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Cognitive capacities for behavioural flexibility in wild chimpanzees (*Pan troglodytes*): the effect of snare injury on complex manual food processing

Received: 20 June 2000 / Accepted after revision: 8 February 2001 / Published online: 11 May 2001

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Abstract In chimpanzees, it is only in the restricted context of tool use that manual and cognitive skills have been described, comparable to those that gorillas and orangutans display in obtaining plant foods. We report the complex food preparation skills used to eat, without tools, the leaves of the tree *Broussonettia papyrifera* in the Sonso community of chimpanzees at Budongo Forest, Uganda. Able-bodied individuals used multi-stage techniques that required bimanual role differentiation at several stages, and were hierarchical in organisation. A total repertoire of 14 techniques was found, with strong preference in all individuals for either of two of these; 6 additional techniques were found when flowers and leaves were eaten together. However, in this community over 20% of individuals suffer from some form of upper- or lower-limb injury as a result of snares. We investigated the manner of compensation for upper-limb injury. Only the most severely injured showed reduced feeding efficiency. Injured individuals were found to use the same repertoire of techniques as able-bodied chimpanzees. We found no evidence to suggest that injured individuals were able to develop wholly novel techniques optimal for their specific injuries, although shifts in preference for particular techniques did occur. Rather, injured individuals used novel ways of achieving particular steps in the process; by “working around” their impairments; in this way, they managed to use the same

techniques as the able-bodied. Since snare injuries generally befall young animals, these results suggest that chimpanzees learn techniques partly through observational learning (of, necessarily, able-bodied individuals).

Keywords Chimpanzee · Feeding technique · Injury · Hierarchical organization · Imitation

Introduction

Until recently, “skill” in primate foraging has been regarded as a matter of learning how to identify and locate edible items (Clutton-Brock and Harvey 1980), avoiding poisons (Hladik 1977), and dealing with complex non-seasonal patterns of food availability in tropical forests (Milton 1981). Only for tool use has it been recognised that technical skills are also important: in chimpanzee insect gathering and nut-cracking (e.g. Teleki 1974; Parker and Gibson 1979; McGrew 1992a; Yamakoshi and Sugiyama 1995) and in orangutan frugivory (van Schaik et al. 1996; Fox et al. 1999).

However, detailed analyses of the behaviour of gorillas (Byrne and Byrne 1991, 1993) and orangutans (Galdikas and Vasey 1992; Russon 1998) in feeding tasks that do not involve tool use have now shown that eating leaves and stems may also involve considerable technical skill. Furthermore, these techniques can exhibit complex logical organization. For instance, mountain gorillas in the Virunga Volcanoes use several different techniques, corresponding to their major food plants (Byrne and Byrne 1991). Each technique exhibits a number of distinct and sequentially organized stages, relies extensively on use of the two hands in coordinated, complementary roles, and invokes strong behavioural laterality. In effect, a technique provides a “solution” to a particular problem set by the mechanical defences or form of a plant: spines, stings, clinging hooks, hard outer casing, and so on. Moreover, despite their complexity, for any one food type techniques are standardised across the population (Byrne and Byrne

Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at <http://dx.doi.org/10.1007/s100710100082>

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1993). Such complexities suggest a level of cognitive ability comparable to that seen in simple craft technology in humans. This is consistent with theoretical proposals (McGrew 1992b; Byrne 1993, 1995; Gibson 1993; Byrne and Russon 1998; Russon 1998) that all great apes, not just humans, possess the ability to keep a number of mental, perceptual or motor elements in mind simultaneously and to combine several of these elements into new wholes, which can then be used as sub-units of other mental constructions. This facility for “hierarchical mental construction” may be lacking in other mammals, even non-human primates. Detecting hierarchical structure in fluid behaviour is not straightforward, but Byrne (1999) has suggested a number of behavioural indices that may serve as clues to underlying organization (for additional possible indices see also Matsuzawa 1996; Russon 1998; A. Russon and B.M.F. Galdikas, unpublished work).

As yet, little is known of the abilities of the chimpanzee in feeding on plants without the use of tools, beyond the relatively rare, non-subsistence activity of medicinal plant-use (e.g. Huffman and Wrangham 1994). Elsewhere, reports of skilled plant processing in chimpanzees are derived at best from anecdotal observations in the field (e.g. Wrangham 1977; Nishida et al. 1983; Tutin et al. 1996). The plant-processing skills of chimpanzees therefore provide the obvious candidate for a comparative study on manual skills in great apes, and a potentially important insight into the evolutionary factors that led to the technical sophistication seen in the human line.

This paper describes dextrous plant-processing skills in a non-provisioned community of wild chimpanzees, paying particular attention to evidence for hierarchical organisation in this feeding behaviour. We focus in particular on the manner in which manual skills vary with hand injury. Injuries to chimpanzees as a result of snares occur at many sites across Africa (Stokes et al. 1999) but the severity and frequency of injuries at Budongo is particularly striking. Here, over 20% of individuals suffer from some form of upper- or lower-limb injury, and the injuries are extreme, typically involving either the loss of a hand or foot or else partial or complete paralysis of at least one limb (Waller 1995). Upper-limb injuries in particular are likely to result in feeding difficulties, specific to those foods that require a degree of manual skill and dexterity in order to process. The ability of an injured individual to overcome their injuries is therefore paramount to their survival. The fact that such a large proportion of this community has sustained and yet survived major limb trauma suggests that these individuals are able to compensate for their injuries. We present data on techniques used by chimpanzees with a plant food that is relatively difficult to process, *Broussonettia papyrifera*, and analyse individual variation in method at both gross and fine-detail levels of analysis. A direct comparison of injured and able-bodied populations is made in order to investigate the nature and extent to which these techniques differ in the case of injury. The manner and extent of compensation in response to injury is used to give evidence of the cognitive processes involved in normal skill acquisition.

Methods

Study site and study population

The Budongo Forest Reserve lies in the western Rift Valley (1°35′–155°N, 31°18′–31°42′E) at a mean altitude of 1050 m (Eggeling 1947). The Reserve covers a total area of 793 km², of which 482 km² is continuous forest cover, classified by Eggeling as medium altitude semi-deciduous.

In August 1997, the Sonso study community of chimpanzees consisted of 51 named individuals: 25 adults (13 males and 12 females), 8 sub-adults (3 males and 5 females), 11 juveniles (6 males and 5 females) and 8 infants (4 males and 4 females). Ten of these individuals have permanent injuries to the upper or lower limbs, comprising nine adults (5 males and 4 females) and one sub-adult female. The majority of these cases are probably the result of having encountered wire snares set on the forest floor. During the study a new injury was sustained by a juvenile female who lost her hand to a snare (E.J. Stokes, personal observations).

Injuries of subjects

The nature and extent of injury are highly idiosyncratic across individuals. This paper focuses on those individuals with debilitating injuries and thus excludes animals with single missing digits. Furthermore, we are interested only in those individuals whose injuries included damage to the arm or hand. Consequently, we present data here on only five individuals from the injured population that meet these criteria (3 adult males, 1 adult female and 1 sub-adult female). The following descriptions are taken from Waller (1995).

Tinka, an adult male, is the most severely injured. Both his left and the right hand exhibit major deformities. Most of the muscles of the left wrist are apparently paralysed, which allows the left hand a limited axis of movement, but in its relaxed posture the wrist is hooked and weakened. Digits 1–4 are permanently flexed and incapable of assuming any independent movement although the thumb has retained some function. The right hand exhibits even greater deformity, with complete paralysis of the wrist and voluntary movement impossible.

Keway, a sub-adult female, has a totally paralysed right hand (see supplementary material at <http://dx.doi.org/10.1007/s100710100082>). The wrist is extremely hooked at all times and considerably stretched and twisted round the forearm. The hand is wasted and the fingers contorted so that the middle finger lies overlapping the forefinger. The hand is still capable of a certain amount of passive movement – swinging limply about the wrist, with movement confined to a small axis.

Kalema, an adult female, shows a similar “claw hand” deformity to that of *Keway*. The right hand is rigidly hooked at the wrist and the fingers are flexed and immobile. The whole hand is emaciated and wasted.

Kikunku and *Muga*, both adult males, have lost entire parts of their entire limbs. *Kikunku* is missing his left limb from a point midway up the forearm. *Muga* is missing his right hand but, in contrast, the point of amputation is distal to the wrist and consequently the majority of the wrist joint is retained and appears to function as normal.

Feeding task

In order to investigate fully the effect of upper-limb injury on feeding skill, we chose a leaf-processing task that demands multi-stage techniques involving delicate manipulation and the use of both hands in complementary, co-ordinated roles, termed “bimanual role-differentiation” by Elliott and Connolly (1984). This paper examines the food-processing technique for the young leaves of the paper mulberry *Broussonettia papyrifera*. This is an exotic species introduced for paper production in the 1950s. It is ubiqui-

tously distributed around forest edges and provides a year-round food source. The young leaves have large fleshy leaf blades with a rough hairy surface. The leaf petioles are tough and are removed before the leaves are eaten, apparently in order to aid digestion and palatability. Eating new leaves of *Broussonettia* accounts for about 5% of the time spent feeding by chimpanzees. There is no significant difference in this proportion between able-bodied and injured chimpanzees, whereas injured individuals spend a greater proportion of time eating figs *Ficus* spp. and a reduced proportion eating the relatively hard-to-process flowers of *Broussonettia* (Stokes 1999).

Data collection

Observations were made on all 25 adult chimpanzees during August 1997 to September 1998, using sequence sampling (Altmann 1974), where the focus of the observation is the interaction sequence between animal and food item rather than any particular individual. In our data, the interaction sequence was a feeding *bout*, which we defined as beginning when an individual first touches the food, and ending when interrupted or terminated by switching to another activity, by moving away from the food item, or periods of inactivity of 20 s or more (since 20 s is approximately the median time required to eat one handful of *Broussonettia*). As *Broussonettia* is a substantial tree, a considerable amount of food can be consumed during a single bout. During consumption, several leaves or stems may be accumulated in the hand before placing into the mouth: this was termed a *handful* and formed the basic unit of sequential analysis. Several handfuls can occur within a single bout; however, for every individual, data were obtained from more than one bout (bouts per individual, able-bodied mean 7.8, range 6–10; injured mean 13.0, range 9–19). In order to ensure that unusual postural demands did not affect feeding, data were only collected from seated individuals. Processing was considered to be made up of sequences of individual elements of action; an *element* was defined as a single action that resulted in a clear change to plant material (see Byrne and Byrne 1993 for further detail on delineation of an element). For each element, the body part(s) used was recorded: left or right hand, both hands together, left or right foot or mouth. Any ordered sequence of elements of manual skill, coordinated so that the whole performance serves to process a handful of food, was defined as a *technique* (Byrne and Byrne 1993; see Appendix for glossary of terms).

An attempt was made to collect equal amounts of data per individual in terms of handfuls, but this was not always easy due to the fission-fusion nature of chimpanzee society. In addition, the dense undergrowth and variable levels of habituation across individuals posed problems of visibility. Consequently, only results from individuals with 10 or more handfuls are used in this paper (able-bodied individuals: $n=9$, total number of handfuls=230, mean number of handfuls per individual=31, range 17–60; injured individuals: $n=5$, total number of handfuls=230, mean number of handfuls per individual=46, range 22–65). Larger data sets were collected for injured individuals to be sure of separating the consequences of injury from any idiosyncratic features of their behaviour; in able-bodied individuals, the commonality of methods in the population makes this determination more straightforward. A voice-operated Sony Dictaphone was used to record the sequences of elements used in processing each handful.

In addition to sequences of feeding actions, rates of processing were calculated from data collected on a hand-held computer (Hewlett Packard 200LX). Key presses were used to record the time at which each handful of processed food was placed in the mouth, and intervals between successive key presses were used to measure the time taken to process a single handful in any given bout.

Results

Feeding technique in able-bodied chimpanzees

In order to process *Broussonettia* leaves, chimpanzees used a variety of techniques (see supplementary material at <http://dx.doi.org/10.1007/s100710100082>). For the able-bodied population, a total of 14 techniques were used in feeding on young leaves (labelled T1–T14; Table 1), with an additional 6 techniques observed when feeding on young leaves together with flowers (labelled Ti–Tvi). Individuals had a mean repertoire of 5.3 techniques (range 4–7). The majority of these techniques hinge around stripping a stem of leaves to form a roll of leaves in the palm with leaf blades aligned parallel. In this way, only a single action is required to remove the petioles from all of the leaves.

Technique T1 or T4 was the preferred technique for six out of nine individuals. Both of these used the “strip-up” element in order to detach leaves. For those six individuals, the preferred technique (either T1 or T4) was used to process a mean 39.7% of handfuls (SD 14.97, range 23.1–57.1%). Of the remaining three individuals studied, all used one or other of these two techniques to process >5% of handfuls. Techniques are then further differentiated by the direction in which the leaves are stripped. Leaves can be stripped towards the individual, in which case leaf blades are first consumed and petioles discarded at the end of the handful; or else leaves can be stripped away from the individual, in which case petioles must first be discarded before the leaf blades are available for eating. T1 (preferred by 2 out of 6 individuals) requires leaves to be stripped towards the individual whereas T4 (preferred by 4 out of 6 individuals) requires leaves to be stripped away from the individual. T3 and Ti accounted for >5% of processing in all individuals, with the one exception of Nkojo. T3 again employs the “strip-up” element, but the leaves are stripped and held and the blades folded over and detached with the lips rather than the hand. Ti was used primarily for processing leaves together with flowers.

Of the remaining, less common, techniques there was considerable variation in frequency of use across individuals. This suggests a degree of flexibility in choice of technique, which is important in order to respond to environmental variations in food efficiently. Linear regression of the number of techniques from the number of handfuls revealed that a good deal of the variance in the number of techniques in an individual’s repertoire is accounted for by the sample size ($r^2=0.62$, $P=0.01$), and thus we are undoubtedly underestimating the number of techniques available to an individual at any one time.

One important feature of these individual techniques is that they overlap at some points: indeed, some strings of elements are used by several techniques. As a result of this, a composite flow diagram can efficiently be created, incorporating all the possible techniques used by able-bodied chimpanzees in processing a handful of young leaves of *Broussonettia* (Fig. 1). Any one technique will form a

Table 1 Techniques of able-bodied chimpanzees feeding on young leaves of *Broussonettia*

Symbol	Method
One-handed	
T2	Branch is brought into range and supported with one hand, whilst leaf blades are picked off with the lips (11.8%).
One-handed, with folding	
Ti	Branch is brought into range and supported with one hand, whilst leaf blades are folded over and detached by the lips. Leaf blades are then gathered into the mouth by the lips (14.6%).
Tii	Branch is brought into range and supported with one hand, whilst leaf blades are folded over and detached by the lips. Leaves are re-grasped by the hand and held in a tight roll with thumb towards petioles. Petioles are bitten off and discarded and the remaining handful is consumed with repeated shear bites (2.8%).
Tiii	Branch is brought into range and supported with one hand, whilst the other hand picks a stem of leaves. Leaf blades are folded over and detached from the stem with the lips and gathered into the mouth with the lips. Petioles and stem are discarded (2.3%).
Two-handed	
T8	Branch is brought into range with one hand and supported, whilst the other hand picks off individual leaf blades with a precision grip. Leaf blades are bundled into the mouth (3.2%).
T12	Branch is brought into range and supported with one hand, whilst the other hand grabs a handful of leaf blades. Leaf blades are bundled into the mouth (1.3%).
T13	Branch is brought into range and supported with one hand, whilst a stem of leaves is detached by the lips. The stem is re-grasped by the hand and held in a tight roll with thumb towards petioles. Petioles and stem are bitten off and discarded and the remaining handful is consumed with repeated shear bites (1.7%).
Tiv	Branch is brought into range and supported with one hand, whilst the other hand picks a stem of leaves. The stem is held in the mouth then re-grasped by the hand and held in a tight roll with thumb towards petioles. Petioles and stem are bitten off and discarded and the remaining handful is consumed with repeated shear bites (1.9%).
Tv	Branch is brought into range and supported with one hand, whilst the other hand picks a stem of leaves. Leaf blades are bitten off and the petioles and stem discarded (0.8%).
Two-handed, with folding	
Tvi	Branch is brought into range and supported with one hand, whilst the other hand picks a stem of leaves. Leaf blades are folded over and detached with the lips and the petioles and stem discarded. Leaf blades are then re-grasped by the hand and held in a tight roll. The handful is consumed with repeated shear bites (0.4%).
Two-handed, with stripping up	
T1	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards leaf blades – and detaches. Leaves are held in a tight roll and eaten with repeated shear bites. The petioles are discarded at the end of the handful (15.4%).
T4	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards petioles – and detaches. Leaves are held in a tight roll and the petioles bitten off and discarded. The remaining handful is consumed with repeated shear bites (22.4%).
T9	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards either leaf blades or the petioles – and detaches. Leaves are bundled into the mouth and petioles removed from the mouth (2.0%).
T10	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards either leaf blades or the petioles – and detaches. Leaves are held in a tight roll and the handful is consumed with repeated shear bites. Petioles are removed from the mouth (0.7%).
T11	Branch is brought into range and supported with one hand, whilst the other hand strips up individual leaf blade from around midrib/petiole with a scissor grip and detaches. Leaf blade is bundled into the mouth (1.15%).
Two-handed, with stripping up and folding	
T3	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards leaf blades – and grips leaf bases. Leaf blades are folded over and detached with the lips and gathered into the mouth by the lips (13.8%).
T5	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards either leaf blades or petioles – and detaches. Leaf blades are folded over and detached with the lips and gathered into the mouth by the lips. Remaining petioles are discarded (0.9%).
T6	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards either leaf blades or the petioles – and detaches. Leaf blades are folded over with the lips and then re-grasped by the hand and held in a tight roll with thumb towards petioles. Petioles are bitten off and discarded and the remaining handful is consumed with repeated shear bites (0.2%).
T7	Branch is brought into range with one hand and the same hand is slid up the branch to strip up leaves – with thumb towards leaf blades- and grip leaf bases. Leaf blades are folded over and detached with the lips and gathered into the mouth by the lips (2.9%).
T14	Branch is brought into range and supported with one hand, whilst the other hand strips up leaves – with thumb towards leaf blades – and grips leaf bases. Leaf blades are folded over and detached with the lips then re-grasped by the hand and held in a tight roll. The handful is consumed with repeated shear bites (0.01%).

Techniques with Arabic numerals (T1–T14) were used in feeding only on young leaves; techniques with Roman numerals (Ti–Tvi) were used when feeding on flowers as well as young leaves. The percentage of handfuls processed by each technique is given in parentheses (for able-bodied chimpanzees)

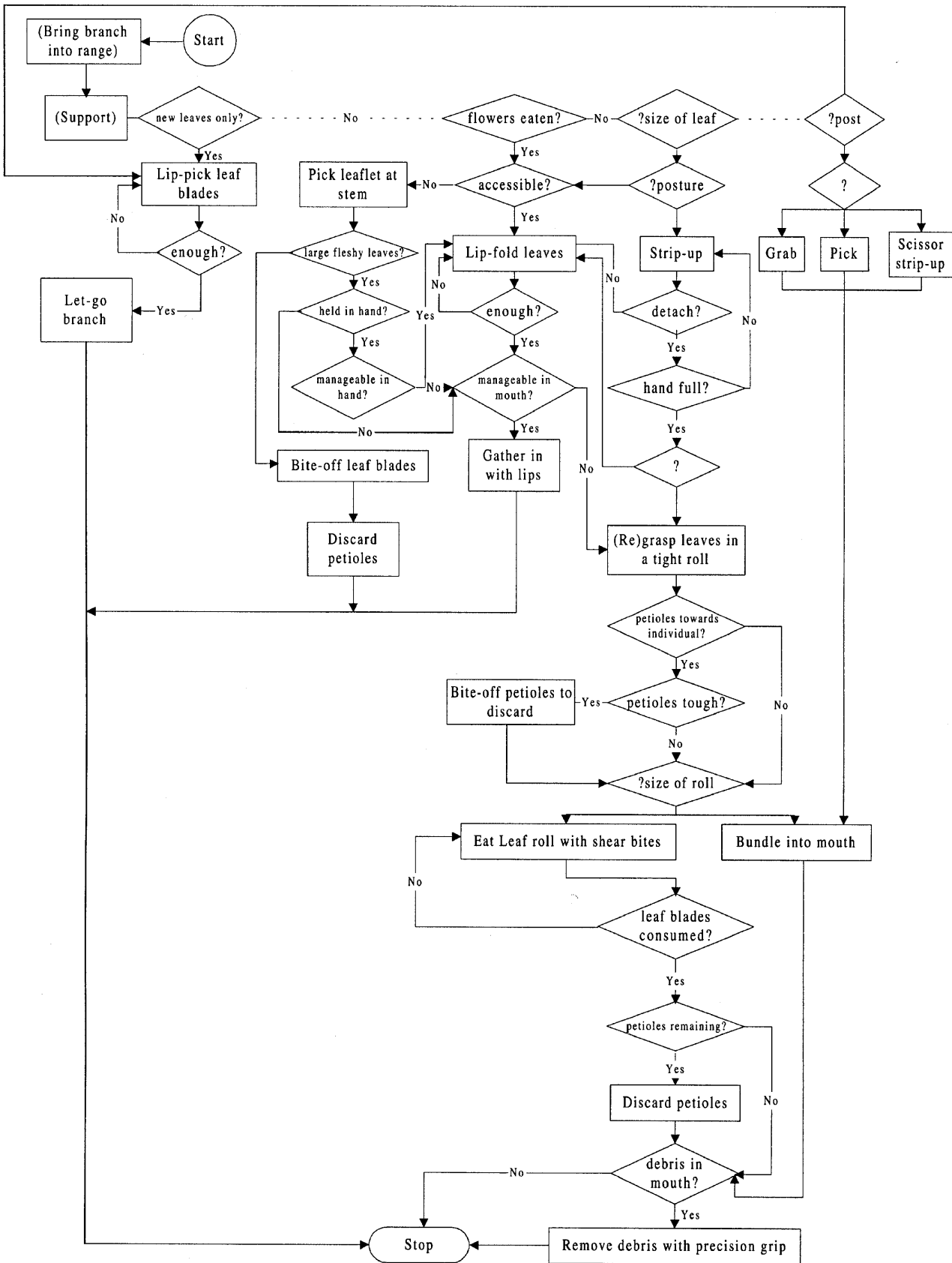


Fig.1 Flowchart for able-bodied individuals feeding on *Broussonetia*. Food manipulation begins at the top and works down; rectangular boxes represent actions and diamonds represent decision processes; a question mark indicates that the factors governing a decision have not been inferred; parentheses around text indicate

that these actions are only performed if necessary. Vertically aligned shapes are performed with the same hand or the mouth; dashed horizontal lines between columns represent coordinated, complementary use of the two hands

single pathway through this diagram, from top to bottom. Note that the precise factors governing a chimpanzee's basis for choice among techniques have had to be deduced in the majority of cases. Figure 1 shows that to successfully complete the task, an ordered sequence of directed elements is required, with bimanual role differentiation necessary at several stages.

A number of features suggest that the underlying organization of *Broussonettia* processing by able-bodied chimpanzees is best seen as modular and hierarchical (Byrne and Russon 1998; Byrne 1999). Evidence that the organization was of this type is given by:

1. *Interruptionality*: When interruptions occur within a module then the handful is aborted, whereas interruptions between modules usually have no effect on progression of the sequence.
2. *Optionality*: Unnecessary stages are omitted on the basis of local circumstance. If petioles are not tough, for example, this stage is skipped without disruption to the entire sequence.
3. *Iteration to criterion*: Repeated use of a module as a subroutine gives a distinctive pattern of several local repeats of a string of elements; for example, leaves are stripped and accumulated before there is a sufficient handful to be held in a tight roll.

In Fig. 1, we have depicted the repertoire of alternative processing sequences in an "economical" fashion, in which techniques share some sequences of elements (visible as common sectors of pathway on the diagram). Between these common sectors, Fig. 1 shows branched pathways, where several alternative ways of doing the same job are possible; most of these pathways were traversed at low frequency. Our impression was that this range of alternatives catered for particular environmental circumstances. As suggested by Fig. 1, then, an able-bodied chimpanzee would carry out certain stages of the process in a rather stereotyped way, but for other stages it would choose among several alternatives on the basis of the local conditions. If we define a *procedure* as an ordered sequence of elements that achieves one stage of processing, their choice is among several alternative procedures. However, since each different sequence that results in processing a handful of food is defined as a separate technique, because an individual chooses among a few different procedures at several points, the total range of techniques become quite large. The reality of this depiction, and the constraints that underlie it, can be tested by examining the consequences of injury.

Effect of injury on choice of technique

The injured individuals exhibited the same 14 (+6) techniques described in the able-bodied population; no novel techniques were identified. Instead, differences between injured and able-bodied individuals arose in their frequency of use of a particular technique. Because of the individual variation in both nature and extent of injury, these differences will be investigated on a case-by-case basis.

When comparing the repertoire of an injured individual to that of the able-bodied population, a number of practical issues arise. The most pressing of these is the question of whether a technique is actually "missing" from the repertoire, or whether it has merely been overlooked as a result of disparities in the quantity of data collected between an injured *individual* on one hand and an able-bodied *population* on the other. Statistical testing is further compromised by the high concentration of zero scores for certain techniques. In order to address these problems, the variation in usage of each technique within the able-bodied population was used to estimate the likelihood of a deviant frequency occurring by chance in a disabled individual. From scores obtained from able-bodied individuals, 95% confidence intervals were calculated for the frequency of use of each technique. Injured individuals whose score fell outside these intervals were considered to vary significantly in their usage of that technique. Figure 2 shows the

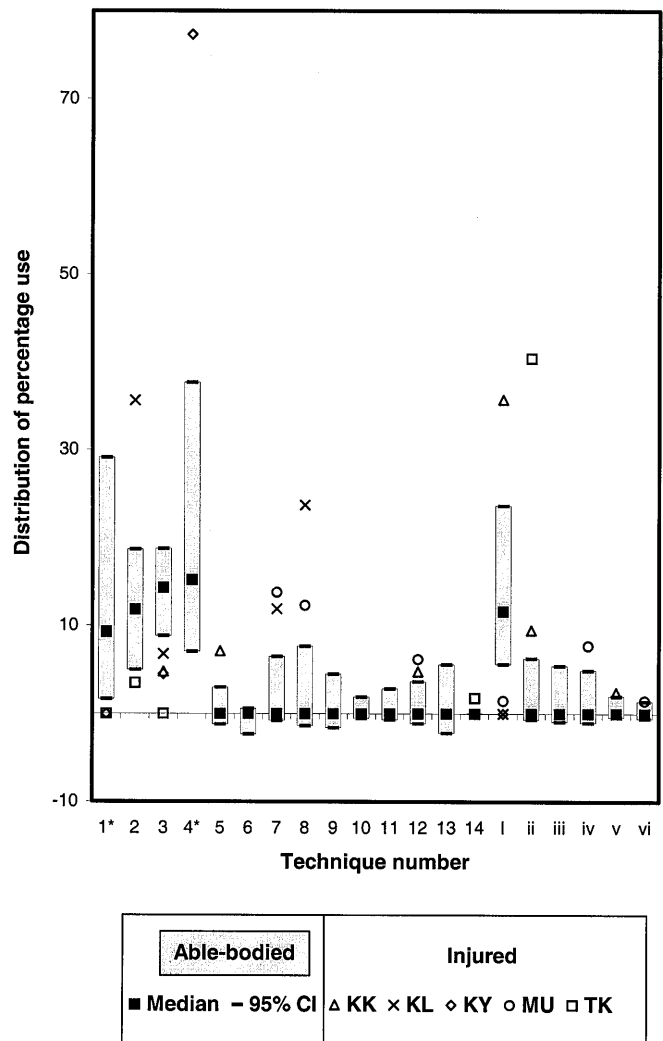


Fig. 2 Frequency of use of technique for able-bodied and injured chimpanzees feeding on *Broussonettia*. Asterisks indicate that T1 and T4 are the preferred techniques (T) of the able-bodied population, "strip-toward-detach" and "strip-away-detach" respectively; T3 is a variant of T1 which does not require leaves to be detached but held tightly and the tips bitten off with the lips

distribution of scores within the able-bodied population for each technique; only those injured individuals whose score falls outside the 95% confidence intervals are shown. Figure 3a–e illustrates the *preferred* repertoire of techniques used by each of the injured chimpanzees. We now examine the injured chimpanzees one by one:

1. Tinka. Those techniques that require leaves to be stripped with the thumb towards the animal, T1 and T3, are missing from his repertoire. On the other hand, T4, which requires leaves to be stripped away with the little finger towards the animal, is present at a frequency within the range of variation of the able-bodied distribution. At the same time, however, Tinka has greatly increased his use of Tii which he used to process 40% of handfuls, in a total repertoire of four techniques (total number of handfuls=58). Tii is less commonly used in the able-bodied population, and requires leaves to be stripped up and then held whilst the leaf blades are folded over and plucked with the lips. The blades, now manoeuvred into a more manageable bundle in the mouth, are then re-grasped in the hand and eaten with repeated shear bites. In terms of Fig. 3a, Tinka thereby bypasses the “stripping and detaching” section and rejoins the normal pathway further down.
2. Kalema. This female, like Tinka, has also significantly reduced her usage of techniques which employ the strip-toward element, T1 and T3, and maintained T4 at a similar frequency to that observed in the able-bodied population. T2 and T8, however, show a significant increase in usage, with 59.3% of handfuls being processed by these two techniques, in a total repertoire of 5 techniques (total number of handfuls=43). Both these techniques involve a simple process: “reach-lip-pick” in the case of T2 and “reach-pick” in the case of T8, with the former used most often by able-bodied individuals when feeding on small or mature leaves (Fig. 3b).
3. Keway. She has considerably reduced her usage of those techniques requiring the strip-toward element (T1 and T3; the former is missing entirely). In dramatic contrast, the technique which uses strip-away, T4, shows an massive increase in usage above that shown by able-bodied individuals, with 73.9% of all handfuls processed with this technique alone, in a total repertoire of 2 techniques (total number of handfuls=22). Figure 3c reveals that Keway shows a far closer resemblance to the pattern displayed by the able-bodied population (Fig. 1) than either Kalema or Tinka, in that she used at least one of the two techniques preferred by the able-bodied population as her preferred technique.
4. Kikunku. This male shows a significant reduction in usage of T3, whereas his usage of T1 and T4 is similar to that of able-bodied individuals. At the same time he shows an increase in other less commonly-used techniques in the able-bodied population, of which Ti is the most marked, accounting for 36% of all processing, in a total repertoire of five techniques (total number of handfuls=42). Ti is a monomanual technique, used most often by able-bodied individuals when eating flowers

together with leaves. Thus, although Kikunku shows similar usage of strip-toward-detach and strip-away-detach to that observed in the able-bodied population, neither of these are his preferred techniques (Fig. 3d).

5. Muga. Uniquely among the injured subjects, Muga does not show a significant variation from the able-bodied population in his usage of T1, T3 or T4. However, his use of several techniques, less commonly used in the able-bodied population, is increased – with the result that he exhibits a repertoire of nine techniques which are used at roughly equal frequencies (mean 10.26%, range 6.2–13.8%, total number of handfuls=65). Thus, although the techniques using “strip-toward” and “strip-away” elements are preferred techniques in Muga’s repertoire, they are not relied upon as heavily as in the able-bodied population (Fig. 3e).

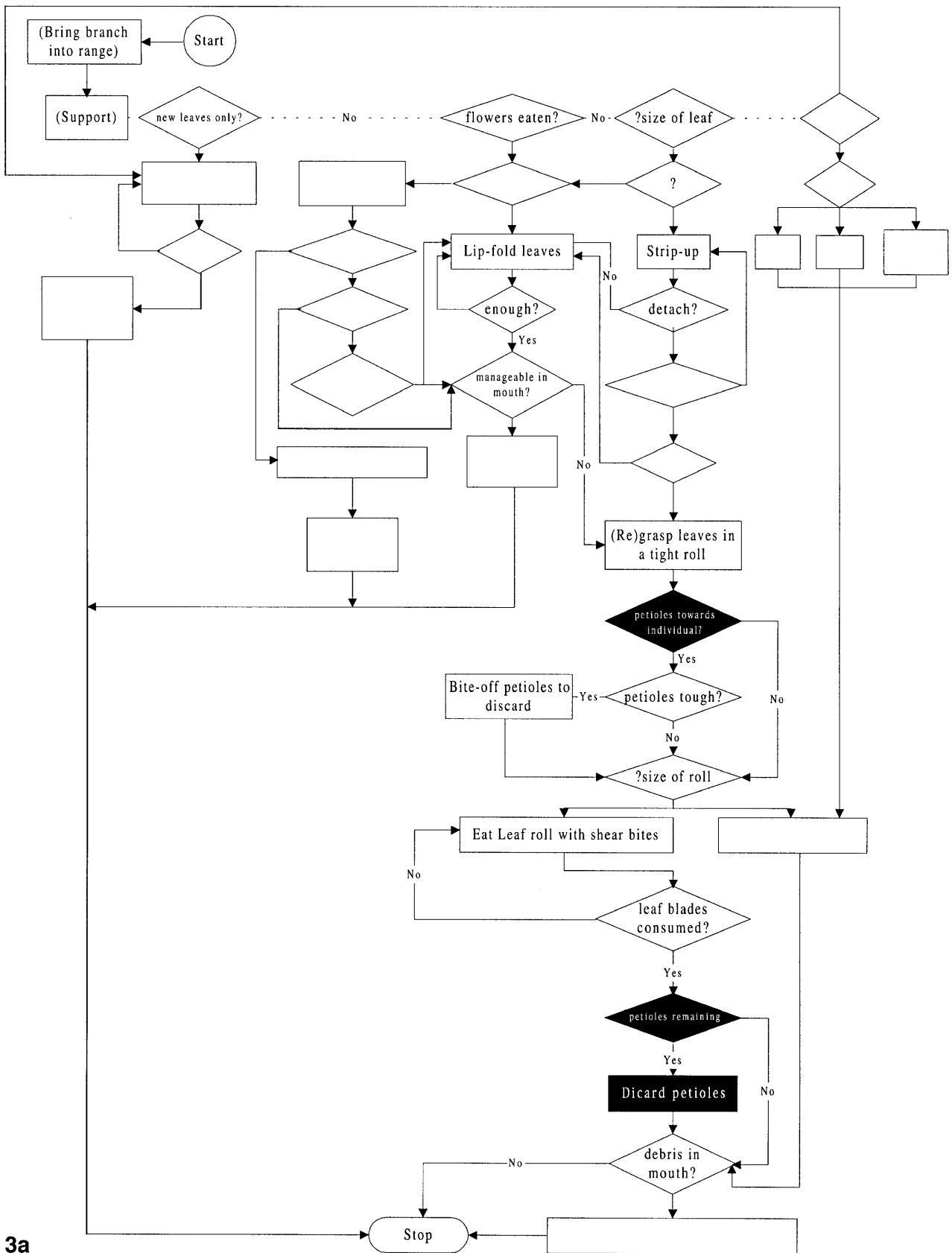
These data may be summarized by two generalizations: (1) the overall, or program-level, *organisation* of leaf-processing behaviour is the same in injured individuals as in the able-bodied, as indicated by the similarity of flowcharts produced by the behaviour of both able-bodied and injured individuals, and (2) the *frequency* of use of the various techniques (i.e. pathways through the flowchart) is determined by the nature of the injury, and some techniques may be missing altogether. It is important to be sure whether the effects we have seen are compensatory strategies as a result of injury and not merely individual idiosyncrasies. Only in the former case would we expect adjustment specifically to the nature of each individual’s impairment. This can be addressed by investigating feeding skills at a finer level of detail, analysing at the level of individual elements of action.

Element repertoire in able-bodied chimpanzees

A total of 69 elements of action were identified for the able-bodied population. These could be divided up into the following functional categories to reflect each stage of processing: *pull into range*, *manoeuvre food item* (prior to detaching), *support*, *detach food item*, *accumulate*, *manoeuvre food item* (after detaching), *remove parts from items*, *put into mouth* (see Stokes 1999 for glossary of individual elements). There was considerable variation in use of elements between individuals (Stokes 1999). Furthermore, as the number of handfuls varies between animals, it is evident that the full set of elements has not reached asymptote for all animals (linear regression $N=0.61H+9.01$, where N is the number of elements recorded in H handfuls, $r^2=0.80$, $F_{1,7}=27.19$, $P=0.01$), and thus we are still underestimating the total number of elements within an individual’s repertoire.

Effect of injury on element repertoire

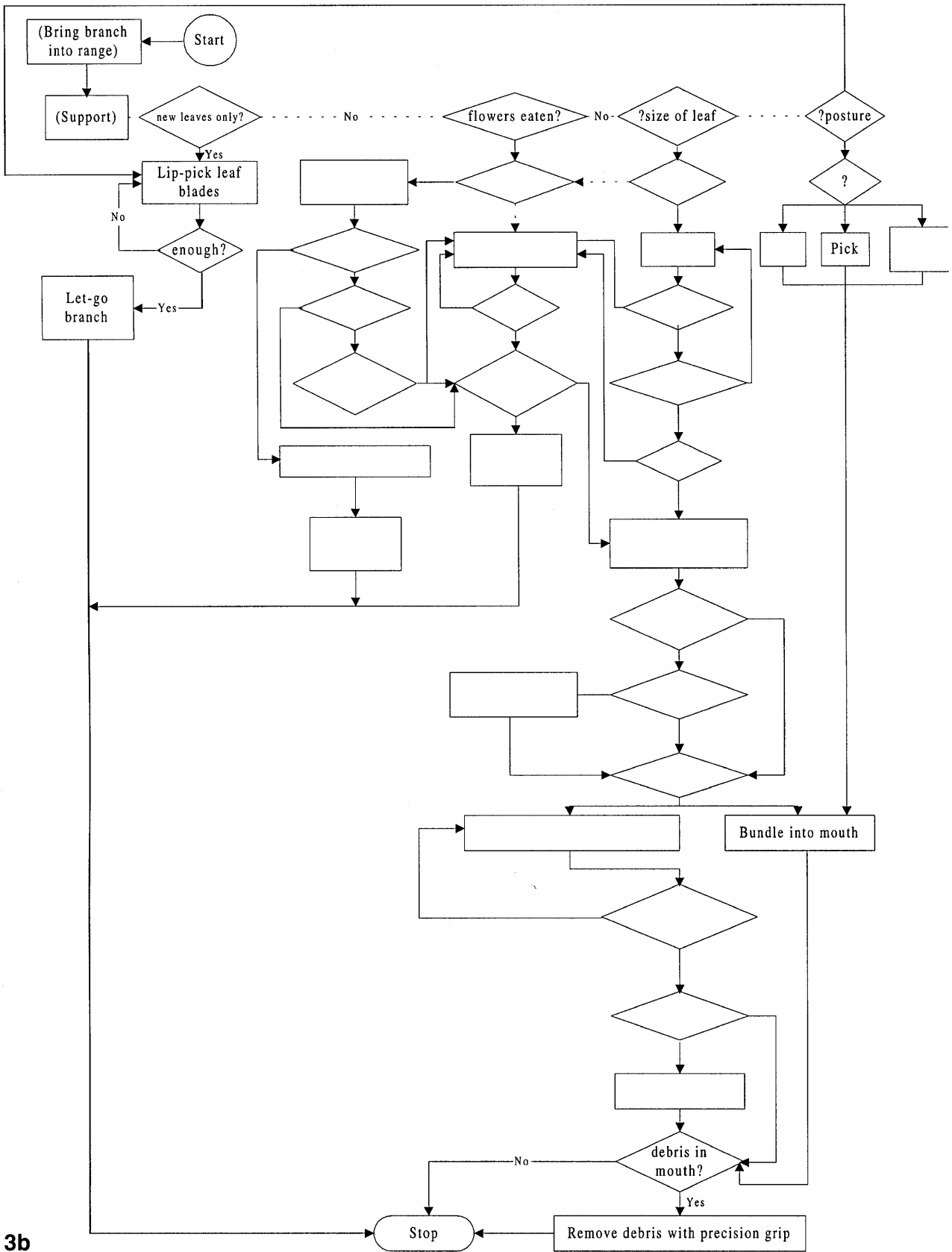
Within the injured population, the number of elements performed by the injured limb is drastically reduced. However,



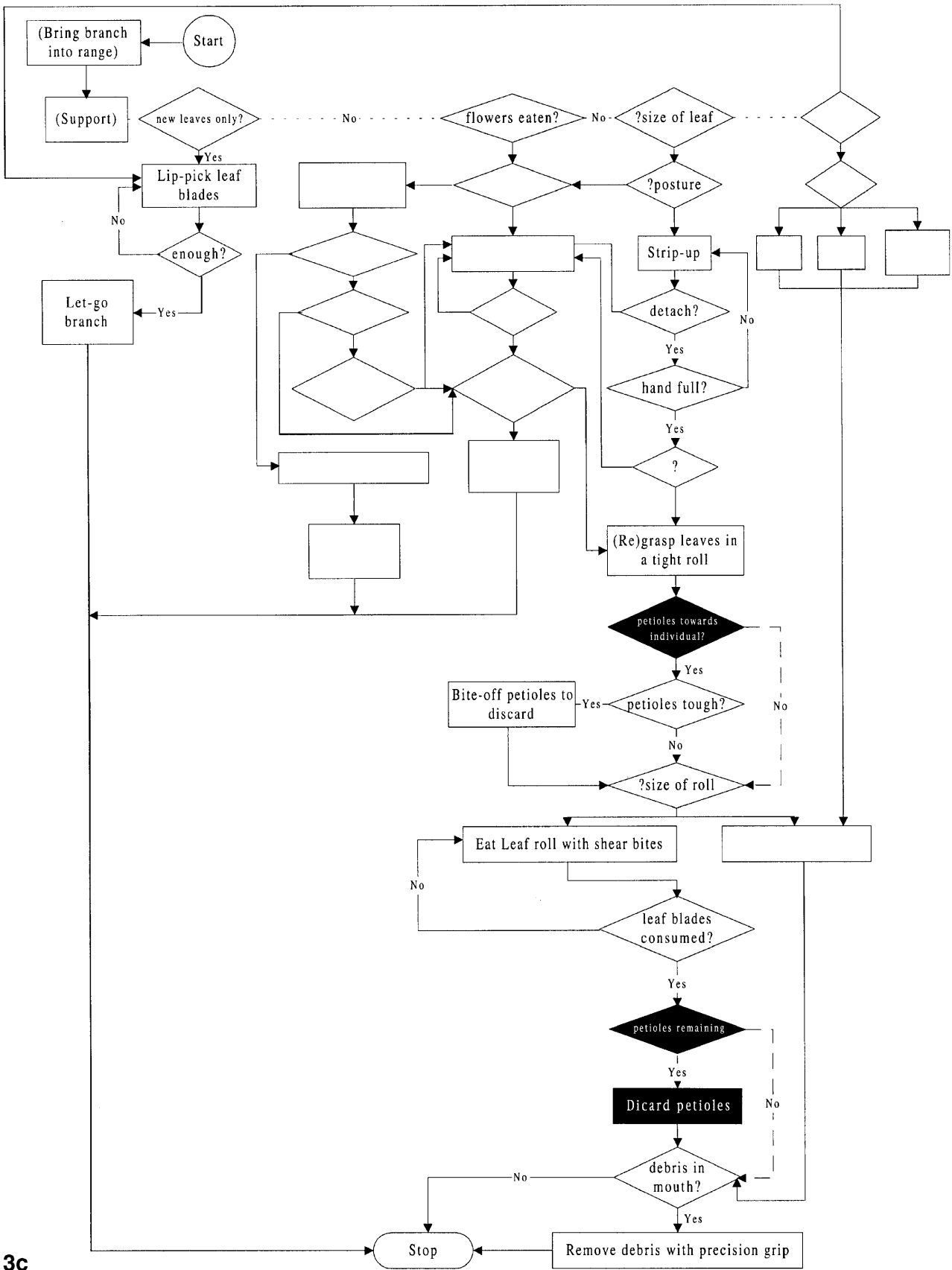
3a

Fig.3 Flowcharts comparing preferred techniques for feeding on *Broussonettia* by injured subjects: **a** Tinka, **b** Kalema, **c** Kewayi, **d** Kikunku, and **e** Muga. Each flowchart uses as a template Fig. 1, the organization of techniques for able-bodied chimpanzees. Only

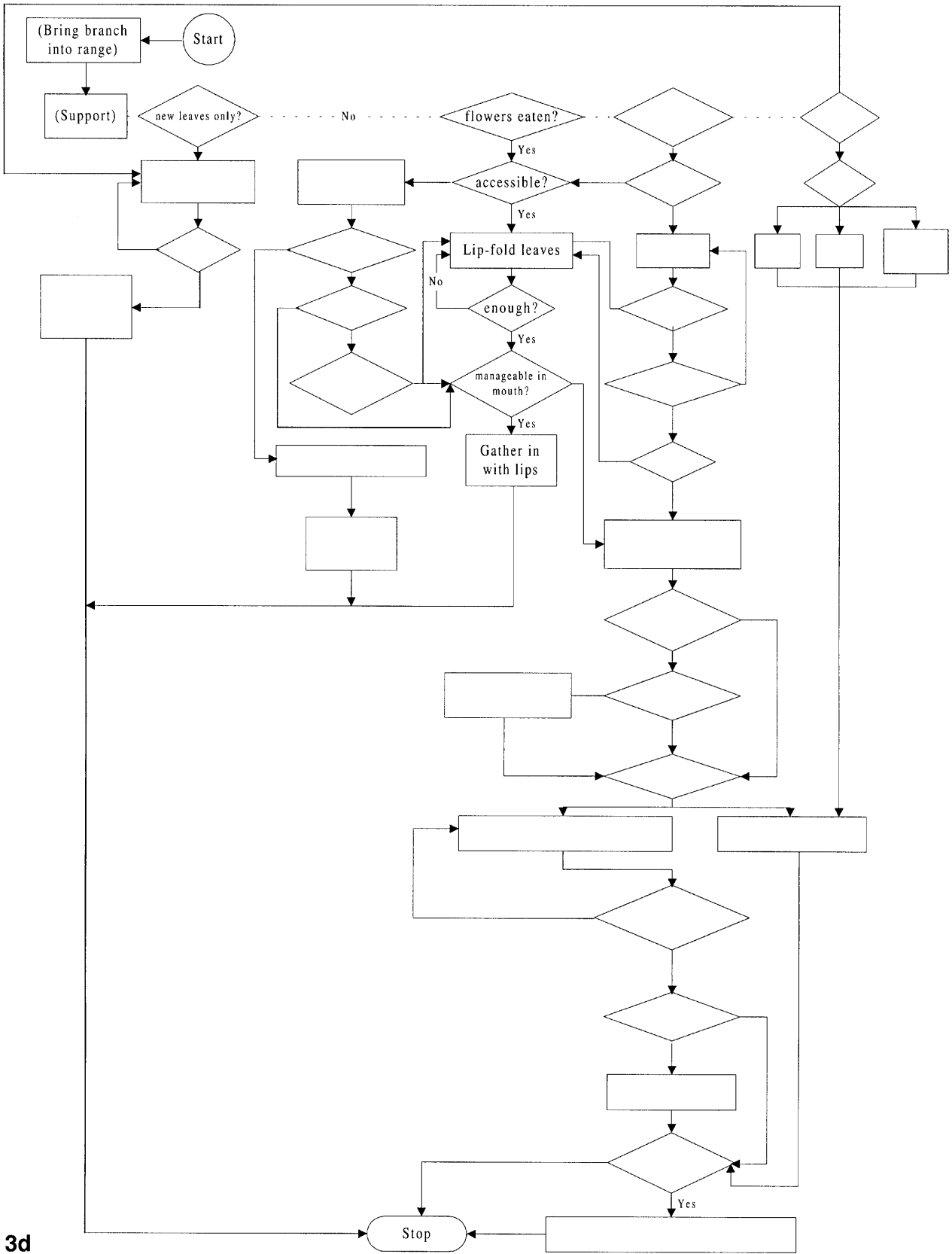
the paths used most often are *highlighted*; *empty boxes* represent uncommon techniques in the repertoire; *shaded boxes* represent techniques that are “missing” from the repertoire



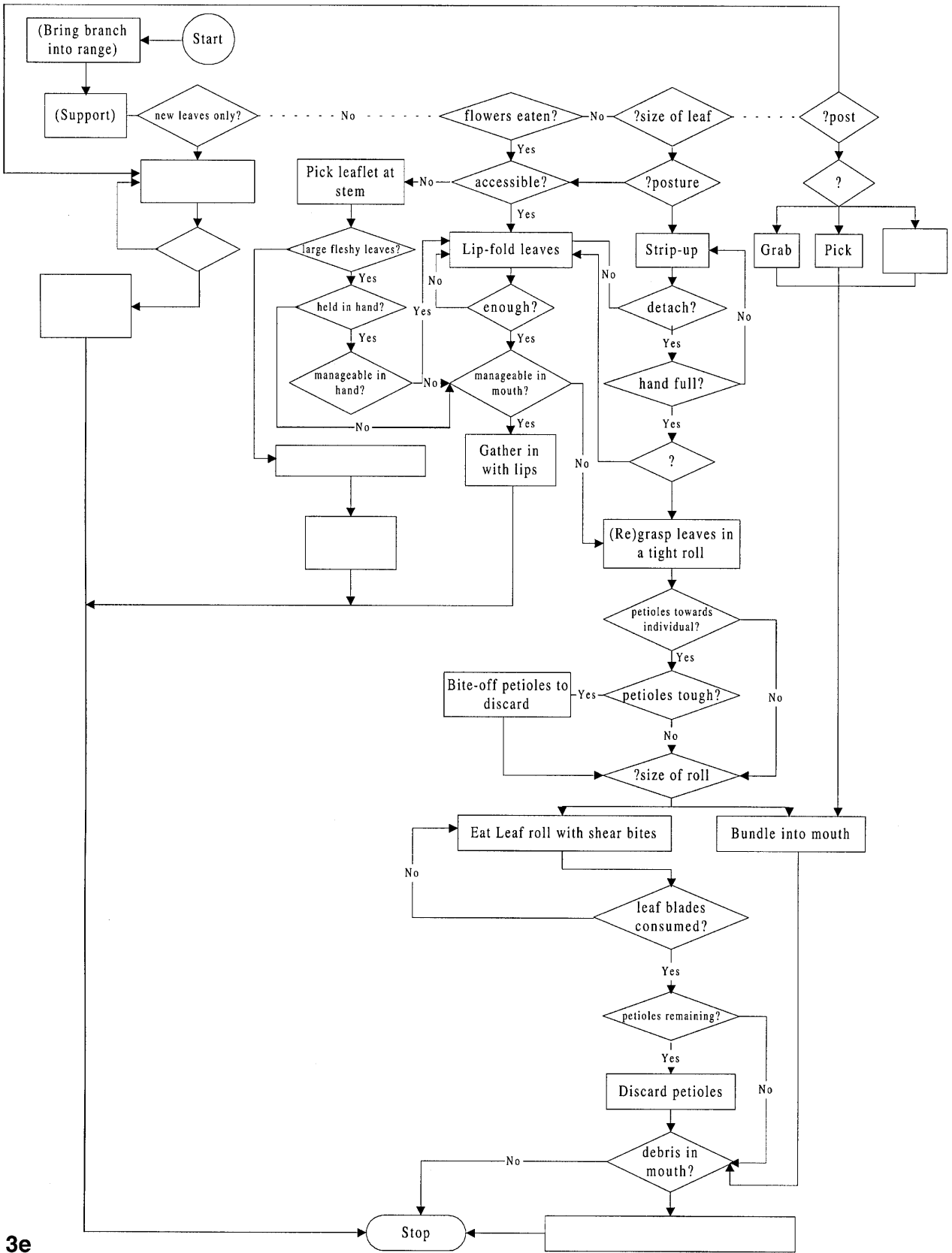
3b



3c



3d



3e

Table 2 Compensatory elements of the injured limb

Element	Kikunku	Kalema	Kewayaya	Muga	Tinka	
					L	R
Pull into range						
Reach (knuckle hook)					*	
Reach (wrist wrap)						*
Reach (back of wrist)		*	*			
Reach (lateral wrist)					*	
Reach (Wrist grasp)				*		
Support						
Back of wrist		*	*			
Wrist-hook		*				
Lateral wrist					*	
Wrist-wrap						*
Knuckle hook					*	
Wrist grasp				*		
Two-hand (back of wrist/pad-side)			*			
Two-hand (wrist grasp/2:3)				*		
Two-hand (knuckle hook/wrist wrap)					*	*
Two-hand (pad-side/wrist wrap)					*	*
Two-hand (lateral wrist/wrist wrap)					*	*
Foot-hand (right foot/passive finger hook)						*
Foot-hand (left foot/knuckle hook)					*	
Foot-hand (right foot/knuckle hook)					*	
Accumulate						
Combine (knuckle hook/strip-away single leaf)					*	

*Present

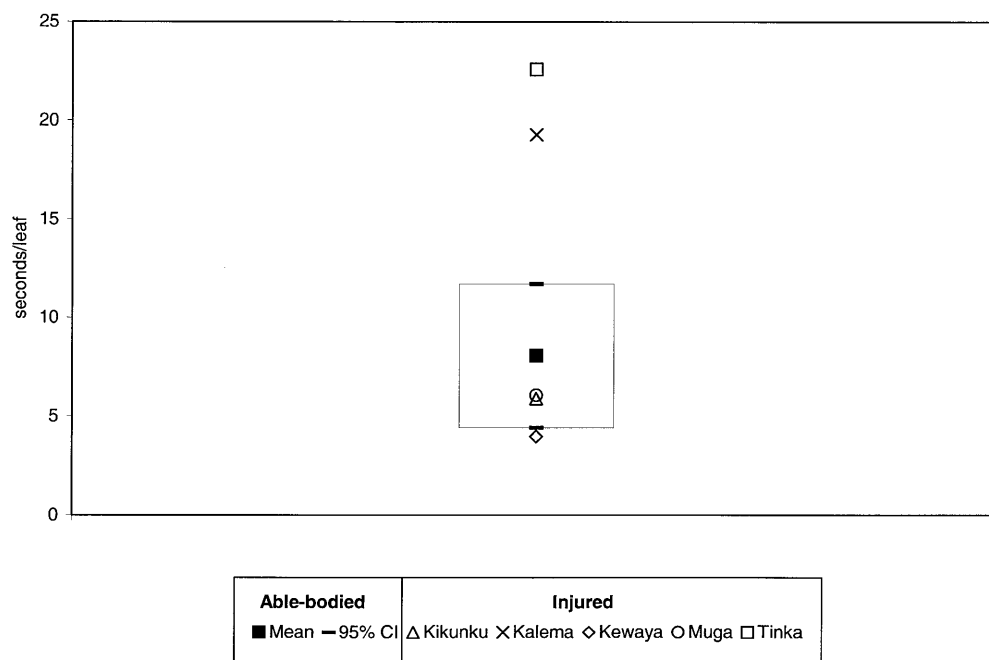
through the adoption of novel elements, the injured limb can still be incorporated into processing, albeit to a lesser extent and for the most part limited to passive supporting actions in the first three functional categories (Table 2). In the case of injured subjects, although asymptote was not yet reached it is probable that we had recorded a substantially greater fraction of the potential repertoire (linear regression $N=0.23H+20.90$, where N is the number of elements recorded in H handfuls, $r^2=0.60$; one-way ANOVA $F_{1,4}=5.99$, $P=0.71$).

For Kewayaya and Kalema, the injured limb is incapable of voluntary movement of either the hand or the wrist. Reaching actions are achieved through movement from either the elbow or the shoulder, and an item is usually supported either by the weight of the limb against the branch or by “trapping” the item between the forearm and the hand. In the case of Muga, the injured limb is capable of functional “grasping” through the retention of a moveable wrist joint, and can manoeuvre food items independently. For all three of these injured individuals, the use of novel elements enables the injured limb to provide an adequate supporting role, leaving the able limb free to perform the more dextrous tasks required in the latter stages of processing. In this way, the injured individual shares some semblance of bimanual control over processing with the able-bodied population. Kikunku, however, shows no use of the injured limb in any of the functional categories and thus in *Broussonettia* processing there is an effective loss of bimanual role differentiation. In the case of Tinka, both limbs are injured, although crucially the nature of

each injury is different. By using the able functions of one limb to compensate for the disabled functions of the other, Tinka maintains bimanual role differentiation. The right hand is used passively in a primarily supportive role in a similar way to that of Kewayaya and Kalema, whereas the left hand is capable of some voluntary controlled precision actions. This is due primarily to the normal functioning of the thumb, which enables a firm precision grip between the thumb and forefinger as used by able-bodied individuals, despite digits I–IV being permanently flexed. Due to the fixed position of the digits, however, Tinka is restricted in his ability to detach multiple items at once and instead is observed to accumulate individual items until he has a sufficient handful.

Although no injured individual completely lacks any of the functional categories of element use identified in the able-bodied population, the majority of elements found were restricted to one hand, the able limb, or in the case of Tinka distributed across both hands in a different way to that of able-bodied chimpanzees. For processing which requires bimanual role-differentiation these restrictions are likely to be extremely limiting, and apparently resulted in a need to “swap” food items from one hand to the other, in order to achieve consecutive stages of the technique. For both Kewayaya and Kalema, for example, the able limb was frequently observed to hand over an item for the injured limb to support. Similarly, Tinka’s limb injuries permitted a limited yet complementary range of functions with each hand, and food items were frequently passed from one hand to the other before processing continued. The percentage

Fig. 4 Efficiency of chimpanzees feeding on *Broussonettia*



of food handfuls in which “hand swapping” occurred was recorded for both injured and able-bodied individuals. The median value in the able-bodied population was calculated, and individuals were then subdivided into four groups: those above and below the median, and those injured or able-bodied. Hand swapping occurred at a significantly greater frequency in the injured population (chi-square test, corrected for continuity, 6.1667 , $df=1$, $P=0.031$). The problem of bimanual role differentiation is likely to be compounded by a predominantly arboreal lifestyle in which one hand is often required for postural support. This in turn may affect the ability to perform a number of processing techniques, for example those involving strip-and-detach, which requires precise positioning of the individual with respect to the food item in order to process the food efficiently. For this reason, an injured individual that may be theoretically capable of performing individual elements with a particular hand, is incapable of coordinating these elements into a feeding technique, and hence these elements may not be incorporated into the repertoire.

Feeding efficiency

Feeding efficiency was calculated from processing rates recorded on the hand-held computer. Although processing rates in themselves provide a useful measure of feeding efficiency, they are not perfect: two individuals may have the same processing rate per handful but one may collect much larger handfuls than the other. This problem is particularly pertinent to injured individuals who through the nature of their injuries necessarily cannot process as large a handful as their able-bodied counterparts (E.J. Stokes, personal observations). From data on the detailed sequences of elements, the mean number of leaves processed in a

single handful was calculated for each individual (only clearly observed, complete sequences were used for this). From the data on processing rates, a value for the time taken to process a single leaf was calculated. This was used as the comparative measure for feeding efficiency.

The mean value and the 95% confidence intervals were calculated, for the time to process a leaf by a member of the able-bodied population. These intervals formed the control against which injured individuals were compared. Individuals whose value fell outside the 95% confidence intervals were considered significantly affected in their feeding efficiency. The results are shown in Fig. 4, where only those individuals whose value falls outside the confidence intervals are shown.

Out of all five injured individuals, only Kalema and Tinka had efficiencies that fall outside the limits of the able-bodied population, in both instances feeding significantly less efficiently than able-bodied chimpanzees, with Tinka showing the lowest feeding efficiency.

Discussion

Hierarchical organisation in chimpanzee leaf processing behaviour

When they process the young leaves of *Broussonettia*, able-bodied chimpanzees generally use an ordered sequence of elements, each achieving a progressive change to the material, coordinated into a structure which includes iterated subroutines and smooth handling of optional and alternative subroutines. Just these features were used by Byrne and Russon (1998), in the case of gorilla and orangutan plant feeding, to infer a hierarchically structured

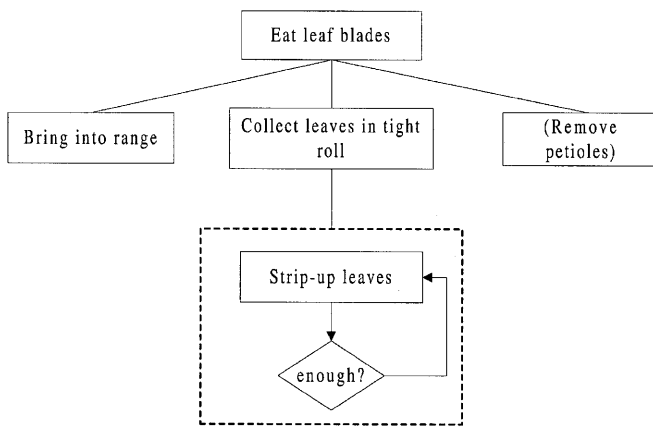


Fig. 5 Goal hierarchy for processing young leaves of *Broussonettia*

process under voluntary control, and we conclude that *Broussonettia* feeding by chimpanzees is similarly structured. Subroutines within the *Broussonettia* technique can be utilized by other techniques, for plants presenting similar difficulties for ingestion. In feeding on the young leaves of *Ficus natalensis* and *F. varifolia*, chimpanzees align the leaf blades parallel in the palm before eating in a tight roll in a similar way to that seen for *Broussonettia* (Stokes 1999). These leaves, like those of *Broussonettia*, have a hairy and abrasive upper surface. The goal structure illustrated in Fig. 5 displays the *minimum* hierarchical complexity that is implied by these behavioural indices, when able-bodied chimpanzees consume these three species of leaf. The relative shallowness of the hierarchy, two-level, is consistent with that noted for gorillas (Byrne and Russon 1998; Byrne 1999).

Individuals also possess a number of other less commonly used techniques, in their repertoire for dealing with *Broussonettia*. This variation is in sharp contrast to the standardization found in the techniques of mountain gorillas (Byrne and Byrne 1993). The contrast may stem from ecological differences. In mountain gorillas, there is low seasonal variation in diet, relatively low feeding competition, and feeding is primarily terrestrial (Watts 1996). Thus the same methods, once optimised, can be employed in nearly all circumstances all year round. Chimpanzees, on the other hand, experience seasonal and spatial variation in diet and significant feeding competition (Hladik 1977; Wrangham 1977; Wrangham et al. 1996), often combined with positional and postural difficulties from arboreal feeding; in facing positional and postural difficulties entailed by arboreal feeding, chimpanzees also resemble orangutans (Russon 1999). The considerably greater variation in feeding methods among chimpanzees is therefore likely to be a response to environmental demands: variations are needed for the many occasions when feeding is compromised by competition, location or peculiarities of the plants themselves. An advantage of hierarchical structure is that it enables this type of low-level decision making to be incorporated (Dawkins 1976). For example, if postural constraints prevent leaves being collected using

bimanual stripping (normally used to collect leaves), then leaves may instead be collected by lip-folding and then re-grasping in the hand. While this matches the definition of a new technique, in fact it only involves an alternative *procedure* for achieving one stage of the process, rather than a wholly new organization. At a level lower than the analyses of this paper, there is also considerable variation in the nature of individual elements and the preferred hand used; this variation has little apparent functional significance. By confining variation primarily to these lower levels – variation in procedures, elements and laterality – the organization of techniques need be altered little to deal with a range of environmental contingencies, thus enabling efficient foraging. At the same time, as found with mountain gorillas, techniques themselves are inherently flexible; for example, if petioles are not sufficiently tough to warrant removing then this stage is omitted.

Compensating for injury: ontogeny

The severity of limb injuries in these chimpanzee subjects poses extreme limitations to both dexterity and control in the injured limb. However, our feeding efficiency measures revealed remarkable compensation in feeding ability, with only two out of five injured chimpanzees showing significantly lower feeding efficiencies than able-bodied individuals. For all but the most severe of injuries, compensation appears sufficient to cancel out potentially negative effects. We found that in all cases this compensation was of the same nature: a matter of working around difficulties in implementing the *same* technique as able-bodied chimpanzees use, by developing novel elements or procedures for effecting some stages in the process, without devising any *new* technique. A priori, it would seem more logical to use a technique that was suited to the nature of the limitation imposed by a particular injury: why did our subjects not do this?

One possibility is that, given time, they might. However, all injuries of the adult individuals studied here were already in place when the Budongo Forest Project was initiated in 1990. Thus we can be sure that in fact their behaviour represents the full compensation that they can achieve, rather than a passing stage in a continuing process. Alternatively, the pattern observed may be a result of the nature of the process of learning to compensate for injury. Three possible ways of compensation seem feasible in principle, broadly relating to the mode of acquisition of feeding skills in able-bodied chimpanzees. We lack any direct developmental data of this process, and for conservation and welfare reasons it is to be hoped that such data does not become available. Given this lacuna, we can instead evaluate the relative plausibility of accounting for our data, according to each of the three possibilities:

1. Individuals might have been injured late in life, after already having learnt efficient techniques as juveniles when they were amenable to learning skills. The techniques were “fixed” or “crystallised” in the behavioural

repertoire of adults to such an extent that injured individuals were unable to learn any new technique, however much more efficient that might prove. Thus they were forced to adapt in minor ways the techniques they learnt as able-bodied juveniles; any that failed in this accommodation died, and we study the survivors. Although, in the absence of any life-history data prior to 1990, we cannot wholly refute this hypothesis, all current evidence on victims of snaring suggests that injuries occur *early* in life, to young animals who by their very nature are inquisitive and therefore most likely to fall victim to snares on the ground (Stokes 1999). Moreover, all new injuries in the 9 years following the initiation of the Budongo Forest Project have occurred to juveniles below the age of four. Finally, the idea that chimpanzees, as adults, are unable to learn new behavioural patterns is hard to sustain given the known flexibility of great ape mental abilities. Consequently, we provisionally reject this hypothesis, and assume from now on that our subjects were injured early in life.

2. Great apes normally acquire the techniques they do because the constraints of the environment, in combination with the natural affordances of the chimpanzee's hand or body anatomy, guiding their trial and error attempts towards a particular technique. This is the particular thesis of Tomasello and Call (1997), who have argued that when able-bodied gorillas acquire their remarkably complex techniques, "each animal is learning individually from its interactions with the plants", rather than gaining anything from direct observation of another individual's behaviour. Applying this hypothesis here, an injured chimpanzee would be expected to learn new techniques that suited the surviving functionality of the hands, in order to feed most efficiently. As both the nature and extent of injury varies considerably between individuals, one would expect feeding techniques to differ not only between able-bodied and injured individuals, but also between individuals with different injuries. The process is a "hill-climbing" algorithm, so local optima would be expected, different for each type of injury. We found nothing like this; there was no sign that new techniques, suited to particular injuries, were ever developed. To rescue the Tomasello and Call hypothesis, it would be necessary to assume that the anatomical constraints and affordance of the chimpanzee hand and limb have essentially no influence on the learning process, which is entirely governed by the nature of *Broussonettia* leaves. We find that highly implausible.
3. Chimpanzees normally acquire food processing techniques partly by imitation of their mother and other members of the community, as well as by other forms of social learning and by individual exploration. For a complex task like dealing with *Broussonettia*, learning the organization of the technique would be guided by seeing the mother's version, whereas details of implementation might often be acquired by individual trial and error. Byrne and Byrne (1993) described this as "program-level imitation", and used it to account for the

pattern of variation among gorillas in how their staple diet plants were processed. Individual gorillas showed great idiosyncratic variation at the detailed level of elements used, but remarkable standardisation in technique; moreover, the techniques were elaborate and complex, and not determined in any obvious way by the form of the plants. Byrne and Russon (1998) have since argued that this may apply to other complex behaviours seen in great apes. On this hypothesis, injured chimpanzees would have no option but to *copy the technique shown by able-bodied individuals*, because no other model is available. To do so, these individuals would need to modify the way in which each stage in the process was achieved, because of the disabling effect of their injuries, or fail at the task. However, since these are just the details normally acquired individually (by a range of means, including trial-and-error learning and mechanisms of social learning other than imitation), that would be possible, provided the injury were not too disabling. This hypothesis is entirely consistent with our data. In the next section, we examine just how accommodation to injury seems to be done.

Compensating for injury: implementation

Just as the goal hierarchy illustrated for able-bodied chimpanzees enables low-level variations in details of technique to be made in response to environmental conditions (Fig. 5), so too does it allow for low-level compensation for injury, and it is at this level that behaviour is influenced by the nature and severity of injury.

Able-bodied individuals have available a range of procedures, shown as alternative branches of pathway through Fig. 1, for achieving important sub-goals. Injured individuals favour particular procedures that suit their individual injuries, whilst sharing with able-bodied chimpanzees the same overall organisation of the process. In extreme cases, a procedure may become unavailable altogether (and as a result, any technique which relies on it). Tinka was the most severely injured of the chimpanzees and as a result was incapable of using the normal procedure for achieving the subgoal, represented in Fig. 5 as "collect leaves in tight roll". As a result he relied more heavily on a technique that was used infrequently by the able-bodied population, but achieved the same eventual goal. At the other end of the scale, Muga, who showed least impairment, used all the techniques observed in the able-bodied population; however, rather than show a preference for a single one, as is normal among the able-bodied, he used them at roughly equal frequencies.

Although they do not appear able to invent novel techniques in response to injury, injured chimpanzees do develop novel elements; in this way they are able to "work around" their impairment, and thus accommodate without any radical re-organization of technique. These actions are "novel" in the sense that they are not observed in the able-bodied population. They include innovative uses of the remaining functional properties of the injured limb;

for example, elbows were often hooked over a branch in order to support the animal in the tree and free an able limb for processing. The feet could be used as a substitute for an injured limb: whereas the feet were often used by both able-bodied and injured chimpanzees to support a branch whilst feeding, only injured individuals were observed to use the feet to first pull the branch into range. In addition to developing novel elements, injured individuals compensated through their use of familiar actions at novel stages of processing: for example, using the lips to detach multiple leaves at once, where the injured limb was unable to do so, and swapping food items between hands to enable bimanual processing. Compensation is also seen in the choice of hand to use at each stage. Injured chimpanzees generally show hand preferences as a result of injury across several different food types, in sharp contrast to able-bodied individuals who are ambipreferent in their hand-use (Stokes 1999). However, injured individuals show stronger hand preferences when feeding on foods that require complex asymmetric processing – such as *Broussonettia* – where it is presumably advantageous to specialize, than on those food types that require simple monomanual processing.

A similar pattern of compensation was found in an analysis of the effects of injury in gorilla feeding skill (Byrne and Stokes, in prep.). Pandora, an adult female gorilla, had snare injuries comparable to those seen in the Sonso chimpanzees. In processing nettle leaves, Pandora used the technique of able-bodied individuals, but modified the fine detail of its implementation by performing certain operations monomanually and at a different point in the sequence. This was evidently effective since her feeding efficiency was in the normal range. In both gorilla and chimpanzees, the variation in use of elements seen *between* able-bodied and injured individuals parallels the idiosyncratic use of individual elements *among* the able-bodied population. Moreover, it is at this level of individual elements that we see the greatest variation among injured individuals, across different feeding tasks (see Stokes 1999 for more detail).

Low-level flexibility underlies compensation to injury in great apes, and imparts the hallmark of each particular injury; it also strongly suggests that at the level of individual elements each individual is learning from *their* own experiences. In contrast, the basic organization of techniques is found in individuals regardless of injury type, which is most consistent with its acquisition by program-level imitation of (able-bodied) adults, most likely the mother. Compensation in this way enables injured chimpanzees to accommodate remarkably well to the effects of severe limb injury, and evidently buffers the population from the effects of snaring. This ability to withstand extreme injury may only be available to those species with extensive capacity to generalize learnt skills to individual circumstances. So far this has only been reported in the great apes and humans, which may well explain why a similar survival rate as a result of comparable injury has not been found in any non-provisioned monkey populations in the wild.

Acknowledgements We thank Professor Vernon Reynolds and the Budongo Forest Project for enabling E.S. to study the Sonso chimpanzees, and to her field assistant James Kakura for his invaluable help in the field. We would also like to acknowledge NORAD, the National Geographic Society and Conservation International's Margot Marsh Fund for their support of chimpanzee research at Budongo. Permission to work in Uganda and the Budongo Forest Reserve was granted by the Uganda National Council for Science and Technology, the Presidents Office and the Forestry Department. Mark Mon-Williams provided useful advice in analysing performance of disabled individuals. This research was funded by a studentship from the Biological and Biotechnological Sciences Research Council.

Appendix: glossary of terms

Bout: a period of feeding, beginning when an individual first touches the food, and ending when interrupted by another individual, or spontaneously terminated by switching to another activity, by moving away from the food item, or periods of inactivity of a defined length appropriate to the feeding task under analysis (for *Broussonettia*, 20 s or more).

Element: a pattern of hand or hand and mouth movement that results in a clear change to plant material by a single action. It is perhaps impossible to define an element of action in a way that is wholly independent of the task in hand; as noted by Byrne and Byrne (1993), "the sense in which we use the term element will be best grasped from the [individual element] definitions themselves". However, the precise effector organs (e.g. left or right hand, particular digits, knuckles, lips) and type of grips (power, scissor, tip-to-tip precision etc) would normally be specified, as well as the movement executed.

Handful: an accumulation of several food items, gathered in the hand before placing into the mouth to eat. During consumption of some foods, such as *Broussonettia* leaves, gathering of several small items is normal, although at times a handful may contain only one item; where pieces are pulled off a larger whole, using the handful as the basic unit of analysis may be inappropriate.

Procedure: a regularly used combination of elements which results in achievement of a specific stage of processing of a food item. In computational terms, a procedure corresponds most closely to the common meaning of a subroutine: however, in practice, it is clear that both an element and a technique may themselves be *used* as subroutines. Thus we suggest that the procedure, intermediate between element and technique, will normally only be useful as a level of analysis when a stage is variously achieved by several procedures within a more fixed overall technique, or when several different techniques overlap for some particular sequence of elements.

Technique: an ordered sequence of elements of manual skill, coordinated so that the whole performance serves to process a handful of food (Byrne and Byrne 1993). A tech-

nique may consist of several stages, achievement of which may be considered as sub-goals of the entire process, and different techniques may overlap with each other at some stages.

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