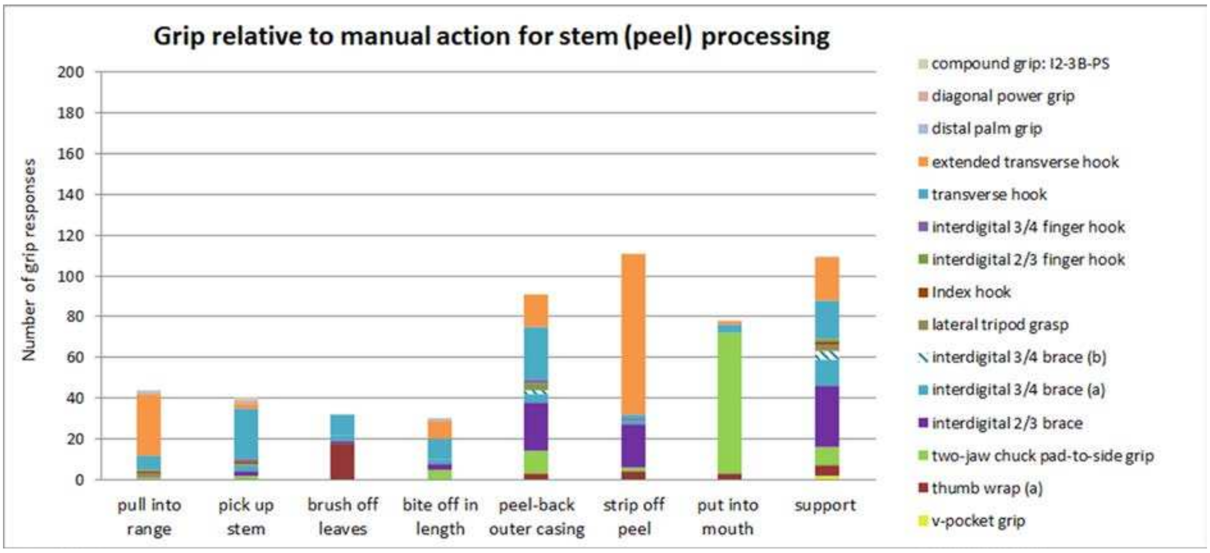


Fig.2. Relative frequencies of grips across the most frequent manual actions for stem-(peel)-processing.

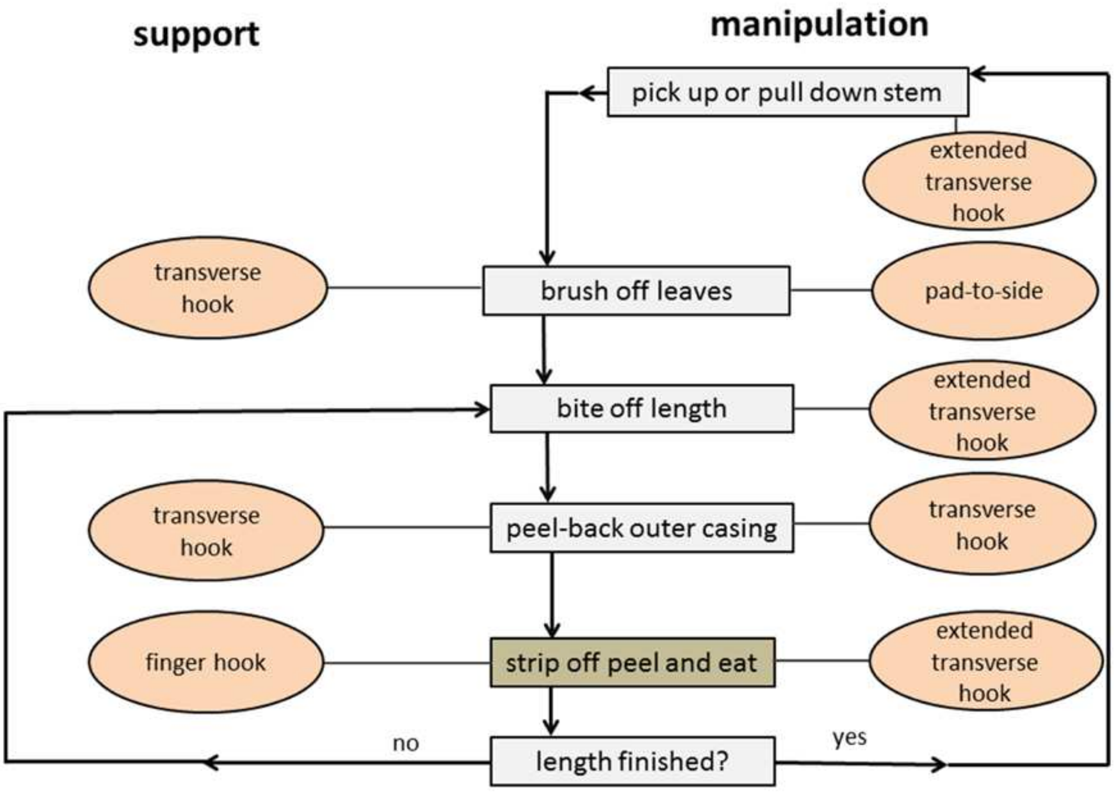


Fig.3: Typical sequence of stem-(peel)-processing and associated hand grips used by all gorilla individuals. Chart is divided into hand functions (manipulation versus. support). Optional actions are highlighted in grey and the obligate action is highlighted in blue. The most frequent grip is indicated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

Stem-(pith)-processing (*Mimulopsis arborescens*) involved 12 hand grips with a significant preference within the group (Q=26.32, N=11, df=3, p <0.001). Precision grasping was significantly more often used than hook (Z=2.63, p=0.009) and compound grasping (Z=2.94, p=0.003) (Figs. 1 and 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). See Figure 5 for the typical processing sequence and associated hand grips used by all gorilla individuals.

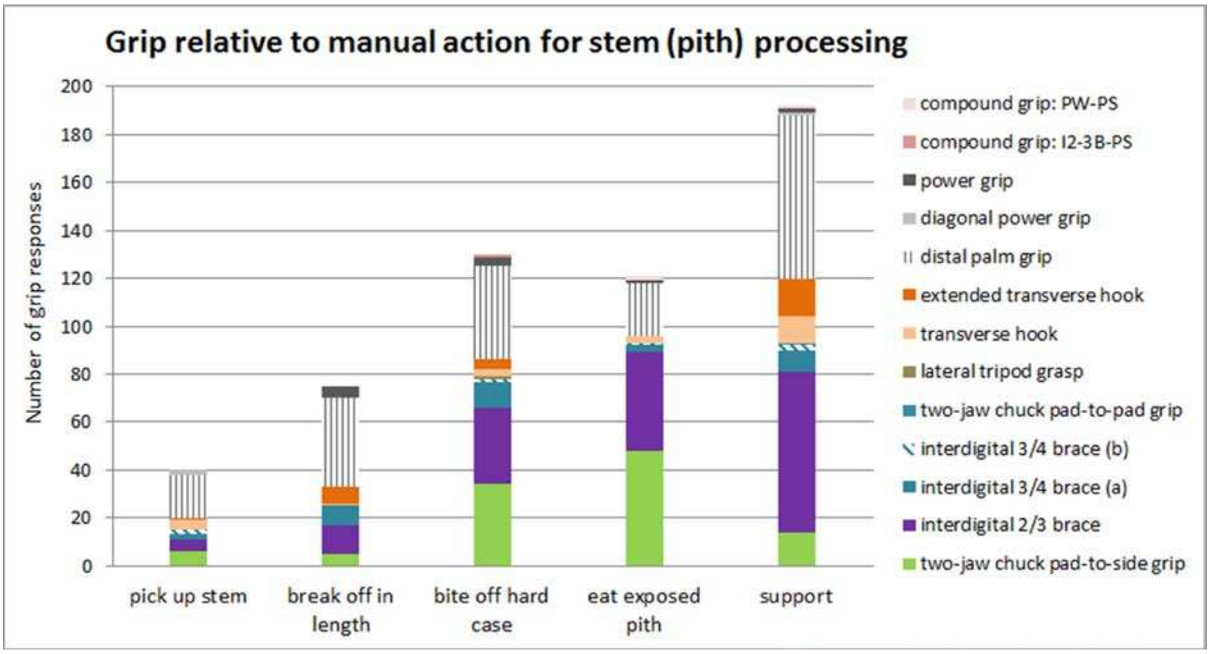


Fig.4: Relative frequencies of grips across the most frequent manual actions for stem-(pith)-processing.

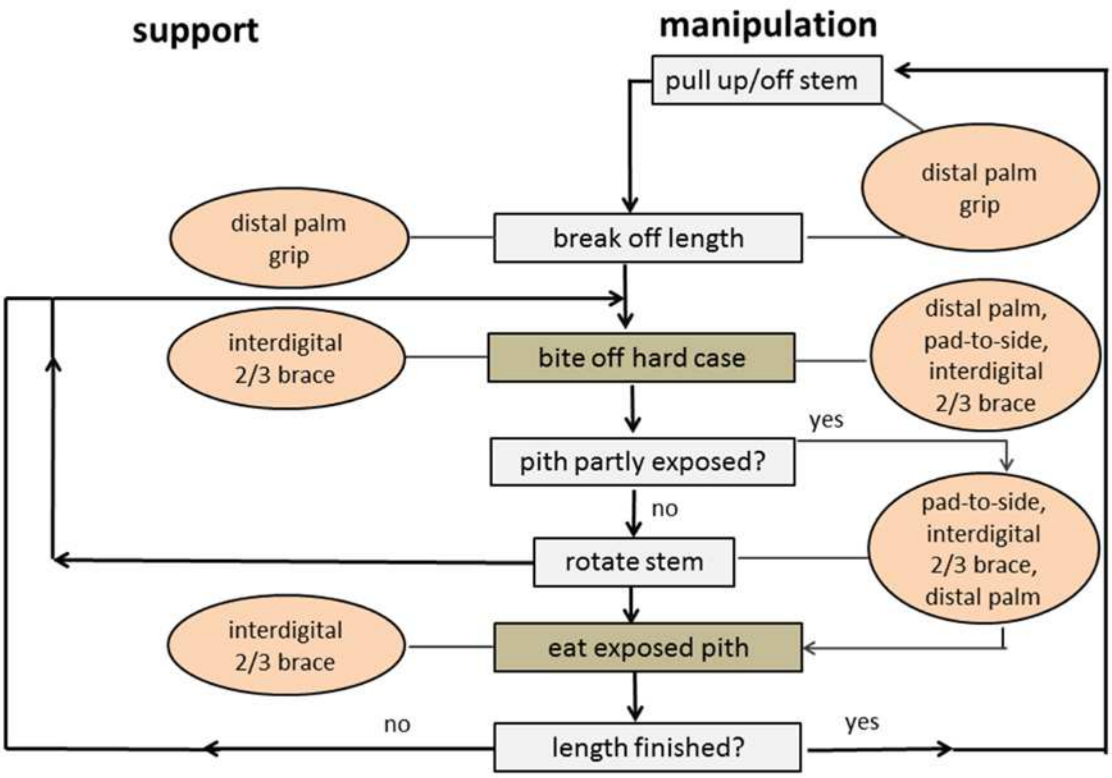


Fig.5: Typical sequence of stem-(pith)-processing and associated hand grips used by all gorilla individuals. Chart is divided into hand functions (manipulation versus. support). Optional actions are highlighted in grey and obligate actions are highlighted in blue. The most frequent grip is indicated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

Leaf-processing (*Mormodica foetida*) elicited 14 hand grips and showed a significant preference within the group (Q=23.53, N=9, df=3, p <0.001), with precision grasping being significantly more often used 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 and 6). See Figure 7 for the typical sequence of processing and associated hand grips used by all subjects.

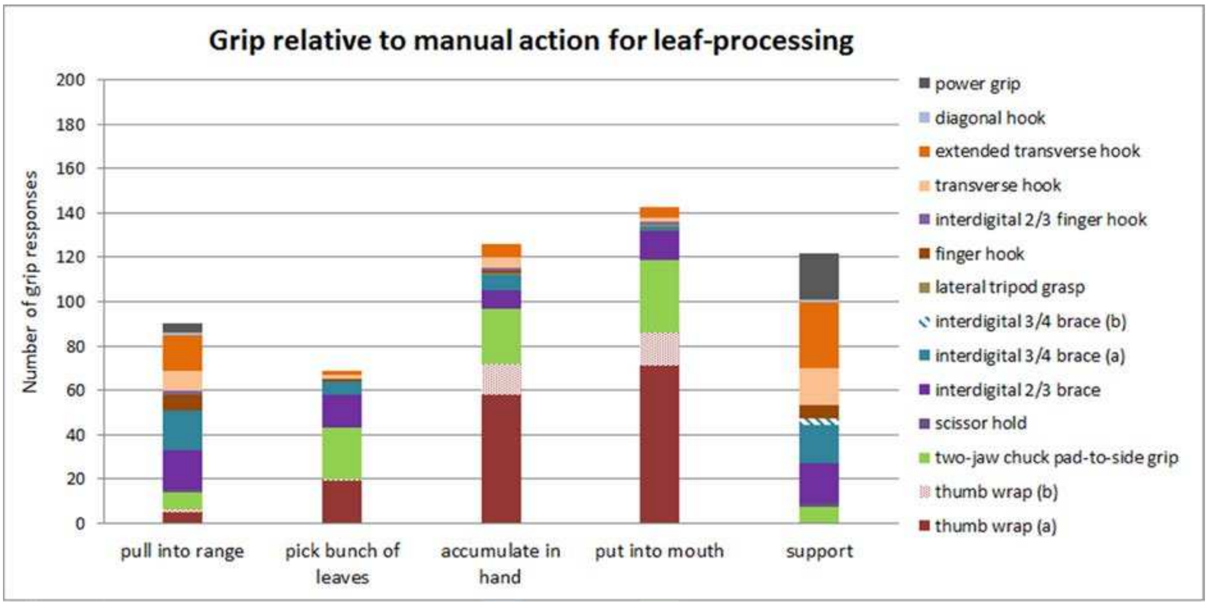


Fig.6: Relative frequencies of grips across the most frequent manual actions for leaf-processing.

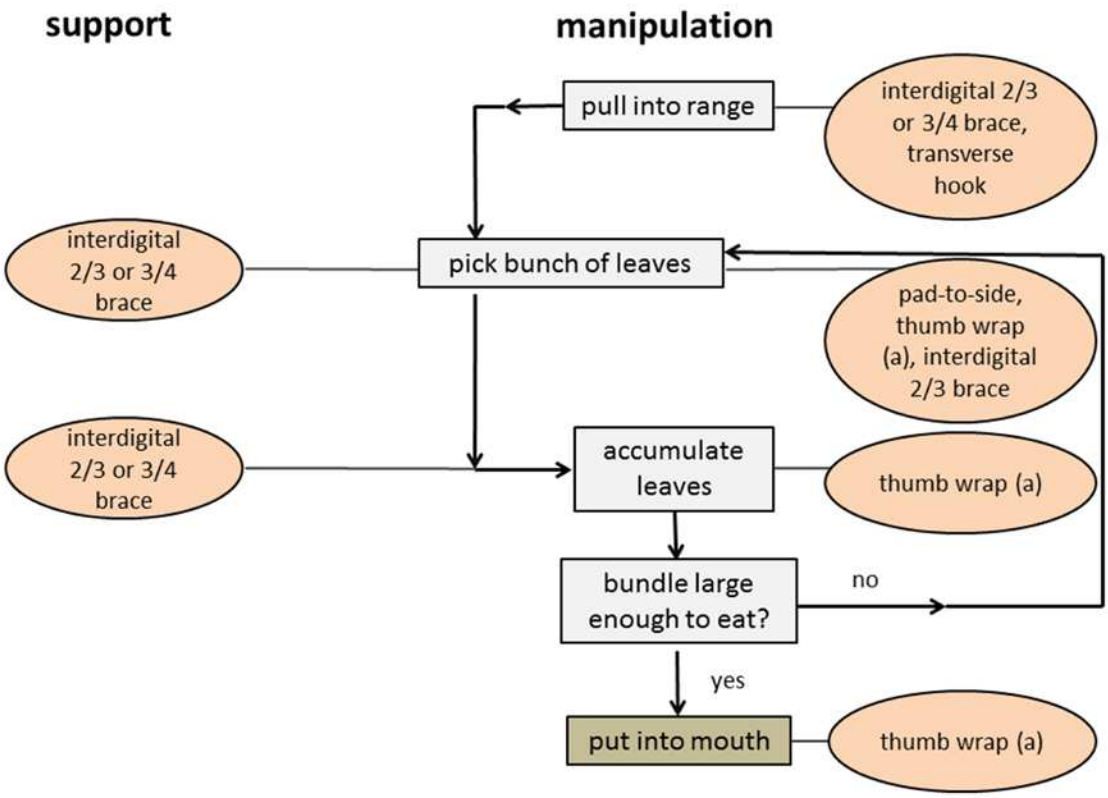
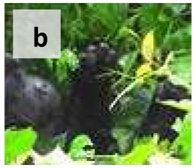
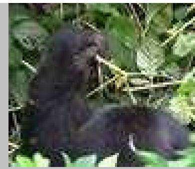
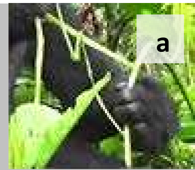
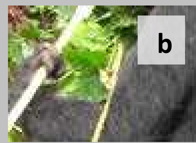
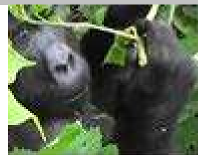
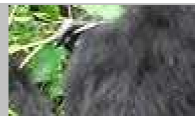
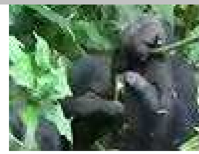


Fig. 7: Typical sequence of leaf-processing and associated hand grips used by all gorilla individuals. Chart is divided into hand functions (manipulation versus. support). Optional actions are highlighted in grey and the obligate action is highlighted in blue. The most frequent grip is indicated with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

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 cross over object and 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 cross with the index over the object.	(peel): 8 % (a), - (b) (pith): 0.9 % (a, b) (leaf): 28 % (a), 6 % (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 bracing 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)	 
	1-2-3	Lateral tripod grasp[5] (LTG)	Object stabilized against radial side of third finger with index 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 four and five. 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 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.	(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 to 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 to the side of index finger or not involved. Distal area of the palm can be partly involved.	(peel): 36 % (pith): 5 % (leaf): 9 %	
	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 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): -	

Discussion

Since the first studies by Byrne and colleagues (1991, 1993) on processing thistle stem and leaves (*Carduus 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 or not they were required by the task (Table 3). The use of 'optional' behavioural components is a feature of hierarchical organisation 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, Corp, Byrne, 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, Corp, Byrne, 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 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 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. Both the preparation of 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 organisation 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 organisation 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, Luncz, Haslam et al., 2016).

Byrne and colleagues (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 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 to thistle preparation in Bwindi gorillas, which consume thistle but more rarely, is needed.

Bwindi gorillas demonstrated a third feature of hierarchical organisation seen in great apes' 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 by Virunga gorillas and wild chimpanzees (Byrne & Byrne, 1993; Byrne & Stokes, 2001). Thus, wild gorillas, like other great apes, use behavioural routines that they repeat until the task is achieved or to maximise efficiency (Russon, 1998).

Processing thistle is also occasionally performed by Bwindi mountain gorillas (e.g., Ganas, Robbins, Nkurunungi et al., 2004; Robbins, Nkurunungi, McNeilage, 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 (Robbins, *pers. observation* 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) 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 in captivity (Tennie, Hedwig, Call 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, Corp, Byrne, 2001a; Marzke, Marchant, McGrew et al., 2015; Lesnik, Sanz, Morgan, 2015; Bardo, Comette, Borel 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, Robbins, Baeumer 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 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 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, Fragaszy, Hayashi, 2009; Bardo, Cornette, Borel 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 and 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 than do synchronous digits (e.g., Christel & Fragaszy, 2000; Byrne, Corp, Byrne, 2001b, Heldstab, Kosonen, Koski 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 to the object (Table 4). The thumb provides counter pressure and appeared 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 and 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 of 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, Marchant, McGrew et al., 2015) and for termite nest perforation in the Goualougo chimpanzees in the Republic of Congo (Lesnik, Sanz, Morgan, 2015). Similar to Virunga gorillas, Bwindi gorillas used precision grips, hook grips, power grips and compound grips across the three plants (7 described grips; Byrne & Byrne, 1993). However, since Byrne's studies (1993, 2001a, b) did not describe most of the grips in more detail beyond these four main categories and did not quantify the relative frequency, 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, Marchant, McGrew 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 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., Marzke, Marchant, McGrew et al., 2015; Lesnik, Sanz, Morgan, 2015; Bardo, Cornette, Borel 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 in captivity tend to focus on precision grips in connection with simple feeding (e.g., Christel, 1993; Jones-Engel & Bard, 1996; Pouydebat, Reghem, Borel 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, Corp, Byrne, 2001a; Marzke, Marchant, McGrew et al., 2015; Lesnik, Sanz, Morgan, 2015; Bardo, Comette, Borel 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, Comette, Meunier 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 plants 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, Marchant, McGrew et al., 2015). In captive studies, large and/or cylindrical-shaped food objects are rarely used (e.g., Christel, 1993; Jones-Engel & Bard, 1996; Pouydebat, Reghem, Borel 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

Gorillas skeletal hand morphology 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 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 suggest 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 stabilise 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 of the food that lays 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 indicates an apparent functional adaptation to variations in requirements for grasp strength, stabilisation 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, Marchant, McGrew et al., 2015).

Gorillas and other apes share long and powerful digital flexors that enable strong grip strength (Myatt, Crompton, Payne-Davis et al., 2012). Strong power grips and hook grips are important for moving safely within an arboreal environment (e.g., Marzke, 1992; Hunt, 1991; Neufuss, Robbins, Baeumer et al., 2017) and arboreal hook grips also enable fine and forceful manipulation of objects, necessary for stick tool-use (e.g., Lesnik, Sanz, Morgan, 2015; Bardo, Comette, Borel et al., 2017) and elaborate preparation of various food types (e.g., Byrne & Byrne, 1993; Byrne, Corp, Byrne, 2001b; Marzke, Marchant, McGrew 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, Robbins, Baeumer 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 feeding behaviours (Preuschoft & Chivers, 1993; Jouffroy, Godinot, Nakano, 1993) and thus, likely 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 recruit the powerful digital flexors and thumb joint (i.e., trapeziometacarpal) features that were likely already adapted to high external forces incurred during the use of arboreal climbing grips (i.e., power and diagonal power grasping; Neufuss, Robbins, Baeumer et al., 2017).

Results of this study lend further support to the idea that humans and other primates may have developed high 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, Sanz, Visalberghi et al., 2012; Heldstab, Kosonen, Koski et al., 2016). Mountain gorillas, for example, demonstrate high 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 (Neufuss *pers. observ.*). These data also add support 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 organise multi-step processing techniques efficiently (Parker & Gibson, 1979). Hierarchical organisation of behavioural programs 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, Manrique, Trapanese et al., 2014; Tan, Luncz, Haslam et al., 2016; Estienne, Stephens, Boesch, 2017). Additionally, digit role differentiation during compound grasping and the pattern of bimanual role differentiation between both hands (i.e., one hand supports and stabilises 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 and colleagues (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 revealed 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 organisation 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.

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