

## RESEARCH ARTICLES

### Complex Leaf-Gathering Skills of Mountain Gorillas (*Gorilla g. beringei*): Variability and Standardization

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The skills that mountain gorillas use to deal with the stings, tiny hooks, and spines protecting common plant leaves in their diet were examined for variation within and between animals. Many elements of uni- and bi-manual performance were identified, often involving delicate precision and coordination, and varying idiosyncratically, each individual having a different set of preferred elements. Many of these elements are functionally equivalent, and all but one weaned animals showed full processing capability; the history of the one exception suggests that early experience with the task may be important. Gorillas' idiosyncrasy in manual skill elements is entirely consistent with trial-and-error learning at this level. By contrast, each individual uses very few techniques (structured sequences of elements) for most processing, and these techniques are the same across the population. Where animals deviate from this generalization, they largely employ the simpler technique normally used for undefended leaves. Lateralization increases from start to finish, consistent with a logical structure in which each stage has a laterality bias and each stage is sequentially dependent on the last. Variations from their commonest techniques occur in all animals (on average, about nine variant techniques were recorded from each animal). The repertoire of techniques increases significantly with age, whereas the repertoire of elements does not. This points to an initial reliance on a single logical structuring that is well established by weaning (about 3.5 years), with subsequent development of the ability to vary the technique used so as to take advantage of variations in the environment. Standardization of logical organization, despite variability between different animals in individual elements and behavioral laterality, suggests that the logical ordering of elements and the interrelationships of processing stages is copied by program-level imitation.

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**Key words:** gorillas, skill, learning, laterality, imitation

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## INTRODUCTION

The prehensile primate hand has long been considered a preadaptation for the manipulative intelligence shown in humans (e.g., Elliot Smith, 1927). More recently, Parker and Gibson [1979] have argued that the need of certain primate species to extract edible material from concealing matrix has selected for both manipulative ability and imaginative foresight. However, most attention has been concentrated on the specialized abilities of a few species to use tools [see Beck, 1980; Goodall, 1986; Izawa & Mizuno, 1977; Sugiyama & Koman, 1979; Boesch & Boesch, 1984; McGrew, 1992], rather than manipulation in general. Where manipulative skill has been studied for its own sake, this is generally in the laboratory [e.g., Napier, 1961; Bishop, 1964; Parker, 1974; Welles, 1975; Torigoe, 1985]. One explanation for the lack of field studies of manual skill may be that most primates, even in the wild, *need* to carry out little manipulation of any skill. The attention devoted to primates' problems of finding, retaining, and digesting adequate food [Clutton-Brock, 1977; Chivers et al., 1984; and much of contemporary primatology] argues that this is widely believed; issues of known biological importance are evidently not being neglected. However, this recent focus on food availability and food chemistry may have obscured interesting differences in the challenges some species face in *manual* food processing, and the skills they employ to overcome them. Mountain gorillas are a particularly suitable species with which to begin to redress this balance, for several reasons.

The diet of the mountain gorilla (*Gorilla g. beringei*) is based on herbaceous vegetation and dominated by consumption of a few species [Watts, 1984]. These herbs, unlike the plants eaten by most primates [Waterman, 1984], are high in digestibility; indeed the herbaceous vegetation in the gorillas' range is generally low in indigestible fibre and tannin-based digestion inhibitors [Waterman et al., 1983]. Thus, learning what foods to eat is neither a complex nor a risky task for a young mountain gorilla. However, these herbs are typically defended by stings, hooks, or fibrous outer casings, and removal of these mechanical defenses requires dexterity. Learning how to eat the main items of diet may therefore be a more serious task, and certainly adult gorillas spend much of their waking lives "eating" [Fossey & Harcourt, 1977], a category of behavior which largely involves removal of plant defenses [Byrne & Byrne, 1991].

Mountain gorillas use different techniques for processing each of their common plant foods, and these techniques are *complex*—each having several stages with quite different actions, involving bimanual coordination of actions which themselves require precision grip and delicate manipulation [Byrne & Byrne, 1991]. The skill involved, and the consequent ergonomic need for manual specialization, is suggested by the very strong behavioral lateralizations observed [Byrne & Byrne, 1991]. The complexity and delicacy of the techniques means that gorillas' feeding is likely to be limited by handling time rather than costs of finding, defending, or digesting the foodstuffs. This is consistent with the argument of Wrangham [1979] that, since female gorillas (unlike female chimpanzees or orangutans) can evidently afford to associate permanently in groups, the costs of direct feeding competition for gorillas must be low. Skills used in plant gathering are therefore important factors in gorilla ecology and sociobiology, and any variations in skill are likely to affect reproductive success.

In this paper, we examine the structure of gorilla leaf-gathering techniques, in particular those for two common and important foods, the leaves of the nettle *Laportea alatis* and the clambering stems and leaves of *Galium ruwenzoriense*. Dexterity is required to deal with the nettle stings, especially prevalent on the upper surface, petiole, and edges of the leaves, and for galium, to deal with the

dense covering of tiny hooks. For these skills, we describe the individual elements of manual processing, the way in which those elements are logically structured into complex overall techniques, and the degree to which elements and techniques vary between animals or show standardization across the population. Since these skills are highly lateralized and involve bimanual coordination, the patterning of lateralization within sequences of processing steps is also examined. The population of mountain gorillas at Karisoke is ideal for this study in ways that go beyond the excellent habituation which makes data collection possible. Known as individuals since 1967, 71% of the study population of 44 had known mothers and probable fathers at the time of this study, and a largely complete record of injury and illness exists in the records of the Research Center. This enables any correlations between motor skill patterns and genealogy, medical history, or individual history to be used as clues to the origin of the variance observed. Our aim is to sort out exactly what a young gorilla must learn in order to exhibit the necessary adult skills in processing leaf foods.

## METHODS

### Study Animals

In August 1989, the study population consisted of three groups totalling 44 individuals: 4 adult males ("silverbacks," aged over 13 years), 7 adolescent males ("blackbacks," aged 9–13 years), 14 adult females (aged 9 years and over), 13 juveniles (aged 3–8 years, six males and seven females), and 6 infants (aged under 3 years, five males and one female). Four further births occurred during the study. All ages quoted in this paper are the animals' ages in August 1989. The three groups are named Group 5, Group 4 (sometimes called Beetsme's Group), and Bilbo's Group. Both the former are breeding groups, whereas Bilbo's Group is a non-breeding association of juvenile and adolescent animals, all but one males.

### Data Collection

During July to December 1989, 106 days were spent observing the gorillas, a total of 510 hours contact time. Focal samples [Altmann, 1974] were used to collect data from all animals of 3 years and upwards ( $n = 38$ ), and where possible from younger animals. Observations were made approximately equally on all juvenile and adult animals, and the final focal sample totals were at least 6 hours 40 min per animal. Since there are no pronounced time of day, seasonal or habitat zone effects upon feeding behavior except when groups occasionally move into bamboo or alpine zones [Watts, 1984], the order in which subjects were observed did not need to be constrained in any way. However, the accumulated total observation times per subject were in fact kept approximately equal throughout the study. Data from occasions when an animal was visibly affected by a temporary hand injury are excluded from the analyses of this paper.

Gorillas often accumulate edible items in a handful before the whole is eaten, and the basic unit for our sequential analyses was the *handful*. Usually, they process and eat several handfuls of a food type one after the other, before switching to a new food, or stopping feeding. A *bout* was defined as a period of feeding on a single food type without any interruption and may include many separate handfuls; bouts were thus terminated by switches to other foods, to other activities altogether, or by periods of inactivity (10 s or more). Since bouts are statistically independent of each other [see Marchant & McGrew, 1991], bout frequencies have been used for examination of handedness [Byrne & Byrne, 1991].

Records were taken of the sequence of acts used to process each handful that

could be seen clearly. Evidently, not all finger movements can be recorded (or indeed seen) in real-time, so a simplified notation was used. Processing was divided into the possible stages: initial procurement of a new plant, actions of holding with one hand and detaching with the other, accumulation of items while continuing processing, any cleaning of food bundles to remove debris, and finally acts of inserting a food bundle into the mouth. For each, the body part(s) used was recorded: left hand, right hand, both hands used together, both hands used separately, lips, or teeth. These data were collected over many days, to a criterion (not reached in all cases) of 50 handfuls for adults and 100 handfuls for juveniles.

Note that these sequences are not statistically independent, since several handfuls could occur in a bout. With the very much larger sample of computer-logged bouts used for laterality analysis [our other methods of data collection are described in Byrne & Byrne, 1991], we can obtain good estimates of the mean number of handfuls per bout: for *Laportea alaticipes* 2.65 (SD 2.17) and for *Galium ruwenzoriense* 3.81 (SD 3.08). Given the small mean sizes of these "runs" compared to the overall sample sizes per animal, our estimates of consistency are still likely to be good ones for comparing animals. Obviously, the sequences of acts within the processing of each handful are also not statistically independent, of necessity; where there is a consistent trend towards lateralized acts, the sequential dependency will tend to increase observed laterality from beginning to end of each sequence.

In order to be certain of the fine details of rapid processing, and to record the inconsistent and variable processing attempts of infants, we used video recording, with a Panasonic compact S-VHS camcorder. Recordings were collected on a schedule to balance approximately the number of bouts of processing of each common food type across age/sex categories for adults, and across individuals for juveniles. Thus not all adults could be compared at this detailed level of analysis on particular techniques, although a representative sample was obtained. For infants (under 3 years at August 1989) particular effort was made to obtain adequate samples of videotaped feeding on the common foods.

## RESULTS

### Repertoire of Elements Used in Leaf Processing

In characterizing the skilled repertoire, all 38 juveniles and adults were treated equivalently, since processing speed does not increase after 3 years old [Byrne & Byrne, 1991]. Using slow motion and stop-frame, the details of hand movements were charted for all filmed processing of galium and nettle leaves by these animals. Since complex behavior is hierarchical, there is always a number of levels at which it can be described, right down to that of individual muscle movements. Even for fine-grain analysis we did not attempt this level of description, instead defining elements of skill such that each results in a clear change to plant material by a single action; the sense in which we use the term "element" will be best grasped from the definitions themselves (see Table I). The term "precision grip" (pad-to-pad or pad-to-side) follows the usage of Napier [1961] and Aiello and Dean [1990]; the gorilla's "power grip" differs from that of humans, since the gorilla saddle joint between trapezium and first metacarpal does not allow such strong support of the thumb as a buttress [Aiello & Dean, 1990]. Digits are numbered 1–5, the thumb being 1. Although only two plant foods were used for constructing the repertoire of Table I, it is likely that this set of elements is representative of leaf-processing. The other very common leaf food, leaves of thistle *Carduus nyassanus*, were dealt with using elements shared by galium and nettle

TABLE I. Skill Elements Used in Leaf-Processing

Grips and supports	
<i>Power-grip</i>	Potentially strong, closed-hand grip (varying as to whether whole-hand or 1 + fingers only; includes using both hands with thumbs pointing same way), on cylindrical object (often stem) for support or for procurement, or on a bundle while accumulating items.
<i>Pencil-grip (power)</i>	Closed-hand grip of one hand on cylindrical object (usually stem) but with object caught between pair of fingers and resting on thumb (specify fingers: 2:3 or 3:4 or 4:5), usually for support. Presumed to be an accidental variant of <i>power-grip</i> .
<i>Loose-grip (power)</i>	Loose, part-open whole hand grip, usually applied to detached objects to allow delicate processing with hand or mouth (e.g., <i>pick-out</i> to clean, or <i>fold</i> ) or to accumulate leaves or stems.
<i>Pinch-grip</i>	Firm precision grip, varying in whether pad-to-pad (1:2 or 1:other) or pad-to-side (1:2 normally); usually either for support or procurement, as if holding in pliers.
<i>Lip-grip</i>	Delicate grip with centre of lips, e.g., when removing debris from bundle.
<i>Two-hand (S)</i>	Strong, closed power grip of both hands, with thumbs pointing towards each other, on cylindrical object to allow processing by mouth.
Actions for procuring items	
<i>Hook</i>	Whole hand or only some fingers (specify) held rather rigidly in open curve to pull attached object (often used to heave down mass of vegetation).
<i>Reach</i>	Various sorts of grip on attached object, which is pulled to bring into range (often used with a similar function to <i>hook</i> ).
<i>Yank</i>	Some sort of <i>power-grip</i> (or grip with teeth) 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 or mouth (often to detach the part).
<i>Pick</i>	Pinch-grip on clearly defined object which is pulled against force of natural attachment, usually to procure the item.
<i>Rotate</i>	Turn or twist a long object held in <i>power-grip</i> to bring into range or into more convenient position for processing (mainly a stem-processing technique).
Actions for detaching parts from items	
<i>Pull-apart</i>	Parts of an object held in the two hands (whatever the grip), the hands then pulled apart in a movement at a tangent to body, thus applying force to object.
<i>Lever-apart</i>	Object (usually leaves) held in both hands using <i>power-grips</i> , then leverage of rocking the hands or knuckles against each other used to tear the object.
<i>Twist-apart</i>	Object (usually leaves) held in both hands using <i>power-grips</i> , then twisting of each hand versus the other used to tear the object (often hard to see if <i>twist-apart</i> or <i>lever-apart</i> ).
<i>Strip-up</i>	Half-open <i>power-grip</i> (often constricted at 1:2, but not always) around leafy stem, slid up stem towards body to detach bunch of leaves, against force of substrate or other hand's supporting grip (thus accumulating leaves, the bunch protruding between 1:2) Sometimes movement in reverse direction, away from body, when constriction normally at 5:palm.
<i>Bite-off</i>	Use teeth to cut off portion of naturally attached or hand-supported object; (mainly a stem-processing technique).
Actions for maneuvering items	
<i>Combine</i>	Ability to carry out separate functions with fingers 1:2 and 3-5 at same time (in various functions), e.g., <i>pinch-grip</i> with 1:2 to pick while <i>loose-grip</i> of 3-5 to accumulate already picked items.
<i>Two-handed-bend</i>	Loosening and re-grasping by the hand holding a long item (e.g., a galium stem), while item is folded into a bundle with the other hand, either once (S), or many times to form a concertina shape as in <i>zig-zag</i> (R).
<i>Zig-zag</i>	Repeated loosening and re-grasping (by the one hand holding a galium strand) with a rocking motion of this hand to enfold the strand into a concertina shape, to allow it to fit into neat bundle, using gravity or the strand's natural attachment to bend the strand, or bending it against an object. Implies <i>combine</i> .
<i>Squeeze-up</i>	Gathering together a bundle of items so that they are finally held in some sort of whole-hand grip in one hand (often <i>loose-grip</i> becoming <i>power-grip</i> ), using closure of first one hand for compression of loose bundle, then the other, alternately. Largely used by infant animals.

(continued on overleaf)

TABLE I. Skill Elements Used in Leaf-Processing (Continued)

Actions for maneuvering items (continued)	
<i>Roll</i>	While holding "untidy" bundle, rolling against flat support (e.g., of chin or hard palate) to produce a tight, roll-shaped bundle.
<i>Pick-out</i>	<i>Pinch-grip</i> or <i>lip-grip</i> on small item which is pulled off an object or out from among a mass of items, requiring discrimination of one item from among many (such as in cleaning a food handful, or accumulating a bundle of food items).
<i>Adjust</i>	Delicately adjusting the position of an item in other hand (usually item held in <i>loose-grip</i> during this), using <i>pinch-grip</i> , a push with the knuckles or just with a single finger.
<i>Fold</i>	A special case of <i>adjust</i> , where nettle leaf-blades are pulled out from grip of other hand, then folded over (sometimes using thumb as fulcrum), often using push with knuckles, and gripped again. Thus a sting-free curved under-surface is presented to lips.
<i>Manipulate</i>	Rearranging, simply using the fingers, the position or shape of item(s) held in one hand without using other hand.
Special ways of biting	
<i>Shear-bite</i>	Shearing bites used to slice off slice of a large, compact handful of items, either singly (S) to finish eating a handful (when remains discarded unless <i>retain-nucleus</i> ) or repeated (R) in order to eat entire handful.
<i>Sausage-feed</i>	Repeated loosening grip and re-grasping lower down an approximately sausage-shaped food bundle, in order to feed it into the mouth as a whole (without the bundle coming apart).
<i>Retain-nucleus</i>	Using the remains of the last handful eaten (bitten off from these remains with a <i>shear-bite</i> ) as a basis for starting to accumulate the next.

leaf [see Fig. 1 of Byrne & Byrne, 1991], while rarer items were largely lacking in physical defenses and so eaten in a far simpler way [Byrne & Byrne, 1991]. The actual number of elements is somewhat arbitrary, since certain elements are perhaps no more than accidental variants of ones more normally used; in some cases, if a slightly broader or narrower category definition were used, a set of less or more elements would be obtained. However, it was evident when devising the classification that if significantly broader categories were used, important aspects of dexterity and skill would be lost. Of course, if the precise configuration of all fingers were recorded, the current categories could be split ad infinitum, as usual with ethological categories. The validity of the present categories must depend on their usefulness in pinpointing interesting variations between animals and over time.

For ten animals (five juvenile and five adult/subadult), videotaped samples of adequate size (four or more complete handfuls) were available for both galium and nettle. These animals were used to investigate variability of repertoires. All elements used by them in processing either food were identified, separated into functional categories since some elements could be employed for very different purposes on occasion. These data, shown in Table II, clearly show the highly idiosyncratic usage of elements. Since the number of handfuls available on video varies between animals, it is possible that the full set of elements has not reached asymptote for all animals. Linear regression of the number of elements from the number of handfuls supports this for both foods (nettle, elements =  $-2.75 + 0.97 \times$  handfuls,  $r^2 = 0.60$ , one-way ANOVA  $F(1,8) = 11.9$ ,  $P < 0.01$ ; galium, elements =  $-3.15 + 0.78 \times$  handfuls,  $r^2 = 0.40$ , one-way ANOVA  $F(1,8) = 5.42$ ,  $P < 0.05$ ). With the extensive overlap in elements between the two tasks and more uniform numbers of total handfuls, it might have been expected that an asymptote would be reached for animals' entire repertoires; this is not the case, as is seen in Figure 1. Here an even greater proportion of the variance in element repertoires is ac-

TABLE II. Elements Recorded in Processing of Nettle and Galium\*

Individuals	KU	AM	IN	UM	MA	DA	SA	TU	BE	LI
<i>Pull into range</i>										
Reach (whole hand)	NG	NG	NG	NG	NG			N	NG	NG
Reach (2, or 2 and 3 only)						N	G	N		
Reach (4 and 5 only)									G	G
Reach (pinch-grip: pad-pad)			N		N	G				
Reach (pinch-grip: pad-side)			N			G				
Reach (pencil-grip 3:4)										G
Hook (whole hand)	G	NG	G	G		G	G	NG		N
Hook (both hands)	G					G			G	
Hook (5, or 4 and 5 only)				N	N					
Hook (2, or 2 and 3 only)			N		N					
Rotate				N				N		N
<i>Support</i>										
Power-grip (whole hand)	G	G	G	G		G	G			G
Power-grip (one finger)						G	N		G	N
Pinch-grip (pad-side)	N	N	N			NG				
Loose-grip	N						N			
Pencil-grip (2:3)	N									
Pencil-grip (3:4)					N					NG
Pencil-grip (4:5)					N					
Two-hand (S)		NG								
Knuckles	N									
Foot			G	G	N					
Mouth					G			NG		
Teeth		G								
<i>Gather into hands</i>										
Yank (power-grip)	NG	G	G	NG	NG	G	G	G	NG	NG
Pick (pinch-grip: pad-side)							N		N	
Pick (pinch-grip: pad-pad)					N					
Strip-up (constricted 1:2)	N			N	N	N	N	N	N	N
Strip-up (constricted 2:3)								N		
Strip-up (constricted 4:5)		N								
Strip-up, reversed (constricted 5)					N					
Strip-up (pencil-grip 3:4)							N			
Pick-out (pinch-grip: pad-side)		G	G	G		G	G	G	G	G
Pick-out (pinch-grip: pad-pad)									G	
Lever-apart				N	N				G	G
Pull-apart		G	G	G				G		G
Bite-off		G								
<i>Tidy-up bundle</i>										
Squeeze-up	N	NG	N							
Zig-zag	G	G	G	G	G	G	G	G	G	G
Two-handed-bend (S)			G	G	G	G	G	G	G	G
Two-handed-bend (R)					G	G	G	G		G
Adjust (pinch-grip: pad-side)	N	N	G	G		G	N	G		
Adjust (knuckles)			N							
Manipulate	G	G	G	G		G		G		G
<i>Repeat till enough</i>										
Combine (pick pad-side/loose)							N			
Combine (yank/power)				G	G	G			G	
Combine (yank/pinch: pad-side)	NG	G	G	G				G		
Combine (yank/loose)	N									
Combine (yank/pencil 3:4)										G
Combine (yank/foot)					N					
Combine (reach/power)		G				NG				

(continued on overleaf)

TABLE II. Elements Recorded in Processing of Nettle and Galium (Continued)

Individuals	KU	AM	IN	UM	MA	DA	SA	TU	BE	LI
<i>Repeat till enough (continued)</i>										
Combine (reach/loose)				N						
Combine (reach/pinch pad-side)			G							G
Combine (pick-out pad-side/power)		G		G		G	G	G	G	G
Combine (pick-out pad-pad/power)									G	
Combine (power/power)	G	G			N					N
Combine (pinch pad-side/power)			G							
<i>Remove unwanted parts</i>										
Adjust (pad-to-side)		N			N	N				
Adjust (knuckles)										
Manipulate							N			
Pick-out (pinch pad-to-side)	NG	G	G	NG	N	G	NG	NG	NG	N
Pick-out (pinch pad-to-pad)				G		G	N			
Pick-out (lips)			G	G	G			NG	G	G
Yank	N	NG			N	N			G	
Slice-down										
Pull-apart	G				N		N			N
Lever-apart	N		N	N	N	N	N		N	N
Twist-apart			N			N	N			
<i>Repeat till enough</i>										
Combine (twist-apart/ power-grip)						N				
Combine (lever-apart/ power-grip)	N				N					N
Combine (lever-apart/ loose-grip)							N			N
<i>Putting in mouth</i>										
Fold	N			N	N	N	N		N	
Fold (over thumb)	N			G	N		N			N
Bite-off		N						N		N
Roll	G	G	G	G	G	G	G	G	G	G
Sausage-feed	G	G	G	G	G	G	G	G	G	G
Shear-bite (S)	G	G	G		G			G	G	G
Shear-bite (R)		G	G	G						
Retain-nucleus	G	G	G	G				G	G	G
Nettle (elements, handfuls)	17,13	10,10	9,5	10,5	22,24	10,9	16,6	10,11	7,4	15,8
Galium (elements, handfuls)	15,13	23,17	21,11	22,22	11,5	21,9	12,5	18,12	20,10	21,8
Total: Elements	28	28	29	29	31	29	27	24	24	33
Total: handfuls	32	33	30	32	33	31	28	28	27	36

\*Ten animals, for whom adequate sample video material was available, were chosen for this analysis: juveniles KURyama, AMahoro, INeza, UMurava, and MAhane; adolescent males DARby and SANDuko; adult females TUCk and LIsa, and adult male BEetsme. Tuck was supporting a young baby during filming of nettle processing sequences. N and G indicate that the corresponding element of skill was noted in the individual's processing of nettle or galium, respectively. Element codes are those given in Table I.

counted for by the amount of processing analysed (elements =  $-0.74 + 0.89 \times$  handfuls,  $r^2 = 0.79$ , one-way ANOVA  $F(1,8) = 29.9$ ,  $P < 0.001$ ). Evidently we must still be underestimating the individual repertoires for all these animals, and it is even possible that eventually all animals would prove to use the same set of elements, most of them very rarely. Given the already high number of elements found, this hypothetical "complete" set may be an illusion: a description in terms of continuous grading between all types might prove more accurate, as with vocal communication [Marler and Tenaza, 1977].



## Element repertoires

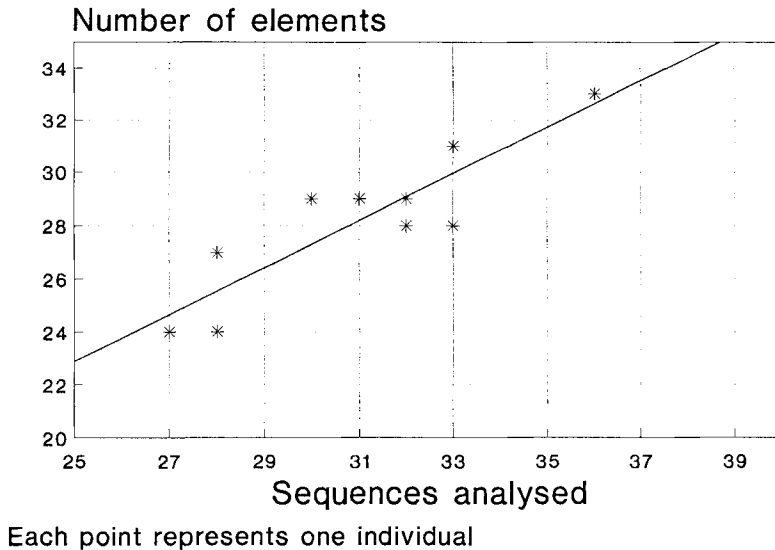


Fig. 1. Association between the number of sequences of leaf-processing analysed and the number of elements of manual skill attributed to an individual's repertoire.

Which set of elements an animal uses with regularity varies greatly among individuals. However, as noted above, some of these elements seem to be variants with little functional significance. Is it the case that all animals possess the same set of functionally equivalent elements, so that their repertoires are *effectively* the same, in terms of "problem-solving" potential? To answer this question, we reduced the categorization of Table I to functional categories, each category grouping all elements that achieve the same result. Elements within a functional category are thus treated as "the same" in the subsequent analysis. We examined all animals for whom we had at least four handfuls of either nettle ( $n = 15$ ) or galium ( $n = 23$ ) processing on videotape; also, for certain elements, such as use of *lip-grip* to remove debris, these data could be supplemented with that of the coded sequences.

This reduced but functionally adequate set of elements, with which both nettle and galium could in principle be fully processed in the flexible, adult manner, consists of *power-grip*, *pinch-grip*, *lip-grip*, *lever-apart* (and/or *twist-apart*), *strip-up*, *combine*, *two-handed-bend*, *zig-zag*, *roll*, *pick-out* (and/or *adjust*), *fold*, *shear-bite*, and *sausage-feed*. With few exceptions, all individuals for whom we had adequate film for either food ( $n = 28$ ) were recorded using all of these 13 elements (11 exceptions were found out of a possible 364). Thus, the variability across animals in preferred elements is not seen when functionally equivalent elements are lumped together.

It might be expected that the youngest animals, three of whom were not weaned, and those animals for whom our samples were smallest, would be those to lack any of these functionally differentiated elements. This is only partially the case. Sanduko's lack of *shear-bite* is no doubt due to small sample size (only five handfuls); Tuck's lack of *fold* is an obvious consequence of all the 11 sequences filmed being from a time when she had a baby only a few days old, needing

constant support; and the youngest, unweaned animals had several omissions (Kuryama, *two-handed-bend*; Amahoro, *lever-apart, two-handed-bend, fold*). However, other omissions do not fit these patterns. Of these, Umurava's lack of *two-handed-bend* has little practical significance, since the more dextrous, one-handed *zig-zag* serves the same purpose and is more versatile, allowing the other hand to be used for support. Picasso, by contrast, is incompetent in eating nettle to the extent that she cannot *fold* the detached bundle of leaf blades, an action which effectively keeps the stings on the upper-leaf from stinging the sensitive lips when eating. Her son, Ineza, also lacks this ability and is also the only animal to fail to show *strip-up*, an essential element in rapid accumulation of nettle-leaves; although quite old, he remained incompletely weaned at the time of the study. A possible reason for Picasso's incompetence, unique among the adults, will be discussed below.

### Logical Organization of Elements Into Techniques

A *technique* consists of an ordered sequence of elements of manual skill, coordinated so that the whole performance serves to process a handful of food. Every animal that possesses elements of motor skill, sufficient to perform the 13 functions identified above, might in principle arrange these elements in an almost limitless range of logical orderings, many of which would succeed in doing the job (and most elements can themselves be performed left- or right-handed, increasing the possible number of techniques still further). In fact, not many different sequences are found. These are examined in Table III, for all adult and juvenile animals ( $n = 38$ ). Only complete sequences were used in this analysis: that is, ones that successfully resulted in a handful being processed, beginning with initial procurement of the plant and ending with eating a food handful. Data where the task was interrupted, or where we failed to see some details, were excluded.

Each animal relies on only a few techniques for most processing. Disregarding stages optional in a complete sequence (cleaning galium, as many plants need no cleaning; accumulating nettle, as single large plants often provide a full handful), shows similarly low variability in technique for both plants (galium, mean 1.53, range 1–4; nettle, mean 1.95, range 1–4).

Most animals in fact have a strong preference for a single sequential order. For galium, all but two animals processed 50% or more of handfuls with a single sequence of elements used with the same laterality (mean 78.7%, range 40–100%); for nettle, all but four animals did so (mean 69.5%, range 33–98%). Even this perhaps underestimates animals' consistency. For instance, eating nettle by the sequences R-(R)-R-(L)-L or L-(L)-L-(R)-R is common. These are, of course, mirror reversals of each other. From laterality analyses of a much larger data set of independent bouts, we know that animals favouring left and right mirror forms of processing are about equally common in these tasks [Byrne & Byrne, 1991]. Inspection of Table III shows a number of cases where a single animal uses both "isomers" of what might better be treated as the same technique (15 cases for galium, but only 3 for nettle).

Furthermore, the exact sequences of elements are often the same in different animals. If sequences identical on mirror reversal are treated as the same, then a huge preponderance of processing is carried out by a single technique: 2,139 handfuls of galium out of 2,213 (96.6%) are processed by the sequence X-X-(Y or mouth)-X (where X, Y can be L, R or R, L), and 1,060 handfuls of nettle out of 1,306 (81.1%) are processed by the sequence X-(X)-X-(Y)-Y. Again this may underestimate the consistency; some "alternative" sequences appear to reflect no more than a slight tendency for initial procurement and final consumption to be carried out

**TABLE IIIa. Sequences of Elements Applied in Processing: Nettle Leaf\***

Animal	Age	P	(A1)	H	(A2)	E	n	%	N
Kuryama	3:00	L	—	L	(R)	R	19	61	31
		R	—	L	(R)	R	8	26	
Amahoro	3:03	R	—	R	(L)	L	16	50	32
		L	—	L	(R)	R	4	13	
		L	—	—	(L)	L	4	13	
Ntambara	3:06	R	—	R	(L)	L	29	63	46
		L	—	—	(L)	L	5	11	
Intwali	3:06	R	—	R	(L)	L	15	65	23
		L	(L)	L	—	L	3	13	
Ineza	3:07	L	(L)	L	—	R	14	32	42
		R	(R)	R	—	R	11	26	
		R	—	—	(R)	R	6	14	
Umurava	3:07	R	—	R	(L)	L	51	90	57
		R	—	L	(R)	R	2	12	
Ndatwa	4:06	L	—	L	(R)	R	14	82	17
		R	—	L	(R)	R	2	12	
Mahane	4:10	R	(R)	R	(L)	L	29	69	42
		L	—	—	(L)	L	5	12	
Mawingu	7:05	R	—	R	(L)	L	13	87	15
		R	—	—	—	R	2	13	
Jenny	8:00	L	—	L	(R)	R	48	83	58
		R	—	—	—	R	7	12	
Kubinya	8:09	L	(L)	L	—	R	8	57	14
		L	(R)	R	—	R	4	29	
Ginseng	8:10	R	—	R	(L)	L	37	90	41
Shengaza	8:10	R	—	R	(L)	L	7	70	10
Maggie	9:02	R	—	R	(L)	L	32	64	50
		R	—	—	(L)	L	8	16	
Benwa	9:09	R	—	R	(L)	L	16	80	20
		L	(L)	L	—	L	3	15	
Darby	10:02	L	(L)	L	(R)	R	48	98	49
Sanduko	10:09	R	(R)	R	—	L	38	97	39
Cantsbee	10:09	R	(R)	R	(L)	L	22	79	28
		L	(L)	L	(L)	L	3	11	
Kwihisha	10:09	R	(R)	R	(L)	L	27	93	29
Bilbo	11:02	L	(L)	L	(R)	R	30	94	32
Shinda	12:05	L	(L)	L	(R)	R	21	48	44
		R	(R)	R	—	L	6	14	
Kwiruka	14:0 +	L	(L)	L	(R)	R	15	58	26
		R	—	L	(R)	R	4	15	
Pablo	15:00	L	(L)	L	(R)	R	7	50	14
		R	—	R	—	L	5	36	
Titus	15:00	R	(R)	R	(L)	L	29	59	49
		R	—	—	(R)	R	6	12	
Picasso	16:0 +	L	(L)	L	(R)	R	19	39	49
		L	—	—	(L)	L	8	16	
		R	—	L	(R)	R	8	16	
Tuck	17:03	R	—	—	(R)	R	7	14	50
		L	—	L	(R)	R	9	18	
Ziz	18:07	R	(R)	R	(L)	L	34	71	48
		L	—	R	(L)	L	7	15	
Simba	21:04	R	(R)	R	—	L	65	86	76
Puck	21:09	L	—	L	(R)	R	45	64	70
		L	—	—	—	L	8	11	
Pantsy	23:05	R	—	R	(L)	L	38	76	50
		L	—	R	—	R	8	16	
Walanza	24:0?	R	(R)	R	(L)	L	39	78	50
Fuddle	23:0 +	R	—	R	(L)	L	25	58	43
		L	—	R	(L)	L	10	23	
Beetsme	25:0?	L	—	L	(R)	R	24	48	50
		R	(L)	L	(R)	R	8	16	
		L	—	—	(R,L)	R	7	7	
Pandora	25:0 +	L	—	—	(L)	L	34	69	49
		L	—	R	(L)	L	8	16	
Papoose	28:0?	R	(R)	R	(L)	L	32	64	50
		L	(R)	R	(L)	L	11	22	
Liza	35:0 +	L	—	L	(R)	R	36	68	53
		R	—	L	(R)	R	9	17	
Effie	35:0 +	L	—	L	(R)	R	36	68	53
		R	—	R	(R)	R	7	13	
		R	—	—	(R)	R	6	11	
Flossie	35:0 +	R	—	R	(L)	L	35	73	48
		R	—	—	—	R	8	17	

(continued)

**TABLE IIIb. Sequences of Elements Applied in Processing: Galium\***

Animal	Age	P	A	(C)	E	n	%	N
Kuryama	3:00	R	R	(L,M)	R	97	99	98
Amahoro	3:03	L	L	(M,R)	L	57	52	110
		—	—	(M)	L	23	21	
		R	R	(L)	R	14	13	
		R	—	(L,M)	R	12	11	
Ntambara	3:06	L	L	(M)	L	79	81	97
		R	R	—	R	15	15	
<i>Intwali</i>	3:06	L	L	(M,R)	L	80	86	93
Ineza	3:07	R	R	(M,L)	R	76	79	96
		L	L	—	L	14	15	
Umurava	3:07	L	L	(R,M)	L	73	80	91
Ndatwa	4:06	R	R	(L,M)	R	52	51	101
		L	L	(R,M)	L	47	47	
<i>Mahane</i>	4:10	L	L	(M,R)	L	84	88	96
<i>Mawingu</i>	7:05	L	L	(M,R)	L	46	98	47
<i>Jenny</i>	8:00	R	R	(M,L)	R	42	89	47
<i>Kubinya</i>	8:09	R	R	(L,M)	R	41	89	46
		L	L	—	L	5	11	
<i>Ginseng</i>	8:10	L	L	(R,M)	L	44	98	45
<i>Shengaza</i>	8:10	L	L	(M,R)	L	42	64	66
		R	R	(L)	R	19	29	
<i>Maggie</i>	9:02	L	L	(M,R)	L	46	92	50
Benwa	9:09	R	R	(M,L)	R	89	76	117
		L	L	(M,R)	L	28	24	
Darby	10:02	R	R	(M,L)	R	52	95	55
Sanduko	10:08	L	L	(R,M)	L	68	99	69
Cantsbee	10:09	L	L	(R,M)	L	35	78	45
		R	L	(R)	L	8	18	
Kwihisha	10:09	L	L	(R,M)	L	40	91	44
Bilbo	11:02	R	R	(M,L)	R	26	59	44
		L	L	(M,R)	L	17	39	
Shinda	12:05	R	R	(M)	R	27	54	50
		L	L	(M)	L	18	36	
<i>Kwiruka</i>	14:0 +	R	R	(M,L)	R	45	90	50
Pablo	15:00	L	L	(M,R)	L	37	95	39
Titus	15:00	L	L	(M,R)	L	47	96	49
<i>Picasso</i>	16:0 +	R	R	(L,M)	R	36	66	55
		L	L	(M)	L	7	13	
		L	L	(M)	R	6	11	
<i>Tuck</i>	17:03	R	R	(M,L)	R	41	84	49
Ziz	18:07	L	L	(M,R)	L	50	96	53
<i>Simba</i>	21:04	L	L	(R,M)	L	34	83	41
<i>Puck</i>	21:09	R	R	(M,L)	R	46	90	51
<i>Pantsy</i>	23:05	L	L	(R,M)	L	44	98	45
<i>Walanza</i>	24:0 +	L	L	(R,M)	L	20	47	43
		R	R	(L,M)	L	17	40	
<i>Fuddle</i>	23:0 +	L	L	(M,R)	L	35	59	59
		R	R	(M)	R	16	32	
Beetsme	25:0?	L	L	(M,R)	L	52	85	61
		R	R	—	R	9	15	
<i>Pandora</i>	25:0 +	L	L	(M,R)	L	49	100	49
<i>Papoose</i>	28:0?	L	L	(M,R)	L	39	83	47
<i>Liza</i>	35:0 +	R	R	(M)	R	38	93	41
<i>Effie</i>	35:0 +	R	R	(L,M)	R	37	76	49
		L	L	(R,M)	L	9	18	
<i>Flossie</i>	35:0 +	R	R	(M)	R	17	40	42
		L	L	(R,M)	L	14	33	
		R	R	(R,L)	L	8	19	

\*Each different sequence is shown as a row in this table. N records the total number of complete sequences available for analysis for each animal, and the number by each technique and its proportion (of N) are shown in the columns headed n and %. Sequences accounting for under 10% of processing are omitted for simplicity. Age of subject where known is given in years and months; females are in italic script. Functions are coded P for initial procurement, H for holding to enable something to be detached with the other hand, E for insertion into the mouth, C for removing debris, and A for accumulation of several items (at two different points, 1 or 2). Since the latter two operations are optional, any options used, however infrequent, are recorded, with their order showing relative frequency.

with the opposite limb to normal. Overwhelmingly, gorillas use a single technique for a single task; these techniques might therefore be termed "modal" for these animals, and are shown in Figure 2.

The commonest alternative sequences to those of the modal techniques are similar for both foods: procuring and eating items with one hand, optionally accumulating nettle with this hand or cleaning galium with the opposite one, but not both. This technique is how gorillas eat a wide range of undefended leaf foods [Byrne & Byrne, 1991, Fig. 1f] and is also that used most often by infants for nettle and galium, presumably with the cost of limiting choice to unusually sting-free nettles and hook-less galium plants, essentially to new growth. These infant techniques account for 1.6% of handfuls of galium and 9.2% of nettle leaves, the latter figure inflated by one adult who employed this technique for a majority of nettle eating. This was Pandora, an adult who is severely maimed, missing much of her right hand.

### Laterality Within Sequences of Elements

Since most handfuls of nettle and galium are eaten by means of one particular, modal sequence of processing elements, we can now ask to what extent stages within this sequence show behavioral lateralization. It is already known that the overall sequences are strongly lateralized [Byrne & Byrne, 1991], as indexed by the hand with which the processed leaves are put into the mouth; indices of left-right prevalence are strongly clumped near 0% or 100%, with approximately equal numbers of animals at each; and lateralization is highly correlated in the two tasks, eating nettle and galium (Pearson's  $R=0.87$ ,  $P=0.001$ ). These data were obtained using statistically independent bouts, but when we come to examine within-sequence variation independence is of course not possible. Here, we simply take all recorded uses of left or right hand in the obligatory stages of the modal sequences (P-A-E for galium, P-H-E for nettle) and calculate percentages with each hand and z-scores (Table IV).

Overall, degree of laterality increases from start to finish in both tasks. Repeated measures ANOVA of this was significant for both nettle (contrasts: P versus A,  $F(1,37)=15.4$ ,  $P=0.001$ ; E versus P,A,  $F(1,37)=36.6$ ,  $P=0.001$ ; overall  $F(2,74)=25.0$ ,  $P=0.001$ ) and galium (contrasts: P versus A,  $F(1,37)=13.9$ ,  $P=0.001$ ; E versus P,A,  $F(1,37)=32.8$ ,  $P=0.001$ ; overall  $F(2,74)=23.3$ ,  $P=0.001$ ). Most lateralization is highly significant (in 53 sequences out of a total 76, laterality is highly significant at all three stages,  $P=0.01$ ), but where it is not, this is generally most likely at the start of sequences (in 17 cases, laterality becomes and remains significant as the sequence advances). For one or other task, a few animals are exceptions to this generalization: for galium, Bilbo (not lateralized at any stage), Shinda, and Flossie; for nettle, Kubinya, Pablo (not lateralized at any stage), and Pandora. Pandora's lack of clear lateralization in holding nettle leaves is unsurprising, given her hand injuries, but otherwise no obvious pattern is apparent.

### Variability of Techniques

Although most handfuls of galium or nettle are processed by one of a very few sequences of elements regardless of the animal concerned, this does not mean that most animals use one or two techniques exclusively and rigidly. Gorillas seem to respond to environmental variations in their foods with efficiency, only doing what processing is necessary for adequate food intake, and responding to individually awkward plants with flexibility. It is also possible that variations reflect learning. With experience, gorillas may add new structural methods to their repertoire, or

TABLE IVa. Lateral Bias in Stages of Processing: Within Nettle Sequences<sup>†</sup>

Name	N	P-LAT	Z-P	H-LAT	Z-H	E-LAT	Z-E
Kuryama	51	22.6	1.26***	91.7	6.35*	100.0	-7.14*
Amahoro	50	6.3	-.35***	28.9	-1.94**	72.0	5.09*
Ntambara	48	47.8	-3.24*	61.9	-4.01*	100.0	6.93*
Intwale	23	39.4	-1.46***	50.0	-2.24**	100.0	4.80*
Ineza	49	14.3	-.93***	26.8	1.72***	100.0	-6.93*
Umurava	65	82.5	-6.23*	96.6	-7.42*	100.0	8.00*
Ndatwa	18	64.7	2.67**	100.0	4.12*	100.0	-4.24*
Mahane	46	61.9	-4.01*	68.6	-4.90*	100.0	6.78*
Mawingu	19	100.0	-3.87*	100.0	-4.36*	79.0	3.44*
Jenny	60	65.5	4.99*	100.0	7.28*	100.0	-7.75*
Kubinya	14	100.0	3.46**	28.6	1.07***	100.0	-3.74*
Ginseng	42	85.4	-5.47*	90.2	-5.78*	95.1	6.09*
Shengaza	10	40.0	-1.26***	77.8	-2.33**	100.0	3.16*
Maggie	50	60.0	-4.24*	57.1	-3.70*	80.0	5.66*
Benwa	22	60.0	-2.68**	71.4	-3.27*	100.0	4.69*
Darby	50	95.9	6.71*	100.0	7.00*	100.0	-7.07*
Sanduko	39	100.0	-6.24*	58.3	-4.04*	100.0	6.24*
Cantsbee	30	71.4	-3.78*	64.3	-3.40*	100.0	5.48*
Kwihisha	29	86.2	-4.64*	93.1	-5.01*	100.0	5.39*
Bilbo	32	87.5	4.95*	93.8	5.30*	100.0	-5.66*
Shinda	45	27.3	1.81***	41.5	2.65**	42.2	-2.83*
Kwiruka	26	38.5	1.96**	66.7	3.27*	76.0	-3.80*
Pablo	15	.0	.00***	.0	.00***	20.0	-.77***
Titus	49	51.0	-3.57*	65.0	-4.11*	56.5	3.83*
Picasso	53	22.5	1.57***	55.6	3.33*	61.5	-4.44*
Tuck	50	24.0	1.70***	73.3	4.92*	75.5	-5.29*
Ziz	50	58.3	-4.04*	100.0	-6.56*	84.0	5.94*
Shimba	76	79.0	-6.88*	94.7	-8.26*	100.0	8.60*
Puck	70	68.6	5.74*	96.4	7.22*	69.7	-5.66*
Pantsy	50	56.0	-3.96*	88.0	-6.22*	56.0	3.96*
Walanza	50	76.0	-5.37*	83.0	-5.69*	70.8	4.91*
Fuddle	50	30.2	-1.98**	87.0	-5.90*	84.0	5.94*
Beetsme	50	44.0	3.11*	79.0	4.87*	96.0	-6.79*
Pandora	50	83.7	5.86*	57.9	-2.52**	100.0	7.07*
Papoose	52	36.0	-2.55**	96.1	-6.86*	91.5	6.27*
Liza	54	50.9	3.71*	84.0	5.94*	69.8	-5.08*
Effie	61	21.3	1.66***	41.8	3.10*	100.0	-7.14*
Flossie	50	83.3	-5.77*	76.7	5.03*	67.4	4.71*
Mean		58.9		70.2		78.2	
S.D.		24.1		30.1		24.9	

(continued)

alternatively they may refine an initially large range of methods into a few optimal ones.

In order to examine these possibilities, two measures of stereotypy were calculated: the number of techniques used by each animal for each food, and the percentage of handfuls processed by that animal's commonest technique. As would be expected, the two measures are inversely correlated (partial correlation of number of techniques with percentage by commonest technique, controlling for the number of handfuls; for nettle,  $R = -0.51$ , for galium,  $R = -0.67$ , both significant at

TABLE IVb. Lateral Bias in Stages of Processing: Within Galium Sequences<sup>†</sup>

Name	N	P-LAT	Z-P	A-LAT	Z-A	E-LAT	Z-E
Kuryama	99	98.0	-9.70*	100.0	-9.95*	100.0	-9.95*
Amahoro	130	24.6	4.96*	12.3	5.90*	55.4	6.31*
Ntambara	100	58.0	6.19*	60.0	6.26*	70.0	7.00*
Intwale	99	63.6	7.15*	73.7	8.95*	100.0	9.95*
Ineza	100	60.0	-5.72*	70.0	-6.46*	70.0	-7.00*
Umurava	97	50.5	5.77*	75.3	7.41*	81.4	8.02*
Ndatwa	115	16.5	-.50***	18.3	-1.87***	23.5	-2.52**
Mahane	100	68.0	7.35*	88.0	8.94*	96.0	9.60*
Mawingu	49	87.8	6.56*	91.8	6.64*	95.9	6.71*
Jenny	49	83.7	-5.69*	83.7	-5.77*	83.7	-5.86*
Kubinya	50	80.0	-5.31*	80.0	-5.31*	80.0	-5.66*
Ginseng	50	76.0	6.41*	96.0	6.79*	96.0	6.79*
Shengaza	67	25.4	2.22**	43.3	3.54*	46.3	3.79*
Maggie	51	80.4	5.94*	92.2	6.58*	96.1	6.86*
Benwa	118	52.5	-5.64*	52.5	-5.64*	52.5	-5.71*
Darby	59	93.2	-6.88*	93.2	-7.16*	93.2	-7.16*
Sanduko	74	83.8	8.07*	100.0	8.60*	100.0	8.60*
Cantsbe	50	40.0	3.73*	92.0	6.51*	96.0	6.79*
Kwihisha	50	60.0	5.43*	96.0	6.79*	100.0	7.07*
Bilbo	51	29.4	-1.21***	17.7	-1.13***	13.7	-.98***
Shinda	51	13.7	-.85***	25.5	-3.45**	17.7	-1.26***
Kwiruka	60	83.3	-5.66*	93.3	-7.23*	96.7	-7.49*
Pablo	51	45.1	5.60*	92.2	6.58*	92.2	6.58*
Titus	52	80.8	6.43*	96.2	6.93*	100.0	7.21*
Picasso	58	34.5	-2.29**	51.7	-3.84*	72.4	-5.51*
Tuck	50	68.9	-4.71*	76.0	-5.37*	88.0	-6.22*
Ziz	55	81.8	6.46*	100.0	7.42*	100.0	7.42*
Simba	49	42.9	4.53*	79.6	5.57*	83.7	5.86*
Puck	52	80.8	-5.74*	84.6	-6.10*	84.6	-6.10*
Pantsy	51	72.6	6.41*	96.1	7.07*	100.0	7.14*
Walanza	51	21.6	-.46***	2.0	.28***	80.4	5.74*
Fuddle	63	17.5	1.95***	36.5	2.90*	52.4	4.16*
Beetsme	71	46.5	5.51*	74.7	6.29*	71.8	6.05*
Pandora	56	75.0	7.00*	96.4	7.42*	100.0	7.48*
Papoose	50	56.0	4.52*	84.0	5.94*	92.0	6.51*
Liza	48	87.5	-5.47*	87.5	-6.06*	91.7	-6.35*
Effie	52	57.7	-3.86*	53.9	-3.78*	69.2	-4.99*
Flossie	49	42.9	-2.16**	2.0	-.14***	30.6	2.14**
Mean		56.1		73.3		85.5	
S.D.		28.1		25.0		19.6	

<sup>†</sup>For each stage the table shows the strength of hand preference: the number of handfuls using the modal hand as a percentage of the total (P-LAT, H-LAT, A-LAT, and E-LAT). Each has an associated z-score (Z-P, etc.), negative for right- and positive for left-handed. Significance level is two-tailed and uses the z-distribution, corrected for continuity if  $n = 20$  or less, unless  $n = 15$  or less when the binomial test was used: \*,  $P = 0.01$ ; \*\*,  $P = 0.05$ ; \*\*\*, n.s.

$P = 0.001$ ). However, they give us somewhat different information. A separate technique was scored for any sequence of steps from P (procure) to E (eat) in which each step was done in a particular way (left-handed, right-handed, using both hands together, using both hands separately, using the mouth, etc.). By this definition, gorillas use a mean of 8.7 techniques ( $SD = 3.8$  and range 3–23) for eating nettle, eating 49% of handfuls by the major one; for galium they use a mean of 9.0

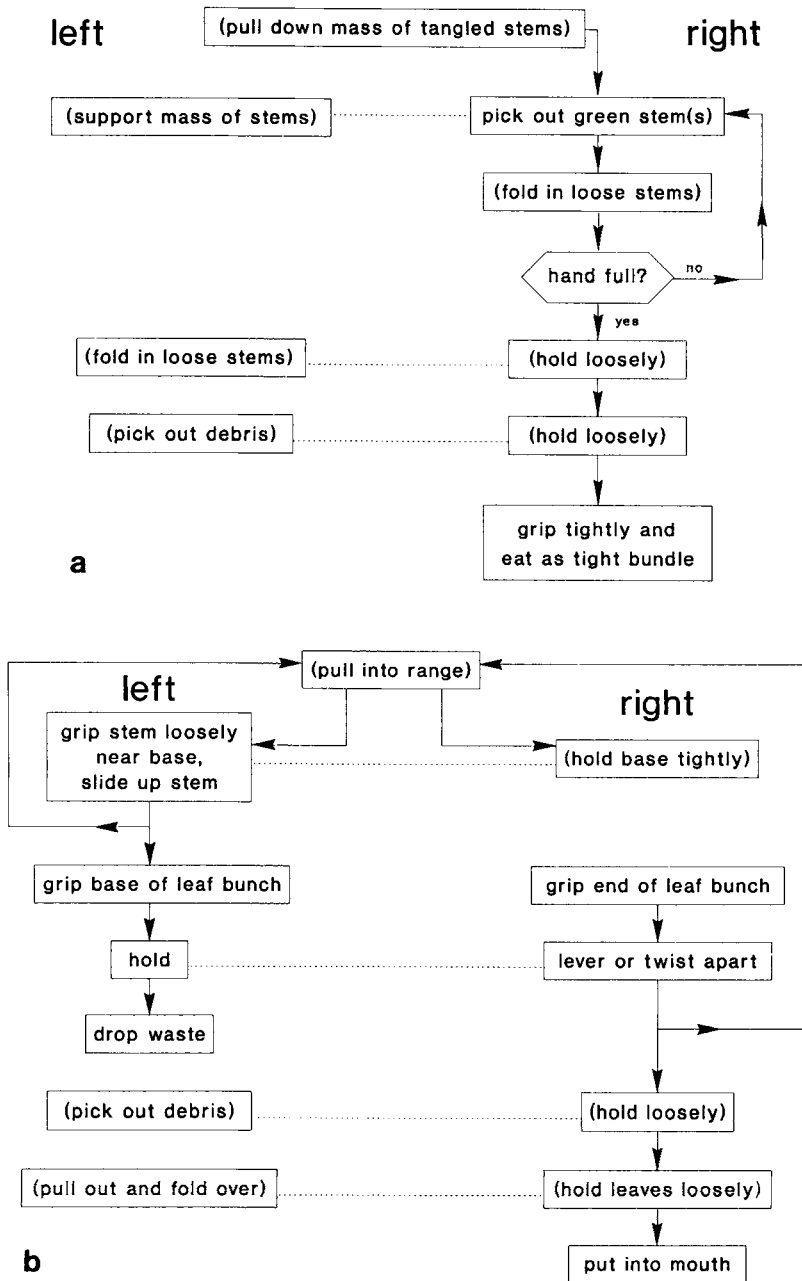


Fig. 2. Flow charts of the modal processing techniques used by adult and juvenile mountain gorillas in the study population on the tasks investigated in this study. Where the logical structure is asymmetric, and mirror form will also occur; the form shown is for an animal coded "right handed." a: *Laportea alatipes* leaves: NET-TLE. b: *Galium ruwenzoriense*: GALIUM. The sequence of actions (which begins when an animal finds a food to eat) starts at the top and moves down: rectangular boxes show actions, described by the words in them, arranged to left and right of the midline to indicate significant lateralities in the hand used (actions with non-significant laterality in some animals are represented on the midline, and brackets show actions which are optional, depending on environmental conditions). Dotted lines indicate bilateral coordination between the separate actions of the two hands. Diamonds represent branch points, with the approximate criteria for the decision indicated in words in the diamond: thus a process may repeat or iterate until an appropriate size of handful is reached. The sequence ends with putting processed food in the mouth.



(SD = 2.6 and range of 5–21), eating 57% by their commonest technique. Like the number of elements in an animal's processing repertoire, the number of techniques increases with our sample size of handfuls processed (nettle,  $R = 0.38$ ,  $P = 0.006$ ; galium,  $R = 0.48$ ,  $P = 0.001$ ).

Does the extent to which gorillas rely on one technique, rather than use several, vary with their age, sex, or group of residence? Animals older than 7 years (for whom equal amounts of data were collected) were examined for effects of sex or group. None were found (nettle,  $F_{1,28} = 0.27$  ns for sex,  $F_{2,27} = 1.5$  ns for groups; galium,  $F_{1,28} = 0.08$  ns for sex,  $F_{2,27} = 0.63$  ns for groups). All 38 adults and juveniles were included for analysis of the influence of age, and partial correlations are used to remove the effect of sample size. This revealed small but significant age effects (partial correlation of number of techniques, with age, for nettle  $R = 0.11$  ns, for galium  $R = 0.41$ ,  $P = 0.006$ ; partial correlation of percentage processed by major technique, with age, for nettle  $R = -0.29$ ,  $P = 0.04$ , for galium  $R = -0.37$ ,  $P = 0.012$ ; controlling for number of handfuls in each case). There is a tendency for the number of techniques to increase with age, and reliance on the commonest technique to decrease.

## DISCUSSION

The techniques gorillas use to process leaves defended by stings or hooks are made up of many elements of manual performance. These elements are used idiosyncratically, each animal having a different set of preferred elements. In the population of adults and juveniles studied here, there is no sign of individual repertoires of elements changing with age. However, the set of elements we attribute to an individual depends on how much processing we analyse in detail, and it is likely that each animal occasionally employs elements from a very large repertoire; the term "element," implying a discrete action pattern, may even be misleading, with some perhaps grading continuously into one another. Many of these elements in the total set of 78 we recorded are functionally equivalent. If we group elements into functional categories (13–15 are required), the appearance of idiosyncrasy largely vanishes: almost all animals show all capabilities of performance.

The exception to this generalization is a revealing one. One female, Picasso, who transferred into Group 5 in late 1984, does not fold nettle leaves before eating them, and thus must often have her lips hurt by the powerful stings on leaf edges and uppersides; nor does her juvenile son. Other than these, the only gorillas to omit this important stage are the youngest, unweaned juveniles, and Pandora, a female with badly maimed hands (Tuck, who did not fold nettles when filmed, because she was continually supporting a recently born baby, showed a normal repertoire at other times). Picasso was born and grew up in Group 11, a group whose range, at lower altitude than the study area, includes few nettles *Laportea alaticipes*. The possibility cannot be ruled out that the action of folding is normally acquired by observation. (Since gorilla adults feed alone, except that infants are permitted to remain with their mother or a silverback, a female transferring as an adult has no model for observation.) With this exception, the variability and idiosyncrasy of usage shown at the level of manual elements is entirely consistent with trial-and-error learning, in which an initially large repertoire of random variations is selected by favourable consequences until only useful elements remain.

Turning to the sequencing of elements into techniques, a wholly different picture is found. Each animal uses very few techniques for most processing, and these techniques (see Fig. 2) are the same across the population. The initial stage of procuring the plants is less strongly lateralized than later stages and shown in

Figure 2 as ambidextrous, although in fact most animals are significantly lateralized at all stages. Lateralization increases from start to finish, consistent with a logical structure in which each stage has some laterality bias and each stage is sequentially dependent on the last. Treating left and right isomers as the same technique, and ignoring the variable lateralization of the first stage, the evidence can be summarized as follows: the vast majority of processing by all animals uses the same multi-stage, lateralized technique with iterative looping and bimanual coordination (87.9% for nettle, 97.0% for galium). The little that deviates from this rule mostly employs the simple technique otherwise used for undefended leaves [Byrne & Byrne, 1991, Fig. 1f] and presumably is used in response to individual plants of nettle and galium that are unusually weakly defended.

The high degree of structuring of the modal techniques and their standardization across the study population are striking, especially compared with the variability in form of the elements comprising them. This is not, however, to suggest that the logical structures are in any way fixed action patterns. Although variations from the modal patterns are in a minority, they occur in all animals (on average, about nine variant techniques were recorded from each animal), and variability increases significantly with age. Rather than implicating a process of trial-and-error selection from an initially large range of randomly varied sequences, this points to an initial reliance on a single logical structuring that is well established by weaning (about 3.5 years), with the ability later to vary the technique in small ways to take advantage of variations in the environment.

How might these complex techniques be acquired? There are three broad options. First, their development might be tightly channeled by genetic constraints, like the fixed action pattern of pecking shown by a newly hatched chick. This is implausible when the close altitudinal zonation of the herb foliage is recalled: the genes would need to be specific to narrow populations of animals. Further, the manipulative behaviour of captive gorillas (who are admittedly lowland gorillas *Gorilla g. gorilla*, and so unlikely in the wild to encounter plants requiring identical techniques to those of mountain gorillas) shows great variation but an almost complete lack of overlap with leaf-processing elements. Parker [1974] noted 69 elements from all the species he studied with only four (coinciding with *yank*, *power-grip*, and *loose-grip*) in common with this study; none of the action patterns he considered unique to gorillas were noted here. No doubt the basic ways of gripping and touching objects are indeed under tight genetic control, but this is inadequate for many of the more complex elements of processing.

Alternatively, the techniques might be learned by trial-and-error learning: high variation in behavior, shaped by the rewards and punishments of experience until the final form is achieved. The social context may be influential in drawing attention to aspects of the environment and stimulating activity, but not in selecting behaviors to be learned. This has been proposed by Watts [1985] for how infant gorillas learn which foods are edible by observation of their mothers eating. We have noted that this is also entirely plausible for acquisition of the repertoire of elements of manual skill, since idiosyncratic variability is the norm. Just such logic has been used to argue that the idiosyncratic gestures of young chimpanzees are acquired by individual learning [Tomasello et al., 1985, 1989]. However, the feeding techniques of mountain gorillas, standardized structures of elements, logically organized into efficient wholes, lack any such idiosyncratic variability. For this pattern to result from trial and error implies that for gorilla food plants the constraints of the environment are so tight that one and only one logical sequence is learnt by individual experience in the first 3 years of life, with no room for idiosyncratic variation. This appears wildly unlikely but cannot be entirely ruled out.

Finally, the techniques may have been acquired by imitation. In considering this possibility, it is important to distinguish the *levels* at which imitation might in principle take place. As normally construed by ethologists, true imitation is “impersonation” [Thorpe, 1956; see Tomasello, 1990], where the detail of motor acts is slavishly copied from a model. We have already noted that the detail of elements is variable and idiosyncratic, so imitation of this level is unlikely; further, hand preferences are not copied from the only available models [the mother and the silverback male: Byrne & Byrne, 1991]. However, an alternative is that what is imitated is the logical ordering of elements and the inter-relationships of processing stages as shown in Figure 2: *program-level imitation*. This would be consistent with the standardization of logical organization despite the variability of individual elements and laterality across animals. An ideal test would be the discovery of an idiosyncratic logical structure, in both a mother and offspring or in a silverback and all the juveniles of his tenure as leader. Unfortunately the standardization is too complete, and no such useful variant was recorded.

Program-level imitation could be achieved quite simply, for instance, by copying the sequence of subgoals in a process, each of which has a distinctive end-point: a bunch of nettle leaves protruding from a first, a folded bundle of leaf-blades held between 1st and 2nd fingers, and so on. This might be encompassed within the original meaning of the term “emulation” [Wood, 1989]; however, in primatology this term has been used specifically to describe copying of the overall goal [e.g., Whiten & Ham, 1992], so to avoid confusion we do not extend the meaning, and employ the less theoretically loaded term “program-level imitation,” since we cannot be sure how this imitation is achieved. The challenge for future research will be to establish exactly how infant gorillas acquire such complex logical programs of action and to compare what they do acquire with the mechanical skills of other primates. Mountain gorillas are certainly remarkable for their array of flexible but complex techniques for the processing of plant material; could they be unique among non-human primates?

## CONCLUSIONS

1. Mountain gorillas use complex manual procedures for processing leaves that are “defended” by stings, tiny hooks, or spines; elementary uni-manual and bi-manual action patterns are sequenced into techniques of 4–5 successive stages, some of which may be iterated.

2. Individual repertoires of elementary action patterns are highly idiosyncratic and variable but do not vary systematically with age after weaning.

3. Despite this variability, almost every animal possesses elements sufficient for all *functionally* different operations (13–15, compared with at least 78 structurally different patterns).

4. For the two plants studied in detail, *Laportea alatipes* and *Galium ruwenzoriense*, individuals use on average about nine techniques (particular structured sequences of elements, coordinated for efficient function), and this repertoire of techniques increases slightly with age.

5. Lateralization increases from start to finish within these sequences for both *Laportea* and *Galium*, but the great majority of variation is between “mirror reflections” of complete sequences of four or five lateralized stages.

6. Recognizing such isomers as structurally identical shows that most processing by all animals is done with the same, standardized logical organization (88% and 97%, respectively).

7. These patterns of variation suggest that elements are acquired by trial-and-error exploration, whereas logical organization is copied by program-level imitation.

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